

CHAPTER 19

Muscle Systems Design and Integration

Fritz-Olaf Lehmann

Summary

The recent advances in experimental technology allows us to assess the mechanical power output and function of the *Drosophila* flight muscle within the context of the flying animal. In an intact animal, production and control of aerodynamic forces during flight depend on several factors including the maximum power output of the musculature and the interplay in neural activation between the two functionally, physiologically and anatomically distinct classes of flight muscles: the asynchronous power muscles and the synchronous flight control muscles. Although the maximum mechanical power output and the efficiency of the locomotory musculature can be estimated from in vitro biophysical experiments, the values determined from such experiments in *Drosophila* are substantially lower than the maxima that must occur in the flying animal. As a consequence, the systems-level perspective on power production is a necessary bridge in any attempt to link the function and performance of flight musculature with its specific role for wing motion and flight force control in the behaving animal.^{1,2} Moreover, the cost of locomotion in flying insects is rarely constant but varies as the animal changes speed and direction. Ultimately the muscles of the insect must compensate for these changing requirements by varying the amount of muscle power that they produce. This chapter considers mainly the mechanisms by which mechanical power output of the asynchronous flight muscles is regulated to match the changing requirements during flight control behaviours and summarizes vital muscle parameters including muscle efficiency, measured in intact fruit flies.

Muscle Function in Intact Animals

Power Requirements for Flight

In a flying insect, the mechanical power generated by the muscular-skeletal flight system drives the wings up and down and must match the power requirements for flight (Fig. 1).³⁻⁵ In a behaving animal, these energetic requirements can be derived by measuring the motion of the insect body and the wings, and the resultant flight force that the animal is producing. Total power requirements for flapping flight may be divided into 4 major power terms: *parasite*, *profile*, *inertial*, and *induced* power.⁶⁻⁸ Parasite power is the rate of work required to overcome the fluid drag on the body as the animal moves through the air. For insects that are hovering and traveling with low speed, parasite power is comparatively small and can be ignored in many instances. At high forward speed, parasite power increases rapidly because it depends on the cube of forward velocity. At high forward velocity parasite cost is the predominant factor of flight costs and distinctly forms the 'classic U- or J-shaped curve' of total power expenditures in flying insects, birds and bats.^{1,9,10} In contrast, profile power is the cost associated with the work required to overcome the drag on the beating wings and is increasing with the cube of the product between stroke amplitude and stroke frequency. Drag, in turn, linearly depends on the drag coefficient that changes with Reynolds number for wing motion. In small insects such as

