

OPTOMOTOR CONTROL OF COURSE AND ALTITUDE IN *DROSOPHILA MELANOGASTER* IS CORRELATED WITH DISTINCT ACTIVITIES OF AT LEAST THREE PAIRS OF FLIGHT STEERING MUSCLES

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Summary

Flight control in the fruitfly *Drosophila melanogaster* is achieved by minute sets of muscles on either side of the thorax. Control responses of wings and muscles were elicited during fixed flight by moving a striped pattern in front of the eyes. For example, pattern motion from the lower right to the upper left signals to the test fly a rotatory course deviation to the right and simultaneously a translatory altitude displacement downwards. The counteracting response to the displacement of the retinal image is an increase in thrust and lift on the right, accomplished mainly by increasing the wingbeat amplitude (WBA) on that side. A comparison of such responses with the simultaneously recorded action potentials in the prominent basalar muscles M.b1 and M.b2 and axillary muscles M.II and M.III1 on either side suggests that three of these muscles act on the WBA more or less independently and contribute to the optomotor control of course and altitude.

During flight, M.b1 is almost continuously active with a frequency equal to or slightly below 1 spike per wingbeat cycle. The spikes occur within a narrow phase interval of this cycle, normally at the beginning of the transition from upstroke to downstroke. However, the visual stimulus described above causes a substantial phase lead in M.b1 on the right; the spikes occur shortly before the end of the upstroke. Such phase shifts are accompanied by comparatively smooth 'tonic' responses of the WBA. The

activities of M.b2 and M.II are normally very low. However, the stimulus described above activates M.b2 on the right in a phase interval approximately two-thirds into the upstroke and M.II on the left in a phase interval at the beginning of the downstroke. The spikes tend to occur in bursts. These bursts are correlated with WBA-increasing 'hitches' (rapid changes in amplitude) on the right and WBA-decreasing hitches on the left. As fast 'phasic' responses, the burst-induced hitches are likely to account for the course-controlling 'body saccades' observed during free flight. For unknown reasons, M.II is activated by pattern motion but cannot conceivably assist the other muscles in altitude control. Unlike its homologues in larger flies (*Musca domestica*, *Calliphora erythrocephala*), M.III1 does not participate in optomotor flight control. Its activation seems to support the termination of flight and wing retraction at rest.

The essential properties of the three pairs of muscles M.b1, M.b2 and M.II resemble those found in larger flies; the muscles are controlled by motion detectors with muscle-specific 'preferred directions' in the hexagonal array of retinal elements. Optomotor control of the three pairs of muscles in *Drosophila melanogaster* could explain most, but not all, of the WBA responses recorded so far.

Key words: insect flight, flight muscles, flight control, optomotor control, *Drosophila melanogaster*.

Introduction

The flight system of Diptera suggests a functional separation into bulky 'power muscles' in the centre of the thorax and comparatively small 'control muscles' on either side. The wingbeat frequency is maintained by activation of the asynchronously responding indirect 'power muscles', which are responsible for both the vertical component (lift) and the horizontal component (thrust) of the average force of flight. The wingbeat on either side can be modified by neuronal

activation of up to 17 possible pairs of synchronously responding direct 'control muscles', which seem to contribute primarily to manoeuvrability.

Little is known about the neuronal origin of spontaneous activity in the flight control system. The neuromuscular output obtained during tethered flight in still air shows, however, that the pattern of activity in several pairs of control muscles is strongly influenced by sensory signals which may be

interpreted as the feedback received during free flight (Heide, 1983). Orientation in space is accomplished by evaluating the directional components of drift within the retinal image of the surroundings. The fruitfly *Drosophila melanogaster*, the housefly *Musca domestica* and the blowfly *Calliphora erythrocephala* use the horizontal drift components to control the difference between the forces of flight on either side (course control) and the vertical drift components to control the sum of these forces (altitude control). The drift is processed by direction-specific arrays of elementary motion detectors in their visual system. In the fruitfly, course and altitude can be stabilized independently of each other by adjusting the difference (R–L) or the sum (R+L) of the wingbeat amplitudes on either side (R, L). A close relationship has been found between R–L and the yaw torque about the vertical axis of the fly, and between R+L and its force of flight (Götz, 1968, 1983a; Götz *et al.* 1979). Alterations in the wingbeat amplitude can be expected to change primarily the magnitude, not the direction, of the average forces exerted by the wings of a tethered fly. A predominant contribution of these alterations to flight control in *Drosophila melanogaster* and *Musca domestica* is compatible with the observed covariance of lift and thrust in still air: the elevation angle between the resulting force of flight and the fixed body axis is constant at approximately 24° (Götz and Wandel, 1984).

Several reasons justify the particular effort of studying neuromuscular aspects of visually induced flight control responses in a lightweight insect of 1 mg body mass. (1) Progress in *Drosophila* research on optomotor reactions (e.g. Buchner, 1984; David, 1978, 1985; Götz, 1968, 1983a,b, 1985, 1987a,b, 1989; Götz *et al.* 1979; Heide, 1983; Heisenberg and Wolf, 1984; Wolf and Heisenberg, 1986; Waldvogel and Bausenwein, 1990, 1991) and related topics of flight performance (e.g. Ewing, 1979a,b; Heide, 1978; Miyan and Ewing, 1985) has raised interest in the muscular origin of behavioural responses. (2) Results regarding flight control in the ‘calyptate’ flies *Calliphora erythrocephala* and *Musca domestica* suggest a comparison with results from the much smaller *Drosophila melanogaster*, where the wings operate at comparatively low Reynolds numbers (e.g. Dickinson and Götz, 1993; Ellington, 1984; Ennos, 1989; Nachtigall, 1989; Vogel, 1967; Zanker, 1990a,b; Zanker and Götz, 1990) and without calyptae, the membranous lobes at the posterior wing base. (3) Hereditary disorders of optomotor responses in *Drosophila melanogaster* mutants (Heisenberg and Wolf, 1984) invite a dissection at the level of the flight control muscles.

The orchestration of flight control in the fruitfly is not yet understood. Here we have tried to identify muscular activities that are correlated with specific response components of the beating wings. To what extent the activation of a muscle really accounts for a covariant optomotor response remains to be established, e.g. by electrical stimulation of this muscle (Lehmann and Götz, 1990, 1996) or by the appropriate transformation of its electrical activity into a response eliciting visual feedback (Götz, 1985, 1989).

The present paper compares the activities of four prominent

pairs of flight control muscles with the optomotor responses of the wingbeat amplitudes during tethered flight in still air. The responses were elicited by continuous motion of a striped pattern in front of the visual system and measured by evaluating the action potentials of the muscles, the angular motion of the wings, or both simultaneously.

Materials and methods

The experiments were performed with 56 female *Drosophila melanogaster* (wild-type ‘Berlin’ from a stock at the Max-Planck-Institut für Biologische Kybernetik, Tübingen, Germany). The legs of a cold-anaesthetized fly were removed and a holder of diameter 0.2 mm was glued to the anterior part of the ventral thorax with dental cement. The tip of the holder was bent in the direction of the animal’s long axis and was glued to the lower posterior portion of the head capsule to prevent head motion. The fly holder was mounted onto one of four miniaturized micromanipulators; the remaining manipulators were used to insert a recording electrode into one or two selected flight control muscles and a reference electrode into the fly’s abdomen.

The tethered fly was positioned in the centre of the photoelectric device (Götz, 1987a) shown in Fig. 1. To record the wing stroke on either side, the wing’s shadow was cast onto the wedge-shaped mask opening of the contralateral photodetector. At the beginning of the downstroke, the wing is still ‘out of sight’: both wings touch, or nearly touch, each other. During the downstroke, the shadow obscures increasing portions of the opening. Maximum obscuration is obtained at the end of the downstroke. The corresponding electrical signal is a measure of the actual wingbeat amplitude minus the lowest amplitude to be detected by the masks of the device. The difference between the signals obtained with either a moving pattern or a resting pattern in front of the eyes represents, in relative units (r.u.), the optomotor response of the wingbeat amplitude (WBA). The angular equivalent of 0.1 r.u. is about 10°. This response of a wing contributes approximately 1.5×10^{-6} N to the force of flight and approximately 3.0×10^{-9} N m to the yaw moment of this force at the centre of the fly (Götz, 1983a). A sample-and-hold circuit facilitated continuous measurements of the two amplitudes (R, L), and their combinations (R–L; R+L). A transient drop in the obscuration of the mask opening occurs at the beginning of the upstroke when the wings flip from the pronated to the supinated state (ventral reversal). The minimum is reached when the wing cord is parallel to the incident light. Figs 3A, 4B, 5A and 8C show examples of the recorded obscuration. The transient minima at the crest of the so-called wingbeat signal (WB) are very sharp because of the extremely fast rotation of the wings about their long axis (Zanker, 1990a,b; Zanker and Götz, 1990). They occur almost simultaneously on both sides (Dickinson *et al.* 1993) and were, therefore, selected as the most reliable ‘absolute’ reference marks for the definition of phase relationships with respect to the wingbeat cycle. The reference marks obtained from the two wings coincide to within less than 2% of the wingbeat cycle of 5 ms that corresponds to the average wingbeat frequency of 200 Hz in *Drosophila melanogaster*.

In some experiments, the photoelectric device was replaced by two sensors, each consisting of a light-emitting and a light-receiving diode. The infrared light beam between these diodes was periodically interrupted by one of the beating wings (Heide, 1971*b*). The light-on or light-off signal of either the upstroke or downstroke can be used as a 'relative' reference mark of the wingbeat cycle. This mark still allows accurate measurements of the wingbeat frequency. The selection of the signal and the alignment of the beam determine the unknown, but fairly constant, phase relationship to the absolute reference mark of the wingbeat cycle.