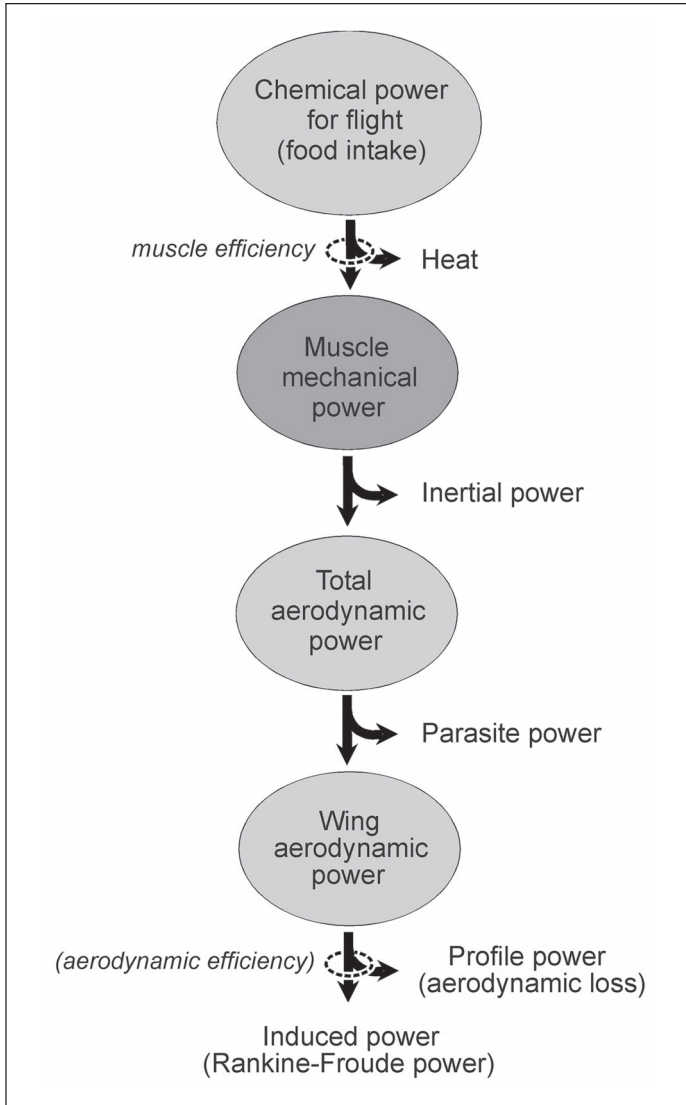


Figure 1. Pathway of power expenditures in flapping flight of insects. Chemical energy due to food intake is converted into muscle mechanical power. In most insects, the efficacy (muscle efficiency) of this conversion process is low ranging from 3.0 to 17%.^{3-6,8,38-40} In endothermic insects metabolic heat production is used to facilitate the mechanical power output of the flight muscles at low ambient temperatures.^{41,42} In freely flying *Drosophila* a minimum ambient temperature of approximately 15 °C is required to produce flight forces that are equal to body weight.⁴³ Inertial power is the cost to accelerate the wings at the beginning of each half stroke. Parasite power, the cost to overcome the drag on the body of the animal, is negligible at low forward speed and hovering. Profile power is the cost associated with aerodynamic drag that the beating wings face when moving through the air. Induced power is the cost to accelerate a fluid momentum downwards and thus representing the cost of lift production. The Rankine-Froude estimate of induced power represents the minimum power requirements for lift production.⁸ Aerodynamic efficiency is the ratio between Rankine-Froude power and the sum of induced and profile power (aerodynamic loss). Modified from Casey.⁶

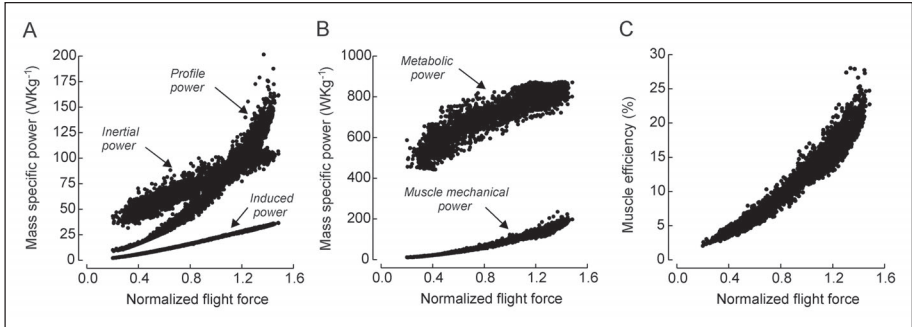


Figure 2. (A) Flight power requirements in *Drosophila* increases with increasing flight force production. Induced power is the smallest cost in total power balance. Profile power estimates based on drag coefficients measured in a robotic fruit fly wing are smaller than inertial power requirements at low flight force but higher when the fly produces flight forces that exceed the body weight of the animal. (B) Aerodynamic power requirements that are estimated from wing kinematics and flight force measurements, match the mechanical power output of the asynchronous flight muscles. The changes in metabolic power are derived from measurements of carbon dioxide release of the fly during flight in a respirometric flight chamber. (C) Muscle efficiency plotted as the ratio between muscle mechanical power output and metabolic power as shown in (B). Due to different slope and offset of both data, muscle efficiency is steeply increasing with flight force. Data are recorded from a single fruit fly flying in a virtual reality flight arena.

Drosophila Reynolds number is relatively low (approximately 90-230) indicating that viscous forces of the air are relatively large and profile cost may dominate. Larger insects that fly at higher Reynolds number benefit from a relative reduction in profile power, and thus muscle mechanical power output can be reduced. In many cases conventional drag coefficient estimates based on Reynolds number ($C_D = 7Re^{-0.5}$)⁸ underestimate profile power because lift production in *Drosophila* and other insects is greatly enhanced by unsteady aerodynamic effects resulting in up to 3-4 times higher profile power cost.^{11,12} In *Drosophila*, profile power rises steeply with increasing locomotor performance and exceeds inertial power expenditures at forces that are approximately equal and above body weight (Table 1, Fig. 2A).