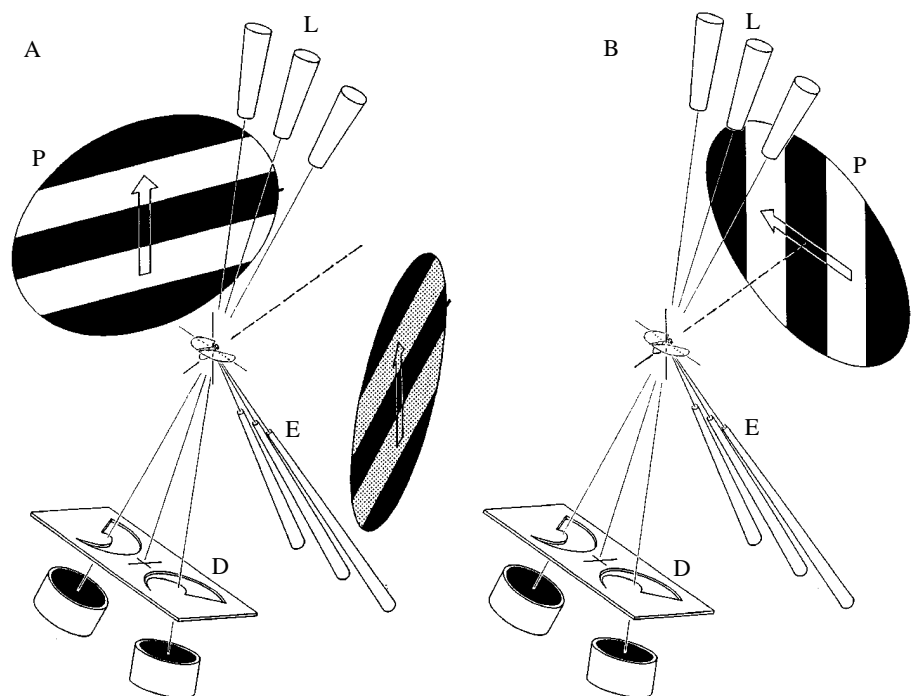
To induce optomotor reactions, a striped pattern moving at a constant velocity was projected from behind onto a translucent screen within the equatorial zone of the fly's visual field (Götz, 1968; Götz and Wenking, 1973). As shown in Fig. 1, the visual stimulus was presented either to the fronto-lateral area of the left and/or right eye (omitting the binocular field) or to the frontal area of both eyes. The visual stimulus received from a single screen is characterized by the following averages: proportion of stimulated ommatidia 140/1400=0.1; luminance of the pattern 200 cd m⁻²; contrast between adjacent stripes 0.75; spatial wavelength of the periodical pattern 30°, or about seven times the angular distance between the optical axes of interacting photoreceptors; speed of the pattern 1 wavelength s⁻¹, corresponding to the most efficient contrast frequency for optomotor flight control in *Drosophila melanogaster* (Götz, 1983*a*). To change the direction of the continuous pattern motion across the stimulated area of an eye field, the projectors could be rotated around their optical axes. The notation used in this paper relates to the direction of motion

as seen by the fly: Fig. 1 shows examples of a stimulus moving upwards (12 o'clock direction) or to the left (9 o'clock direction). The two-projector arrangement in Fig. 1A made it possible to combine different motion directions on either side. Some of these combinations simulate rotatory or translatory components of retinal displacements perceived during free flight in a stationary environment (Spüler, 1980; Heide *et al.* 1985). In the present investigation, we induced the optomotor responses of yaw torque (course control) or lift/thrust (altitude control) by presenting the 'same' direction of motion to the left and the right eye, either in a two-projector arrangement (Fig. 1A) or with only one projector in front of the fly (Fig. 1B).

The action potentials (spikes) from the flight control muscles were recorded using electrolytically tapered tungsten electrodes. After appropriate positioning, the non-insulated electrodes were inserted through the cuticle directly into the muscles. The reference electrode was placed between the comparatively small air sacs in the abdomen. The fly holder and the reference electrode were earthed during the measurements. Flight muscle anatomy is surprisingly uniform in all Diptera. The configuration of the flight muscles in *Drosophila melanogaster* is known from several investigations; in Fig. 2, we refer to the description given by Zolotar (1947) and Heide (1971*a*).

In order to identify the very small flight control muscles in *Drosophila melanogaster*, the following criteria were applied. (1) *Anatomical assignment.* Marks on the cuticle can be used to guide the insertion of electrodes into identified muscles. The tip of an electrode was allowed to just penetrate the cuticle without moving deeper into the thorax. The identification of the control

Fig. 1. Experimental set-up for simultaneous bilateral measurement of muscle activity and wingbeat amplitude in response to continuous motion of a striped pattern on a projector screen P. The arrows show examples of motion presented in the fronto-lateral (A) or frontal (B) part of the visual field. The drawings of the fly indicate the horizontal body axis (broken line) and the envelopes of the beating wings. In A, the screen facing the fly's right eye is shown shaded to indicate that the reader is viewing it from behind. The fly is mounted on an adjustable holder (not shown) between the recording electrodes E. The central spotlight L used for the adjustment is flanked by two infrared light sources, each casting a shadow of the ipsilateral wing onto the mask opening of the contralateral infrared detector D. The light flux through a wedge-shaped mask opening depends on the angular position of the corresponding wing: the minimum of the light flux during the wiper-like motion of its shadow is used as a measure of the actual wingbeat amplitude. Unlike measurements of force or torque, the present method is extremely fast, indicates the beginning of a wingbeat cycle, processes the actions of the two wings separately from each other and allows the insertion of electrodes into selected muscles of the flight control system.



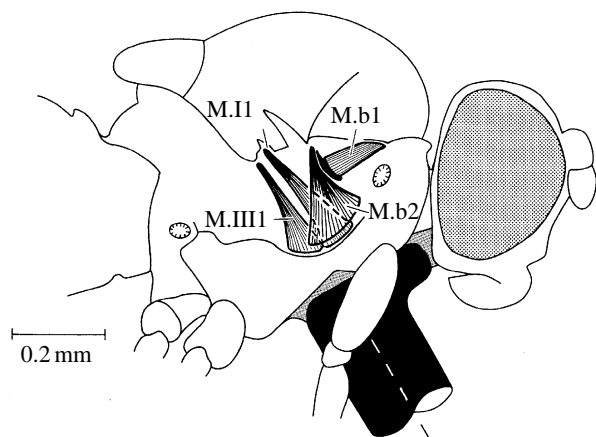


Fig. 2. Lateral view of the most conspicuous flight control muscles on the right side of the thorax, just below the cuticle, of the fruitfly *Drosophila melanogaster*: M.b1 and M.b2 (inserting on the basalar sclerite), M.II (inserting on the first axillary sclerite) and M.III1 (inserting on the third axillary sclerite). Redrawn from Zalokar (1947). Notation of the muscles according to Heide (1971a). For synonyms, see King and Tanouye (1983). The figure shows the thin layer of dental cement (light shading) used to attach the fly holder (black shading) to ventral portions of the thorax and head. Orientation of the fly as in Fig. 1.

muscles penetrated according to such cuticular marks has been verified in recent experiments by current-induced coagulation of the tissue near the electrode tip and subsequent inspection of this area under a polarizing microscope (Lehmann, 1994). To record from muscles M.b1 or M.b2, the electrode was aimed at a position near their respective origin on the thoracic wall; to record from muscles M.II or M.III1, the electrode was inserted into the appropriate position at the ventral rim of the dorsal episternum. The electrodes do not seem to restrict normal wing motion. (2) *Electrophysiological assignment*. The characteristic pattern of activity found in a flight muscle of *Drosophila melanogaster* under defined stimulus conditions was compared with the analogous pattern of activity in the corresponding flight muscle of the larger flies *Calliphora erythrocephala* and *Musca domestica* (Heide, 1971a,b, 1975, 1983), where the muscular target for the electrode is more easily identified by direct microscopical inspection. (3) *Phase relationship*. As shown in Fig. 6, the recorded action potentials of the prominent flight control muscles are phase-locked with respect to the wingbeat cycle. The action potentials occupy characteristic phase bands, which can be used to distinguish the different muscles.

Problems caused by cross-talk between neighbouring muscles were minimized as follows: unwanted spikes from asynchronous power muscles were eliminated, to some extent, by a high-pass filter with a cut-off frequency of approximately 1 kHz. Such filters selectively attenuate the essential frequency components of the power muscle spikes. As a rule, unwanted spikes from other control muscles were significantly smaller than the spikes obtained from the impaled muscle. Under these conditions, the cross-talk could be reliably eliminated by means of a threshold discriminator. To improve the signal-to-

noise ratio, a low-pass filter with a cut-off frequency of approximately 3 kHz was added in most of the present experiments. Spike amplitudes between 1 and 5 mV were obtained under these conditions.

The action potentials of one or two muscles, the actual wingbeat amplitudes (R, L), their differences (R–L) and sums (R+L), the wingbeat signals containing the absolute reference marks of the wingbeat cycle, and the signals controlling the pattern motion on the projector screens were recorded on tape. Simultaneously, the wingbeat amplitudes obtained during the time period of a given stimulus were averaged on-line using analogue devices developed in cooperation with M. Herre and H. Wenking (Max-Planck-Institut für Biologische Kybernetik, Tübingen, Germany). The electrical signals from the muscles were subsequently played back and the threshold was set to respond to the action potentials of the most prominent source. This was verified by continuous inspection of the size and shape of the triggering signal on the oscilloscope screen. The signal indicated the occurrence of a muscle spike approximately 0.5 ms after its onset. Hard- and software for the evaluation and graphical representation of the time of occurrence of spikes in relation to the reference marks of a wingbeat cycle were developed by M. Spüler, K. Kamper and D. Schrage (Institut für Zoology, Universität Düsseldorf).

The distribution of muscle spikes over the wingbeat cycle is shown in a phase histogram. Using the absolute reference marks derived from the wingbeat signals WB R or WB L, the wingbeat cycle is considered to begin and end with the fast transition from the downstroke to the upstroke (ventral reversal). According to the notation introduced by Wyman (1969), the phase ϕ of a muscle spike is simply the ratio of the latency between the spike and the preceding reference mark to the time period between the ensuing and the preceding reference mark. This definition assigns to each of the spikes a 'trailing' phase ϕ or a 'leading' phase $1-\phi$, both with values in the range 0–1. In earlier publications (Götz, 1983a,b), the results were multiplied by 360 to express the phase in degrees.

Data pooling

Assuming lateral symmetry of both the visual system and the flight control system, we pooled the results obtained under mirror-symmetrical conditions with respect to the median plane of the fly. For example, pattern motion in a 2 o'clock direction on the left is the mirror-inverted equivalent of pattern motion in a 10 o'clock direction on the right. To pool the results of these two experiments, the responses of the wings and muscles in the first experiment were supplemented by the responses of their respective lateral counterparts in the second experiment. The presentation of pooled data in a figure is explicitly mentioned in its legend.

Results

Muscle-specific patterns of spike activity

The flight system in *Drosophila melanogaster* comprises up to 17 possible control muscles on either side. Four of the most

prominent muscles are shown in Fig. 2. These muscles have been accessible to electrical recording over extended periods of tethered flight (Heide, 1978, 1983; Ewing, 1979*a,b*; Götz, 1983*a,b*, 1987*b*, 1989; Lehmann, 1994). The present examples illustrate specific patterns of activity found in the basalar muscle M.b1 (Fig. 3A), the sternobasalar muscle M.b2 (Fig. 3B), the axillary muscle M.II (Fig. 3C) and the axillary muscle M.III1 (Fig. 4). Flight is a prerequisite for visually induced activity in the first three of these muscles. With the wings at rest, action potentials occur only rarely or not at all.

During flight, M.b1 was almost continuously active. The frequency of the action potentials (spike rate) was equal to, or slightly below, the frequency of the wingbeat (156 Hz in the present example). A comparison of the muscle spikes and the simultaneously recorded wingbeat signals (Fig. 3A, uppermost and central trace, respectively) generally showed the occurrence of one spike per wingbeat cycle. Increased time resolution in the example on the right revealed a phase relationship between the muscle spikes and the wingbeat signal. This relationship was not disturbed by occasional interruptions in the spike train (Fig. 3A, arrow).

A qualitatively different action pattern was found in M.b2 and M.II. The average rate of spontaneous spike activity in these muscles was comparatively low. The activity was characterized by occasional bursts (see arrows in Fig. 8A,B). The maximum spike rate in these bursts rarely reached or exceeded the frequency of the wingbeat. The contribution of these muscles to induced responses of the optomotor course control system was investigated under the conditions shown in Fig. 1B. The moving stripes on the screen in front of a tethered *Drosophila melanogaster* simulate the effect of continuous deviation from a straight course. To counteract this deviation, the fly tries to follow the stripes by increasing the wingbeat amplitude on the outer side and decreasing the wingbeat amplitude on the inner side of the intended turn. The direction-specific effect of pattern motion on the spike activity of the muscles on the right side (R) of the thorax is shown for M.b2R

(Fig. 3B) and M.IIR (Fig. 3C). Motion to the left (central trace low) activated M.b2R but not M.IIR. Motion to the right (central trace high) activated M.IIR but not M.b2R. The mirror symmetry of the control system has been confirmed by an investigation of the corresponding muscles on the left side (L) of the thorax. As expected, M.b2L was activated by motion to the right and M.IIL by motion to the left. Further results suggest that spike activity in any of these muscles is accompanied by a muscle-specific increase (M.b2) or decrease (M.II) in the difference between the beat amplitudes or between the average forces of flight of the ipsilateral and the contralateral wing.

The contribution of M.III1 to flight control in *Drosophila melanogaster* deviated considerably from this scheme. During tethered flight, the spontaneous spike activity of this muscle was extremely low and could not be increased by horizontal or vertical components of pattern motion. At rest, however, the muscle was easily activated by a puff of air blown from below to separate the wings from the abdomen. Note the coincidence of spike activity with the sound of the stimulus (Fig. 4A, uppermost and central traces, respectively). The muscle seemed to support the retraction of the wings towards their resting position but did not participate in optomotor flight control. Retraction of the wings towards the resting position was imminent whenever a burst of spikes occurred. A long-lasting burst in M.III1 was often accompanied by a transient ventral deflection of the abdomen and the wing tips. The wingbeat signals WB R and WB L in Fig. 4B show an example of loosely coordinated flight interruption for about 0.2 s which coincided with spike activities in M.III1 and M.II.

Muscle-specific spike patterns within the wingbeat cycle

The spikes recorded from flight control muscles in *Drosophila melanogaster* appear to be phase-locked with respect to the wingbeat cycle (Heide, 1978, 1983; Ewing, 1979*a,b*). The objectives of the following experiments were (1) to determine the position of the expected 'windows' for spike occurrence within the wingbeat cycle, (2) to investigate the

Fig. 3. Characteristic patterns of spike activity in the flight control muscles M.b1 (A), M.b2 (B) and M.II (C) (see Fig. 2). Uppermost traces: spike activities recorded in identified muscles. Central traces: simultaneous recordings of either the wingbeat signal, indicating the wingbeat cycle (A), or the direction of the optomotor stimulus (B,C). Lowermost traces: time marks. (A) Continuous activity of approximately 1 spike per wingbeat cycle, or about $156 \text{ spikes s}^{-1}$, in the left (L) M.b1. The time marks correspond to 20 ms per interval for the example on the left and to 10 ms per interval for the example on the right. The latter example illustrates the phase relationship between the muscle spikes and the dips on the crests of the wingbeat signal. The dips indicate the transition from downstroke to upstroke. Occasionally, a spike was missing (arrow). (B) Direction-specific activity of the right (R) M.b2 in response to visual stimulation on a screen in front of the fly (see Fig. 1B). The pattern moved alternately to the left (central trace low) and to the right (central trace high). Time marks, 1 s per interval. (C) Direction-specific activity of the right M.II under similar conditions.

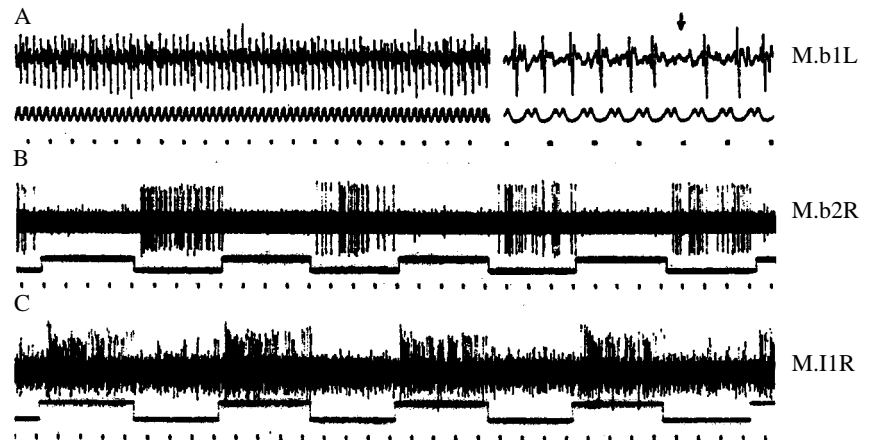
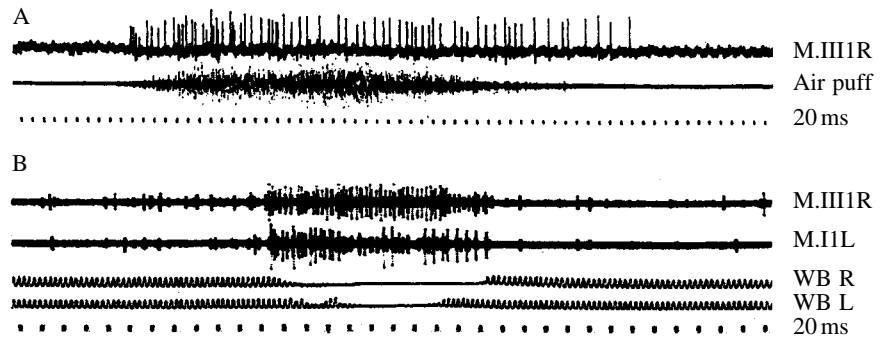


Fig. 4. Characteristic pattern of spike activity in the flight control muscle M.III1 (see Fig. 2). (A) Activation by a puff of air blown from below to lift the resting wings. From top to bottom: spikes of the right M.III1; electro-acoustic signal of the stimulus; time marks, 20 ms per interval.

In *Drosophila melanogaster*, this muscle does not seem to participate in optomotor flight control. (B) Coincidence of activity in the otherwise silent muscle M.III1 with a 0.2 s period of spontaneous flight interruption. From top to bottom: spikes of the right M.III1, assignment inferred from the recording site of the electrode

and from the exclusion of motion-sensitive flight control responses; spikes of the left M.I1, the smaller spikes in this trace are likely to belong to the left M.III1; wingbeat signals on either side (WB R, WB L); time marks, 20 ms per interval. Simultaneous recordings from the same fly. Retraction of the wings towards the resting position by muscles M.I1 and M.III1 could explain their activity during flight suppression, flight termination or flight interruption.



preferred phase of spike activity under different conditions of visual stimulation, and (3) to compare the results obtained with different muscles of the flight control system.

The recordings in Fig. 5A represent a complete upstroke–downstroke cycle. The upper two traces of the three diagrams show a number of superimposed action potentials from M.b1 on the right (R) or on the left (L). The potentials were recorded together with the wingbeat signals (WB), which are superimposed on the lowermost trace. The arrows indicate the direction of pattern motion in front of the eyes. Motion to the left induced spike activity both in M.b2R and M.I1L. The results show the accumulation of the spikes in muscle-specific windows of the wingbeat cycle. The visually induced spikes of the otherwise inactive muscles coincided either with the comparatively fast upstroke (M.b2) or with the comparatively slow downstroke (M.I1) of the wings. The spikes of the almost continuously active muscles (M.b1) accompanied the transition from upstroke to downstroke. However, the actual phase of the muscle spikes depended on visual stimulation: a comparison of the upper two diagrams reveals a motion-induced direction-specific shift of the phase within the muscle-specific window. The existence of a muscle-specific phase relationship facilitates the identification of the investigated flight control muscles, either by comparison of the muscle spikes with the reference signal from a wingbeat processor or by stroboscopic inspection of the spike-related wing posture. Fig. 5B shows a photograph of the early downstroke obtained by exposure to a volley of flashes triggered by the spikes of muscle M.b1.

The influence of visual stimulation on the frequency of the muscle spikes and their distribution over the wingbeat cycle is shown in more detail by the phase histograms in Fig. 6A. The results were derived from the activities of corresponding muscles on either side. However, the data have been combined and are presented as if they had been derived from the muscles on the right (R in parentheses). To facilitate the comparison of spike activities in response to motion in a 9 o'clock direction (broken line) with those in response to motion in a 3 o'clock direction (solid line), we used identical sampling time intervals

in corresponding experiments. The histograms confirm the conclusions drawn from the results in Fig. 5 and reveal the following peculiarities of visual flight control in *Drosophila melanogaster*. (1) The direction-specific control of the frequency of the muscle spikes is represented by the area of the corresponding histograms. The comparatively high rate of spikes in M.b1 is almost independent of the direction of pattern motion. A 'preferred direction' and a 'null direction' of pattern motion can be distinguished by the direction-dependent frequencies of spikes in both M.b2 and M.I1: spikes were rarely evoked by front-to-back motion in M.b2 (solid line) or by back-to-front motion in M.I1 (broken line). Sporadic ambiguity of the direction-specific input to 'unidirectional' motion detectors may account for some if not all of the spikes obtained in response to pattern motion in the null direction. (2) The direction-specific control of the phase of the muscle spikes within the wingbeat cycle was significant in M.b1, but apparently missing in M.b2 and M.I1. Sporadic ambiguity of the direction-specific input may account for a small second peak in the distribution of the M.b1 spikes. Resulting from the apparent motion in the opposite direction, this peak was expected and found at the corresponding phase of the wingbeat cycle: in Fig. 6A (upper panel), the first and the second peaks are either fused (solid line) or distinct (broken line). The lack of direction-specific phase shifts in M.b2 is most easily explained by the assumption of unidirectional detectors which respond only to real or, sporadically, to apparent motion in their preferred direction. (3) Identical simultaneous phase shifts in the spikes of M.b1, M.b2 and M.I1 would be equivalent to a shift of the wingbeat cycle with respect to an invariant pattern of spike occurrence in these muscles. The present results rule out such effects.

The frequency and distribution of interspike intervals in units of the actual wingbeat period are shown for the different flight control muscles on either side (R, L) by the interval histograms in Fig. 6B. The preferred interspike interval of 1 wingbeat period (WBP) in M.b1 deviates from the corresponding intervals of at least 2 or 3 wingbeat periods in visually induced spike activities of M.I1 and M.b2,

respectively. The pattern of the comparatively long interburst intervals of these muscles (shown in Fig. 8) reveals no significant regularities.

Wingbeat amplitude versus spike phase in *M.b1*

Flies tend to stabilize the retinal image of their surroundings, presumably in an attempt to counteract involuntary deviations from a straight course. *Drosophila melanogaster* tries to follow horizontal components of motion in front of its eyes mainly by controlling the difference (WBA R–L) between the wingbeat amplitudes: motion to the left increases WBA R on the outer side and decreases WBA L on the inner side of the intended turn to the left (Götz *et al.* 1979).

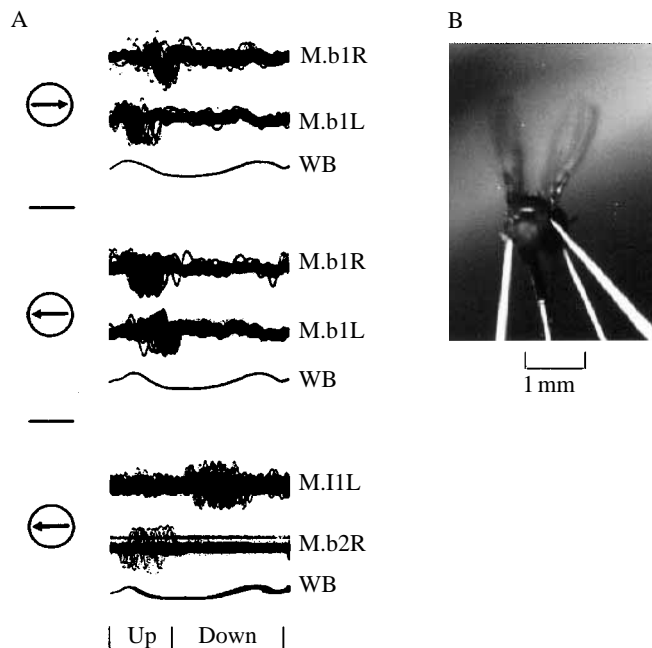


Fig. 5. Phase relationship between muscle spikes and wingbeat cycle. (A) The width of the three panels corresponds to a complete wingbeat cycle, beginning with the transition from downstroke to upstroke. Every second reference pulse indicating this transition was used to trigger an oscilloscope in order to superimpose, on the upper two traces, the simultaneously recorded action potentials from a flight control muscle on either side (R, L) and, on the lowermost trace, the corresponding wingbeat signal (WB). The arrows in circles on the left indicate the direction of pattern motion on the two screens in front of the eyes (see Fig. 1A). The upper two panels show the superposition of approximately 80 cycles of 6.2 ms duration obtained from the same fly. A comparison of the results reveals motion-induced shifts within the specific phase band of the M.b1 spikes. Specific phase bands also exist for the spikes of M.b2 and M.II. This is shown in the lower panel by superposition of approximately 750 cycles of 5.0–5.6 ms duration. (B) The spikes can be used to trigger a stroboscopic illumination of the wingbeat. The frontal view of a *Drosophila melanogaster* (with fly holder and three electrodes) shows the effect of multiple illumination in a narrow range of the early downstroke, obtained using a 1.5 s volley of M.b1 spikes. Spike-induced visualization of the phase band helps to identify the corresponding flight control muscle in experiments where the reference signal from a wingbeat processor is missing.

Fig. 7 shows the relationship between course control response (WBA R–L) and spike phase in M.b1R and M.b1L. The results indicate (1) the stochastic distribution of the phase of consecutive spikes within the preferred phase band, (2) the motion-induced shift of this band, suggesting the participation of these muscles in the control of the wingbeat amplitudes, and (3) the asymmetry of this effect: pattern motion in a horizontal direction elicits a continuous phase lead of the spikes in the M.b1 on the outer side of the intended turn to the left (M.b1R)

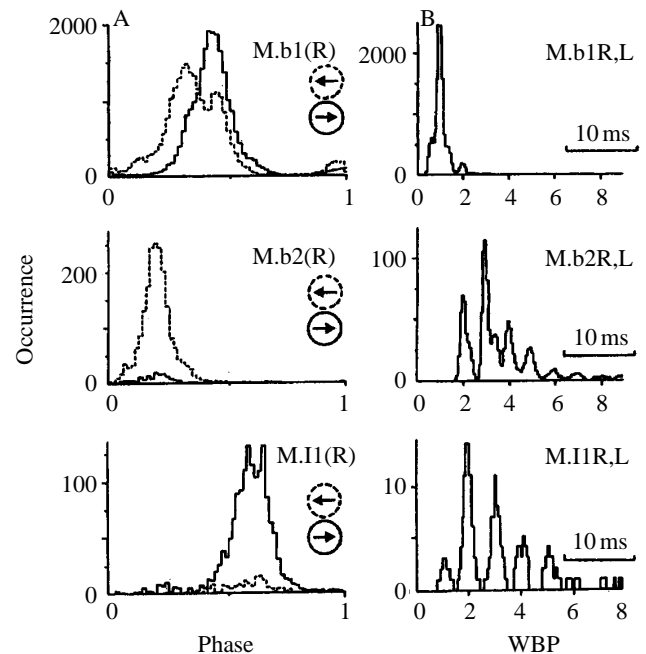


Fig. 6. Characterization of the spike activity in the flight muscles M.b1, M.b2 and M.II of *Drosophila melanogaster*. (A) Phase histograms of the spikes in three different muscles. The histograms show the influence of visual stimulation on the distribution of the occurrence of spikes over the wingbeat cycle. The phase ϕ of the cycle begins with the transition from downstroke to upstroke. The bin width is 1/64 of the complete cycle. The patterns on the screen on either side of the insect (see Fig. 1A) moved alternately to the left for 9 s (broken line) and to the right for 9 s (solid line). The results are plotted for muscles on the right side (R) of the thorax. The parentheses indicate the inclusion of the data obtained from the corresponding muscles on the left side under mirror-inverted conditions (see Materials and methods). The three diagrams show, from top to bottom, the direction-selective effects of pattern motion on the phase of the M.b1 spikes (six muscles; three flies), on the frequency of the M.b2 spikes (five muscles; three flies) and, antagonistically, on the frequency of the M.II spikes (six muscles, four flies). (B) Interval histograms of the spike activities presented in A. The histograms show the distribution of the occurrence of interspike intervals over the time of their duration, scaled in average wingbeat periods (WBP). A time interval of 10 ms is given for comparison. Each of the histograms represents the data derived from spike sequences of the corresponding muscles on either side (R, L) in three different flies. Appropriate visual stimulation was applied to enhance the spike activities of M.b2 and M.II. Nevertheless, the preferred interspike interval is clearly 1 wingbeat period for M.b1, and at least 2 or 3 wingbeat periods for M.b2 and M.II.

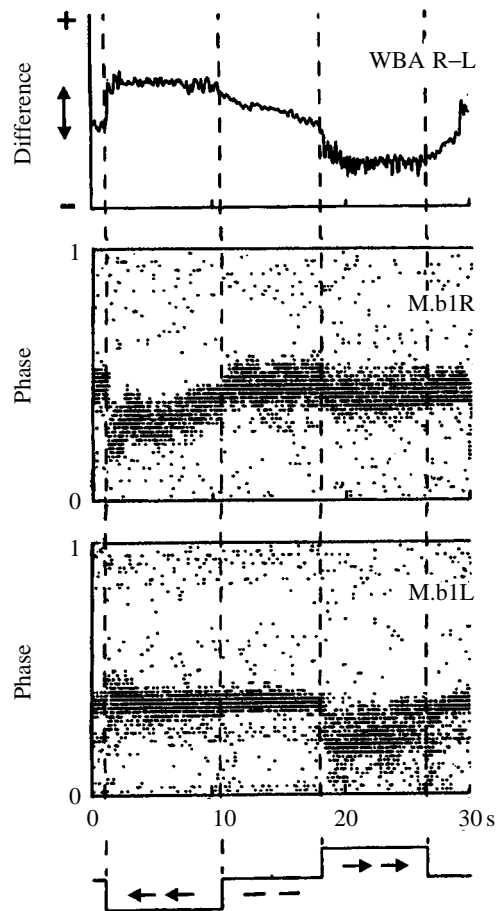


Fig. 7. Motion-induced course control response given by the difference between the wingbeat amplitudes on either side (WBA R-L) in comparison with the direction-specific phases of the spikes in the right (R) and left (L) M.b1 within the wingbeat cycle. The dots represent the phases of subsequent spikes in a single experiment. The trace at the bottom indicates the temporal sequence of the visual stimuli projected on the screens in front of the two eyes: motion to the left (low), no motion (medium), motion to the right (high). Simultaneous recordings from the same fly. The wingbeat response demonstrates the well-known tendency of the fly to follow the pattern motion on the screens. The response of the muscles suggests a stochastic distribution of the spikes within the phase band. The motion-induced shift of this band suggests a participation of M.b1 in the control of the wingbeat amplitudes.

or to the right (M.b1L). An equivalent phase lag of the spikes in the M.b1 on the inner side of the intended turn to the left (M.b1L) or to the right (M.b1R) is apparently missing. The insensitivity to visual stimulation observed under these conditions should diminish the fluctuation of the phase. The width of distribution in the phase histograms shown for M.b1(R) in Fig. 6A is indeed smaller for the ineffective motion to the right (solid line) than for the effective motion to the left (broken line).

Wingbeat amplitude versus spike rate in M.b2 and M.II

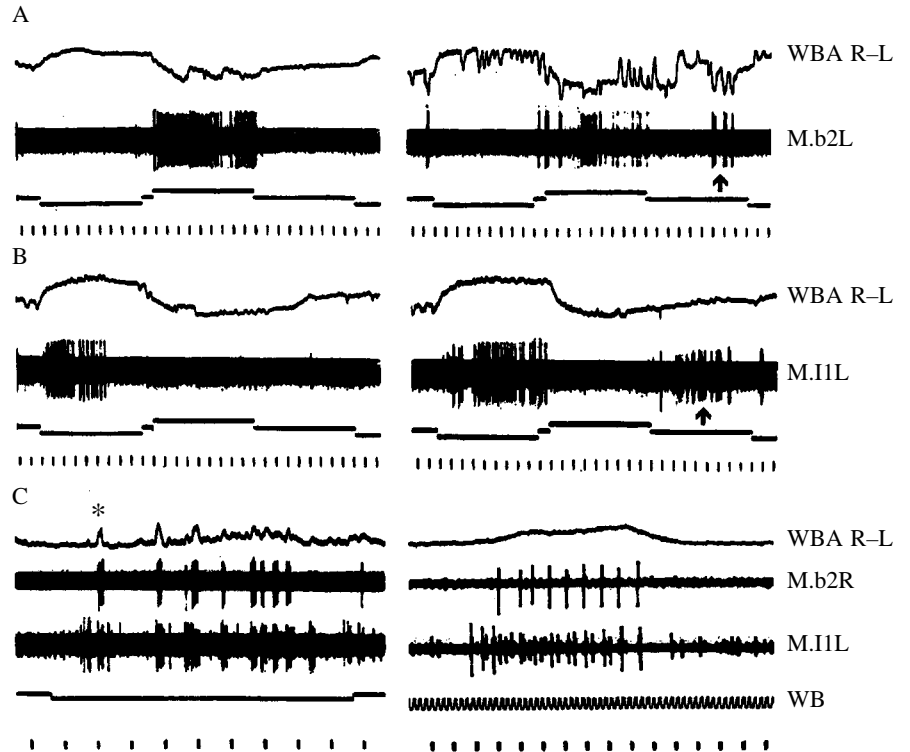
The relationship between the motion-induced course control response (WBA R-L) and the spike activities of the apparent

antagonists M.b2L (Fig. 8A) and M.IIL (Fig. 8B) or of the apparent synergists M.b2R and M.IIR (Fig. 8C) suggests the participation of these muscles in optomotor flight control because of the coincidence of repeated bursts of spikes with slightly delayed volleys of fast 'hitches' in the wing response (Götz, 1989; Götz *et al.* 1979) which are likely to elicit abrupt turns ('body saccades') in free flight (Heisenberg and Wolf, 1984). A comparison of the simultaneously recorded activities of the apparent synergists in Fig. 8C shows a partial coincidence of both the spike bursts (panel on the left) and the spikes within the bursts (panel on the right). The fixed delay between associated spikes in M.b2R and M.IIR and the occasional occurrence of a (slightly smaller) M.II spike in the subsequent wingbeat cycle is consistent with the results shown in Fig. 6. A few conspicuous differences in the spike patterns of M.b2R and M.IIR in Fig. 8C indicate partial independence of activation in these muscles. The time course of spike activity observed in the two successive runs of the experiments in Fig. 8A,B varies considerably and cannot be attributed to a fixed template. Results published previously (Heide, 1983) confirm this observation (Fig. 9): superposition of the data from several runs of these experiments smooths the average time course of the responses. This is a consequence of the irregular distribution of both the bursts of spikes and the concomitant hitches of the wing stroke. The different time course of the responses of muscles and wings in Fig. 9 suggests a contribution of M.b2 and M.II to the 'phasic' components of optomotor course control in *Drosophila melanogaster*. The muscles do not seem to account for all of the 'tonic' components of this reaction.

Direction-specific response components in muscles and wings

Partially independent spike activity in two synergists of the course control system, the muscles M.b2R and M.IIR in Fig. 8C, raised questions about the origin and function of the response components that do not occur simultaneously in these muscles. Presumably, the cooperation of these muscles during course control is conditional if the muscles must be independently activated in the context of other control functions. To prove this conjecture, it would be necessary to separate the stimulus components which activate different combinations of the flight control muscles under investigation. Fig. 10 summarizes the results of the experimental approach used. The arrows on the abscissa specify different directions of pattern motion on the screen in front of the fly (see Fig. 1B). The panels show the effects of the corresponding stimuli on the wingbeat amplitude (WBA), the spike phase of M.b1, and the spike activity of M.b2 and of M.II for the wings or muscles on either side (R, L) of the thorax. Motion detection in *Drosophila melanogaster* is mainly accomplished by nearest-neighbour interaction along the three main axes of the hexagonal array of visual elements in the compound eyes (Buchner, 1976, 1984; Götz *et al.* 1979; see Fig. 11). Accordingly, the pooled data from a total of 25 flies were fitted by periodic functions comprising harmonics up to an order of three, the highest order likely to occur under these conditions.

Fig. 8. Comparison of the motion-induced course control response with the direction-specific spike activity in two pairs of flight control muscles. A–C show, each for a different fly, from top to bottom: the difference between the wingbeat amplitudes on either side (WBA R–L); the simultaneously recorded action potentials from one or two of the muscles (M.b2; M.I1) on the right or left side (R, L); the signal indicating the visual stimulus on the screens in front of the eyes, motion to the left (low), no motion (medium) or motion to the right (high); and time marks. (A,B) The response of the wingbeat amplitudes demonstrates the attempt to follow the pattern motion on the screens. The slow component and the occasional volleys of fast ‘hitches’ characterize the optomotor behaviour of *Drosophila melanogaster*. The coincidence of some of the hitches with perceivably antecedent bursts of spike activity suggests a participation of M.b2 and M.I1 in the control of the wingbeat amplitudes. Neither the hitches nor the spike bursts seem to occur in reproducible temporal succession. Different configurations of a spike train were obtained in two successive runs of the same experiment (panels on the left and on the right). Arrows indicate the transient occurrence of spontaneous bursts in the absence of visual stimulation. Time scale, 1 s per interval. (C) Comparison of a succession of spikes in the simultaneously active ‘synergists’ M.b2R and M.I1L shows partial coincidence between their responses to visually perceived motion to the left. Panel on the left: the bursts of spikes are accompanied by hitches (sudden changes) in the difference (R–L) between the wingbeat amplitudes on either side; the fly tries to follow the visual stimulus. Time scale, 1 s per interval. Panel on the right: an expanded view of the reactions marked by an asterisk on the left shows the resolution of the two bursts into single spikes. Trace WB indicates the wingbeat cycle. Time scale, 20 ms per interval.



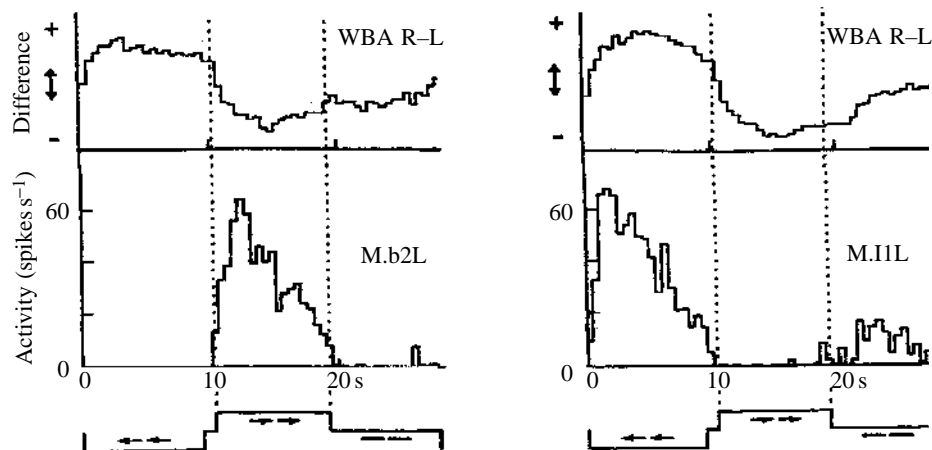
Conspicuous similarities between the butterfly-shaped response curves of the wings and the muscles suggest the participation of M.b1, M.b2 and M.I1 in a common scheme of flight control. The strongest responses were elicited by pattern motion in oblique directions (approximately 11 o'clock and 1 o'clock), which deviate considerably from the preferred directions for course control (9 o'clock and 3 o'clock). Qualitatively, M.b1R, M.b2R and M.I1L or their counterparts M.b1L, M.b2L and M.I1R act like synergists in this scheme. However, significant quantitative differences can be observed, for instance in their response to horizontal motion. Independent control of cooperating muscles was even more evident for the homologous counterparts (L, R) within each of the four panels. In a simplified classification, the response of a wing or muscle may be either high (HI) or low (LO). Four combinations of such responses are conceivable in a pair of wings or muscles: HI/HI or LO/LO for synergists and HI/LO or LO/HI for antagonists. All of these combinations occur in each of the panels. The corresponding homologous counterparts seem to be engaged in at least two different control functions: their variable role as synergists or antagonists depends on the actual direction of pattern motion in front of the fly. Much of the wingbeat response can be explained by the combined actions of the muscles in Fig. 10. However, a significant portion of the

response requires contributions from additional control muscles with preferred sensitivity to pattern motion in a 4–5 o'clock direction on one side and the mirror-inverted 7–8 o'clock direction on the other side. Among the up to 17 possible pairs of flight control muscles in *Drosophila melanogaster* there are still about 13 potential candidates for these reactions.

The Fourier components of the curves fitted to the experimental data in Fig. 10 can be interpreted as ‘fingerprints’ of the direction-specific responses of a particular wing or muscle. The control of these responses requires a direction-specific array of elementary motion detectors. The fingerprint also applies to this array, provided that the responses of its muscle or wing are proportional to the strength of the sensory signal. Otherwise, the fingerprint describes a reduced array of detectors which is compatible with the actual responses and their preferred direction of stimulation. Fingerprints of such arrays may be useful as a tool in comparative studies on optomotor-disturbed mutants or on other species.

Fig. 11 shows the principal direction and relative magnitude of the harmonic components of the order 1, 2 and 3 for the right wingbeat amplitude WBA R and the contributions of the apparent synergists M.b1R, M.b2R and M.I1L. (To approximate the responses of the contralateral pairs to this wing and these muscles, namely WBA L, M.b1L, M.b2L and M.I1R,

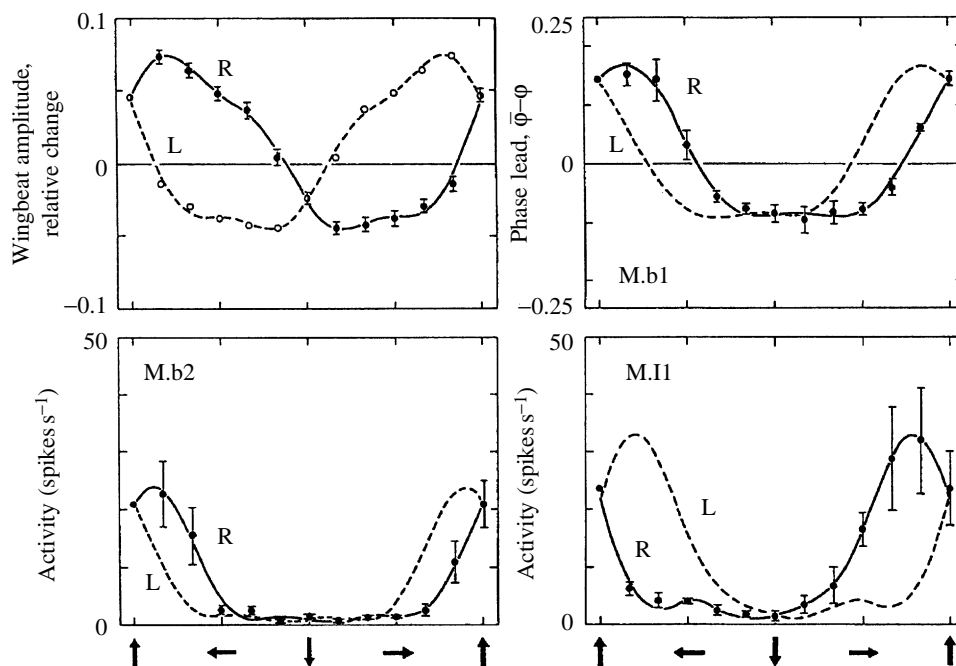
Fig. 9. Average time course of the motion-induced wingbeat response (WBA R-L) in comparison with the spike rate of the 'antagonists' M.b2L (panel on the left) and M.IIL (panel on the right). The trace at the bottom indicates the visual stimulation in front of the two eyes. The diagrams show the averages obtained from five runs of the experiments in Fig. 8A,B. The spike activity of the two muscles does not seem to account for all of the 'tonic' components of the wingbeat response. This suggests the participation of additional muscles of the flight control system.



the bars must be plotted in reverse order. A comparison of diagrams R and L in Fig. 13 illustrates the 'reversed succession' of similar components.) The harmonic component 1 indicates, by its position, the preferred direction of the array of motion detectors fitted to the selected response curve in Fig. 10. Without substantial contributions of higher harmonics (2, 3), component 1 stands for the sinusoidal response curve of bidirectional detectors which discriminate, by the sign or strength of their response, motion in the preferred direction from motion in the opposite direction (right wingbeat amplitude

in Fig. 11). A coincidence of component 1 with a smaller component 2 (the theoretical optimum of the ratio 1:2 is 0.42) stands for the half-sine response curve of unidirectional detectors which respond only to motion in their preferred direction (M.b1R, M.b2R and M.IIL in Fig. 11). Component 3 merely sharpens the peak(s) in the response curves if its main direction coincides with 1 (M.b2R, M.IIL), and flattens the peak(s) if this direction is about $\pm 60^\circ$ away from 1 (right wingbeat amplitude). The theoretical optima of the ratio 1:3 are 0.11 and 0.33, respectively. Unidirectional motion detectors

Fig. 10. Influence of the direction of pattern motion on the flight control responses of wings and muscles on either side (R, L). The arrows below the diagrams denote different movement directions of the pattern on the screen in front of the fly (see Fig. 1B). The means and standard errors of the means of the responses refer to pooled data obtained under mirror-inverted conditions (see Materials and methods). The wingbeat amplitude data show, in relative units, the direction-specific deviation of actual amplitudes from their average value (1952 measurements on 20 wings, 10 flies). The M.b1 data relate to the leading phase $1-\phi$ of a muscle spike within a wingbeat cycle: the data show the direction-specific deviation of actual phases from their average $1-\phi$ (70 measurements on five muscles, three flies). The M.b2 data indicate the activity in spikes s⁻¹ (144 measurements on eight muscles, eight flies), as do the M.II data (81 measurements on four muscles, four flies). As periodic functions of the direction of motion, the data were subjected to Fourier analysis. The curves in the diagrams represent the best fits obtained by waveforms comprising harmonics up to the order of three, the highest 'significant' order likely to occur if motion detection is achieved by nearest-neighbour interaction in a hexagonal array of photoreceptors. (Fig. 11 shows the most probable harmonic components of the fitted curves.) The correspondence between the curves in the four diagrams suggests the participation of the three pairs of muscles in a common scheme of flight control. However, the responses of a muscle and its counterpart on the other side of the fly can be controlled independently, the direction of pattern motion eliciting maximum response is neither horizontal nor vertical, and the wingbeat response cannot be completely attributed to the actions of the investigated flight control muscles.



appear to be sufficient for the activation of M.b2 and M.I1: the very low level of spontaneous activity does not allow these muscles to respond to motion against their preferred direction. However, this does not hold for the motion-induced phase lead in M.b1. An induction of phase lag by motion against the preferred direction of this muscle is conceivable, but obviously missing (Fig. 7). Here, unidirectional motion detectors could be necessary for a suppression of induced phase lag.

The preferred direction of actual motion detectors in *Drosophila melanogaster* is likely to coincide with the axes of the hexagonal array of visual elements in the eyes on either side. The directions of these axes are marked on the abscissa of the diagrams. The preferred direction of the array for wingbeat control (1) coincides with a nearest-neighbour direction in the hexagonal array of visual elements (10 o'clock in the right eye, 2 o'clock in the left eye). However, this is not

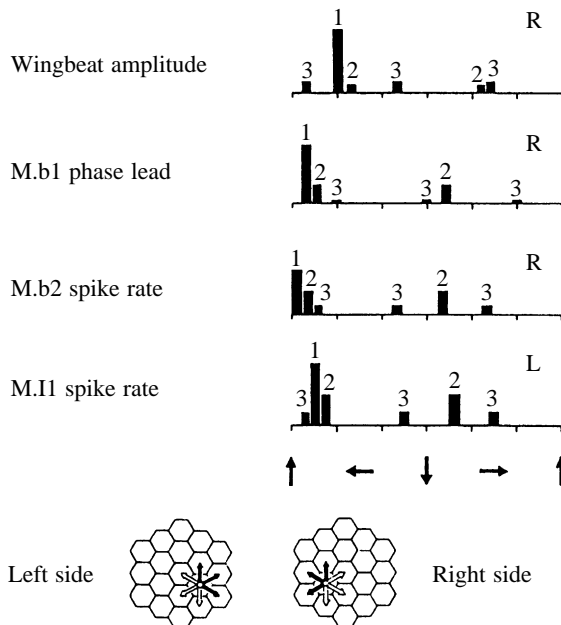


Fig. 11. Principal direction and relative magnitude of the harmonic components (1-3) required to approximate, in Fig. 10, the motion-specific responses of the right wingbeat amplitude and muscles M.b1R, M.b2R and M.I1L. To approximate the responses of the contralateral pairs to this wing and these muscles, the bars must be plotted in reverse order. The position of the fundamental component (1) indicates the preferred direction of a fitted array of unidirectional or bidirectional motion detectors within the visual field of the fly. The higher-order components (2, 3) determine the specific properties of these detectors. Nearest-neighbour interaction within the hexagonal array of visual elements in *Drosophila melanogaster* is restricted to the six main directions shown in the lower diagrams in a projection of representative groups of visual elements onto the frontal visual field. These directions are marked with ticks on the abscissa of the upper diagrams. The preferred direction of actual motion detectors is expected to coincide with one of these directions. This is valid for the wingbeat response. However, the preferred directions of the muscles do not cluster around the corresponding marks on the abscissa. A combination of responses from directionally different sources could explain this discrepancy.

true for the constituents of the wingbeat response: the preferred directions for the control of the three pairs of muscles deviate significantly from the preferred directions of the wingbeat control system and do not coincide with other nearest-neighbour directions. The results in Fig. 11 show at a glance that the control of these muscles requires a combination of responses from directionally diverging detectors.

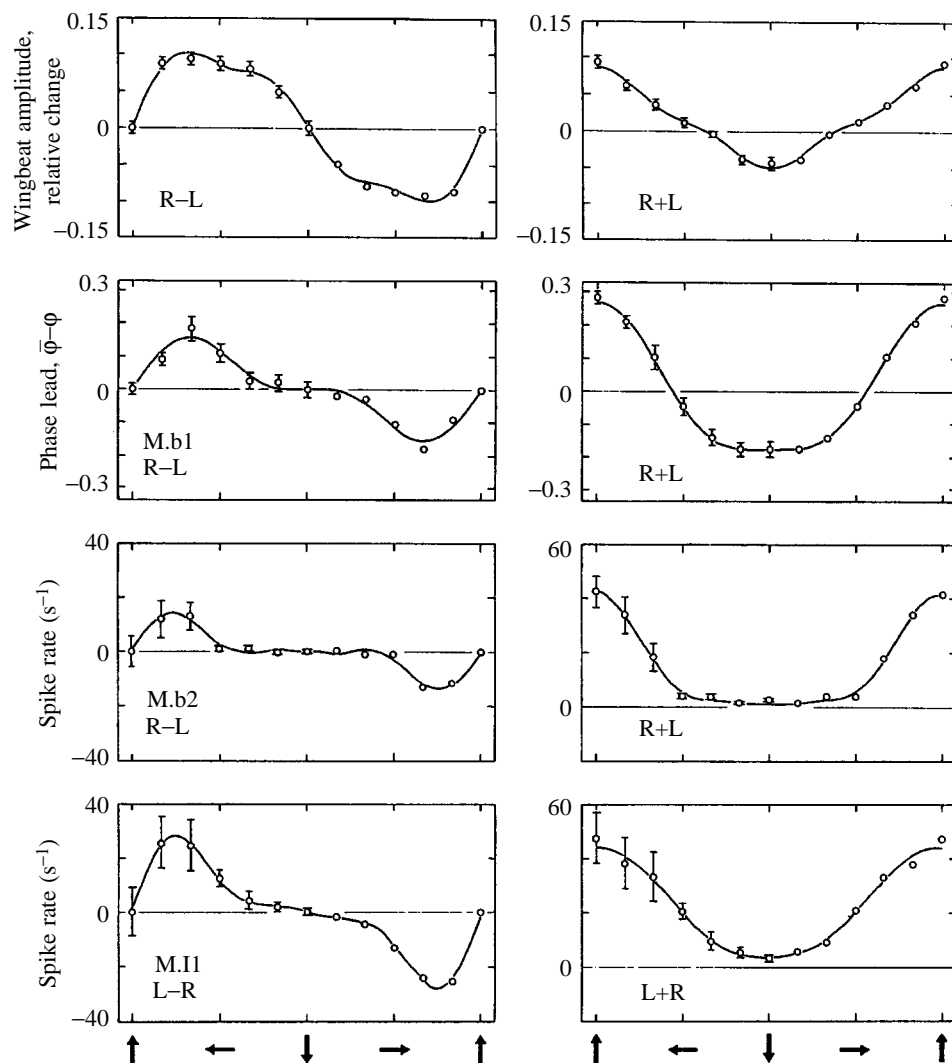
Direction-specific control of course and altitude

At least two independent functions in wingbeat control have been assigned to each of the three pairs of muscles in Fig. 10. However, these functions are not immediately evident from the data. The relationship between wingbeat amplitude and the corresponding force of flight in *Drosophila melanogaster* was mentioned above. The results suggest that, during free flight in a stationary environment, the difference in the wingbeat amplitudes (R-L) accounts for the yaw torque required to stabilize the course, whereas the sum of the wingbeat amplitudes (R+L) accounts for the lift/thrust required to stabilize the altitude. This has led to the conclusion that the optomotor control of course and altitude is achieved by independently controlling the difference R-L and sum R+L of the wingbeat amplitude in response to the visually perceived components of motion in a horizontal and in a vertical direction, respectively. Superposition of these two functions is likely to explain the independent control of homologous wings and muscles in Fig. 10.

To demonstrate the influence of the direction of pattern motion on the difference and on the sum of the flight control responses of wings and muscles on either side, the available data were rearranged accordingly (published previously in Götz 1983a,b). Fig. 12 shows the results derived from the pooled responses shown in Fig. 10. Again, the curves represent the best fit obtained by waveforms comprising harmonics up to the third order. The fundamental components of these curves are either sine functions for the course control responses in the column of diagrams on the left or cosine functions for the altitude control responses in the column of diagrams on the right. The responses are mutually independent: the horizontal motion component controls exclusively the difference and the vertical component controls exclusively the sum of WBA R and WBA L. Similar properties of the fundamentals within the columns suggest, but do not prove, the participation of all three pairs of muscles in the control of both course and altitude. The muscles inserting on the basalar sclerite seem to support the control of course and altitude by an increase in the ipsilateral wingbeat amplitude with either the phase lead of the M.b1 spikes or the rate of the M.b2 spikes. The muscles inserting on the first axillary sclerite could achieve similar results by an increase in the contralateral wingbeat amplitude with the rate of the M.I1 spikes. However, this appears improbable and fails to explain their activity during wing retraction (Fig. 4). A decrease in the ipsilateral wingbeat amplitude would support wing retraction and course control, but simultaneously counteract the altitude control response shown in the uppermost diagram. The seemingly paradoxical role of M.I1 remains to be understood.

The present interpretation of these data has led to alternative

Fig. 12. Influence of the direction of pattern motion on the difference (left column) and the sum (right column) of the flight control responses of wings and muscles on either side (R, L) of the *Drosophila melanogaster* thorax. The arrows below the diagrams denote the movement direction of the pattern on the screen in front of the fly (see Fig. 1B). The means and standard errors of the means of the responses were derived from the pooled data in Fig. 10. The curves represent the best fit obtained by waveforms comprising harmonics up to the order of three. The uppermost diagrams relate to the control of the wingbeat amplitudes: the 90° shift between the sine-shaped curve of the yaw torque response R-L and the cosine-shaped curve of the lift/thrust response R+L demonstrates the 'orthogonality' of these responses: the flight control system adjusts, simultaneously and independently, the difference between the amplitudes to counteract retinal slip in a horizontal direction (course control) and the sum of the amplitudes to counteract slip in a vertical direction (altitude control). The similarity of the response curves within the columns on either side suggests, but does not prove, the participation of the three pairs of muscles in the control of both course and altitude *via* the phase (M.b1) or the rate of occurrence (M.b2, M.I1) of their action potentials.



configurations of the hypothetical detectors representing the responses of wings and muscles in Figs 10 and 12. The wingbeat responses required for the stabilization of course and altitude during free flight can be accomplished either directly by separate sets of motion detectors for the control of the difference (R-L) and the sum (R+L) of the amplitudes or indirectly by separate sets of motion detectors for the corresponding control of the right (R) and the left (L) amplitude. Fig. 13 shows, by analogy to Fig. 11, the direction and relative magnitude of the harmonic components (1-3) in the two alternative configurations for the control of the wingbeat amplitude on either side. The preferred direction (1) of the configuration shown in the upper diagrams is horizontal (9 o'clock) for course control, and vertical (12 o'clock, all three components) for altitude control. The 9 o'clock preferred direction does not coincide with nearest-neighbour directions in the hexagonal array of visual elements. However, this direction is likely to result from a combination of nearest-neighbour interactions with 8 o'clock and 10 o'clock preferred directions (Buchner, 1976, 1984). Direct control of course and altitude is suggested, for instance, by the partial coincidence of the spike activity of conditional synergists such as M.b2R and

M.I1L in a response to motion in a horizontal direction (Fig. 8C). Moreover, stimulation of only one eye was sufficient to elicit synergy of these muscles across the midline of the fly (K. G. Götz and G. Heide, unpublished data).

Discussion

Optomotor control of course and altitude in *Drosophila melanogaster* is accompanied by conspicuous adjustments in the wingbeat amplitude (up to $\pm 10\%$ of the stroke angle) and/or by minute adjustments in the phase difference of their oscillation (up to $\pm 1\%$ of the wingbeat cycle). Indirect evidence rules out a significant adjustment of wing angle of attack or stroke plane (Götz and Wandel, 1984). The average force exerted by a wing during tethered flight in still air acts at a distance of approximately 2 mm from the midline of the body. The variation in this force is approximately proportional to the angular variation in the wingbeat amplitude. The wingbeat amplitude (WBA) on either side (R, L) can be optically recorded as described in this paper. Unlike measurements of force and torque, the present method accurately indicates the beginning of a wingbeat cycle,

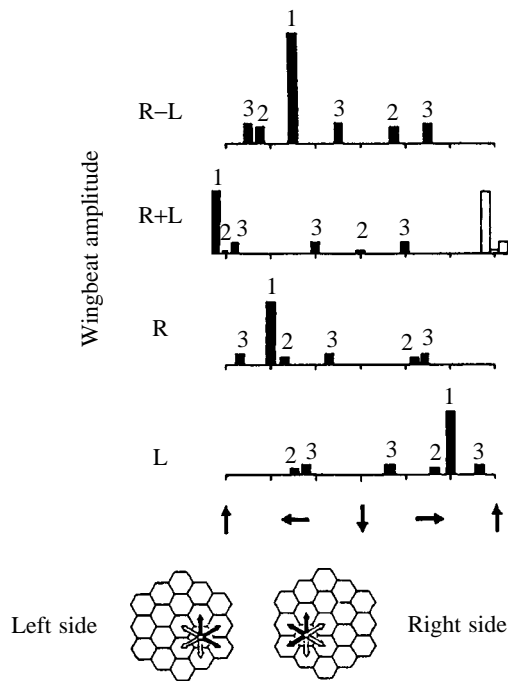


Fig. 13. Principal direction and relative magnitude of the harmonic components (1–3) required to approximate, in Figs 10 and 12, the motion-specific responses derived from the wingbeat amplitudes on either side. The prevailing contribution comes from the first harmonic. The position of the corresponding bars (1) indicates the preferred direction of a fitted array of motion detectors; their height is a measure of the positive response to pattern motion in this direction. A negative response of similar strength is expected for motion in the opposite direction. The wingbeat responses required to maintain a given course and altitude during free flight can be accomplished directly by the independent control of the difference (R–L) and the sum (R+L) of the amplitudes on either side or indirectly by the functionally equivalent control of the right (R) and the left (L) amplitude. The preferred directions of the fundamental components (1) of the corresponding detector systems coincide either with the 9 o'clock and 12 o'clock directions (upper diagrams), or with the 10 o'clock and 2 o'clock directions (lower diagrams, identical to the uppermost diagram in Fig. 11 and its mirror-inverted counterpart). The three components (1–3) shown side by side in the diagram for R+L actually coincide with the 12 o'clock direction. Several observations suggest a direct control of course and altitude. The 9 o'clock preferred direction of the course control system in the uppermost diagram is not available in the hexagonal array of visual elements (shown at the bottom) and is likely to result from a combination of detectors with the 8 o'clock and 10 o'clock preferred directions found by Buchner (1976, 1984).

records the WBA with the highest possible temporal resolution of 1 sample per cycle (approximately 5 ms), processes the actions of the two wings separately from each other and allows the insertion of electrodes into selected muscles of the flight control system (Götz, 1987a, 1989; Dickinson *et al.* 1993).

General results

Three of the four investigated pairs of prominent flight control muscles in *Drosophila melanogaster* respond to visual stimulation. Each of these muscles seems to be involved

simultaneously in at least two functionally independent activities: course control and altitude control. Spontaneous muscle spikes are rarely recorded with the wings at rest. Flight is required to enable the activation of the three pairs of control muscles. In this state, the spike-phase-controlled muscles (M.b1) are continuously active. The spike-rate-controlled muscles (M.b2, M.I1) show (1) sporadic bursts of spontaneous activity which do not seem to be elicited by external sensory signals, (2) individual excitatory or inhibitory responses to motion within the visual field and, often simultaneously, (3) cooperative activity of spikes and spike bursts in distinct muscles observed, for instance, during a course control manoeuvre (Fig. 8C). The responses elicited by repeated presentations of a given stimulus are rarely identical with respect to the time course of spike activity (Figs 8A,B, 9).

The three pairs of muscles do not account for all of the investigated wingbeat responses (Fig. 10). These responses are characterized by the preferred direction of the contributing sets of motion detectors in the hexagonal array of visual elements (10 o'clock for WBA R, 2 o'clock for WBA L; Fig. 13). The source of the missing response components is thought to be either in the up to 13 largely unspecified pairs of control muscles (Ewing, 1979a; King and Tanouye, 1983; Miyan and Ewing, 1985; Zalokar, 1947) or in a visually induced residual modulation of the asynchronous spike activity in one of the power muscles (e.g. the dorso-ventral muscle; Heide *et al.* 1985). Most of the minor control muscles in *Drosophila melanogaster* are not accessible for in-flight spike recording. However, their metabolic activity in response to visual stimulation during stationary flight has successfully been determined by high-resolution deoxyglucose autoradiography (Waldvogel and Bausenwein, 1990, 1991).

Homologous types of prominent flight control muscles also exist in *Calliphora* sp. and *Musca domestica*. In spite of aerodynamically significant differences in wingbeat kinematics (the 'squeeze-clap-peel' sequence at the dorsal reversal of the beating wings is almost completely absent in the larger flies), the three species are surprisingly similar with respect to both the general properties of flight control mentioned above and the specific contributions of the different types of control muscles. However, a species-specific comparison is necessarily incomplete. Numerous aspects of flight control have only been, or can only be, studied on larger calyptrate flies; for instance, flight mechanics and kinematics (e.g. Boettiger and Furspan, 1952; Miyan and Ewing, 1985; Nachtigall, 1989; Nalbach, 1989; Pfau, 1987; Pringle, 1965; Wisser, 1987, 1988; Wisser and Nachtigall, 1984), muscle physiology and the time course of muscular contraction (Bergmann-Erb and Heide, 1990; Heide, 1971b; Nachtigall and Wilson, 1967; Schrage and Heide, 1990; Tu and Dickinson, 1994, 1996) and the patterning of control muscle activities by wingbeat-synchronous afferences (Heide, 1975, 1983). Other investigations of the control muscles require simultaneous recordings of wing motion on either side, the derivation of the corresponding forces and moments from visually induced WBA responses and/or the evaluation of the phase of muscle spikes within the wingbeat

cycle. Most of these procedures are described for the first time in the present paper and have been applied so far in experiments with *Drosophila melanogaster* to investigate flexibility and genetic disorders of flight control at the muscular level, to determine the contribution of single muscle pairs to the fixation and tracking of visual objects under closed-loop conditions in a flight simulator and to stimulate a muscle electrically in selected phases of the wingbeat cycle (Götz, 1983b, 1985, 1987b, 1989; Götz and Lehmann, 1990, 1996).

Muscle-specific properties

The spontaneous activity and the visually induced activity of the different types of flight control muscles can be characterized by (1) the range around the muscle-specific phase ϕ of the wingbeat cycle in which most of the spontaneous or motion-induced spikes occur, (2) the rate at which these spikes occur, (3) the preferred direction of pattern motion in front of the eyes that is most efficient in the control of the spike activity of a particular muscle, and (4) the WBA response that appears to be correlated with the activity of this muscle. The corresponding data for the control muscles M.b1, M.b2 and M.I1 are shown in Fig. 6 (1 and 2), Figs 11 and 13 (3) and Figs 10 and 12 (4). Muscle M.III1 does not contribute to motion-induced flight control in *Drosophila melanogaster*. Analogous responses of these four muscles have been studied in *Calliphora erythrocephala* and *vicina* for arbitrary directions of motion (Heide, 1971b, 1975, 1983; Hirth, 1981; Hirth and Heide, 1980; Spüler, 1980; Spüler and Heide, 1980; Tu and Dickinson, 1996) and in *Musca domestica* for horizontal motions (Egelhaaf, 1989; Heide, 1975; Spüler and Heide, 1978).

In *Drosophila melanogaster*, the basalar muscle M.b1 is spontaneously active at a rate of nearly 1 spike per wingbeat cycle (Fig. 3). Motion in the preferred direction (11 o'clock in M.b1R, 1 o'clock in M.b1L) elicits 'phase lead', a transition of the average spike phase ϕ from 0.42 to 0.31, i.e. the spikes occur earlier in the wingbeat cycle. This effect is correlated with an increase in the ipsilateral WBA and is likely to account for tonic components of the flight control responses. Motion in the opposite direction decreased the spike rate in a few preparations. The spike phase was independent of the rate at which the spikes occurred. Essentially the same control responses have been found in M.b1 of *Calliphora erythrocephala* and also in *Musca domestica* (Heide, 1975, 1983). However, in similar experiments with *Musca domestica*, the motion-induced phase lead was accompanied by an increase in the comparatively low spontaneous spike rate of approximately 1 spike every second wingbeat cycle (Egelhaaf, 1989). The connection between spike phase and flight performance was first observed in insects with a lower degree of separation between the muscle systems for force generation and force control, such as moths *Rothschildia jacobaeae* (Kammer and Nachtigall, 1973) or locusts *Locusta migratoria* (Zarnack and Möhl, 1977).

In the sternobasalar muscle M.b2, spontaneous activity is a rare event. However, a transient spike rate of up to 830 Hz has been observed during attempted take-off (Lehmann and Götz, 1996). Motion in the preferred direction (11:30 o'clock in

M.b2R, 0:30 o'clock in M.b2L) elicits up to 1 spike in every other wingbeat cycle; the average phase of the spikes ($\phi=0.19$ in M.b2) seems to be independent of the visual stimulus and of the spike activity (Fig. 6). The time course of the spikes can be regular or irregular: volleys of spike bursts were frequently observed (Fig. 8A,C). Single spikes and spike bursts were correlated with a slightly delayed transient increase in the ipsilateral WBA which seems to account for phasic components of flight control in *Drosophila melanogaster* (Götz, 1989). Spike bursts coincide with WBA-increasing 'hitches' of the ipsilateral wing (Götz *et al.* 1979) and are likely to coincide with the course-controlling 'body saccades' observed during free flight (Heisenberg and Wolf, 1984; for a discussion, see Kirschfeld, 1994). Hitches can be induced by electrical stimulation of M.b2: maximum efficiency of the stimulus is obtained by activation of the fibres at the muscle-specific phase of the wingbeat cycle (Lehmann and Götz, 1990, 1996). The control responses found in M.b2 of *Calliphora erythrocephala* and *Musca domestica* were compatible with the present results.

The axillary muscle M.I1 resembles M.b2 with respect to the low level of spontaneous activity, the regular or irregular responses composed of spikes, spike bursts or volleys of spike bursts (Fig. 8B,C), and the stimulus- and activity-independent spike phase. However, M.I1 seems to cause a decrease in the ipsilateral WBA which accounts for phasic components of flight control in *Drosophila melanogaster*. Comparison with M.b2 underlines the individual properties of this muscle: the greater spike rate of up to 1 spike per wingbeat cycle, the muscle-specific spike phase ($\phi=0.60$ in M.I1) and the mirror-inverted preferred direction (1:30 o'clock in M.I1R, 10:30 o'clock in M.I1L). The M.I1 muscles seem to support course control by retraction of the beating wing on the inner side of an intended turn. Bilateral wing retraction in response to motion in a 12 o'clock direction would diminish the average force of flight, whereas an increase in this force is required to counteract the simulated loss of altitude. Selective elimination of the sensory signal for altitude control, as found in the optomotor responses of the walking fly (Götz and Wenking, 1973), could, but does not, suppress the apparently counterproductive altitude control response of M.I1.

The seemingly paradoxical action of M.I1 in the control of course and altitude is in keeping with its ambivalence in the fixation of an object in the frontal visual field, an autonomously controlled variant of optomotor course control in *Drosophila melanogaster* (Heisenberg and Wolf, 1984; Wolf and Heisenberg, 1986). Object fixation on the level of the control muscles has been investigated under closed-loop conditions in a flight simulator. The fly on the wingbeat processor (Fig. 1) was held in a fixed position and orientation at the centre of an artificial panorama. The contribution of either the wings or a pair of flight control muscles to the intended turns was converted into the appropriate rotation of the panorama around the fly. Each of the investigated pairs of muscles was found to respond to the rotatory displacements of a visual object and to contribute to its fixation. Muscles M.b1 or muscles M.b2 support a rigid procedure of

'instructional' fixation. Muscles M.II, however, engage in a flexible procedure of 'operant' fixation also suitable for coping with artificially reversed displacements of the visual object. To achieve fixation, the fly has to turn away from the object – a response without relevance to natural conditions. This ambivalence of the M.II system is missing in the mutant '*small optic lobes*', where the optomotor control of course and altitude appears to be normal, and is present in the mutant '*optomotor-blind*', where the optomotor course control is selectively blocked, but obviously not at the level of the control muscles (Götz, 1983b, 1985, 1987b, 1989). At least the basic control responses of M.II are similar in *Calliphora erythrocephala*, and probably also in *Musca domestica*, where the applicability of the different muscles for the two variants of optomotor course control has been assessed under open-loop conditions. The course-stabilizing responses to slow large-field displacements increase, and the fixation responses to fast small-field displacements decrease, in the order M.b2, M.II/M.III1, M.b1 (Egelhaaf, 1989).

The axillary muscle M.III1 is activated in the context of flight suppression, termination or interruption, but does not contribute to the motion-induced flight control responses investigated so far. The corresponding muscles in *Calliphora erythrocephala* and *Musca domestica* are actively engaged in optomotor flight control. The action of M.III1 is similar to the action of M.b2: activation of these muscles increases the WBA of the ipsilateral wing, although this appears to be in conflict with the classification of the third axillary muscles as wing retractors. These observations are reconciled by a posture-dependent direction of the M.III1-induced wing excursion (Heide, 1975). Moreover, the third axillary muscles seem to control the mode of operation (Nalbach, 1989). For unknown reasons, this may be impossible in *Drosophila melanogaster*. The different role of M.III1 and the different sign of a control response of the dorso-ventral muscle mentioned above are the only major discrepancies detected so far when comparing the flight control systems of *Drosophila melanogaster* and the larger flies.

In the discussion above, the actions of the different flight control muscles were considered to be a cause of the concomitant increase or decrease in wingbeat amplitudes. This appears to be justified for M.b2 and most probably also for M.II, where the minute effect of a single spike can be recorded in a low-noise preparation. So far, this has not been achieved for the graded responses of M.b1.

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