Inertial power is needed to accelerate the wings and the surrounding fluid (virtual wing mass) from rest to maximum velocity within the first half of each half stroke cycle. Inertial power depends on several factors including wing mass, mass distribution given by the wing shape and length, wing velocity and the wing's acceleration profile throughout the stroke cycle. The most conservative model of motion is one in which the wing movements are described by a pure sinusoidal function. Under these conditions inertial cost is approximately 20% higher compared to the most liberal model of wing motion in which the wings have a short period of high acceleration followed by a long region of constant velocity kinematics (triangular function). In the case of varying flight forces in an intact flying fruit fly, inertial cost can be estimated from the product of wing velocity squared and stroke frequency. Induced power is the cost to generate a downward jet of air that keeps the insect airborne. This term is equal to the total flight force produced by the beating wings multiplied by the mean velocity of the wake that the flying animal leaves behind. Producing flight forces at relatively low wing velocities are energetically favorable and may lower the energetic expenditures of the insect's flight muscles.

Power Reduction

Elastic Energy Recycling

The total flight cost in an insect is not a simple linear relationship between profile, inertial and induced power but rather depends on the complex interaction between the costs that are associated with the motion of the fluid around the wing (profile and induced power) and the

Table 1. Flight parameters of *Drosophila melanogaster*[‡]

| | Minimum | Hovering | Maximum |
|--|------------------------|------------------------|------------------------|
| Stroke amplitude (deg) | 148 ± 9 | 162 ± 8 | 169 ± 7 |
| Stroke frequency (Hz) | 190 ± 18 | 209 ± 15 | 212 ± 12 |
| Wing velocity (m s ⁻¹) | 1.38 ± 0.14 | 1.66 ± 0.14 | 1.76 ± 0.14 |
| Flight force (μN) | 4.4 ± 2.0 | 10.3 ± 1.2 | 13.6 ± 1.5 |
| Muscle strain amplitude (%) | 2.7 – 4.6 [†] | 2.7 – 4.6 [†] | 2.7 – 4.6 [†] |
| Mean C _L | 0.97 ± 0.40 | 1.59 ± 0.20 | 1.88 ± 0.29 |
| Mean C _D | 0.50 ± 0.21 | 1.02 ± 0.13 | 1.74 ± 0.27 |
| P [*] _{MR} (W kg ⁻¹) | 519 ± 123 | 664 ± 100 | 727 ± 119 |
| P [*] _{ind} (W kg ⁻¹) | 7.1 ± 5.3 | 21.4 ± 1.0 | 32.4 ± 6.1 |
| P [*] _{pro} (W kg ⁻¹) | 22.0 ± 6.1 | 69.9 ± 12 | 139 ± 26 |
| P [*] _{aero} (W kg ⁻¹) | 29.1 ± 11.4 | 91.3 ± 13 | 171 ± 32 |
| P [*] _{acc} (W kg ⁻¹) | 43.5 ± 13.5 | 67.4 ± 13.5 | 77.0 ± 16.5 |
| η _M <i>in vivo</i> (%) | 5.6 ± 1.2 [§] | 13.8 ± 1.8 | 23.5 ± 2.6 |

[‡]Flight parameters were measured during extremes of force production that fell within the top 1% (maximum muscle power output) or bottom 1% (minimum muscle power output) of flight force or within 1% of body weight (muscle power output during hovering flight). Oscillations in mean muscle strain (strain amplitude) were derived from the length changes of the thoracic exoskeleton in flying *Drosophila virilis* during an entire contraction-relaxation cycle.³⁷ Mean drag coefficient (C_D) of the moving wings was derived from mean lift coefficient (C_L) during translational motion of a robotic fruit fly wing moving at Reynolds number of 134 that is typical for *Drosophila* flight.¹² Flight specific power is given in units of W kg⁻¹ flight muscle mass that amounts to approximately 30% of total body mass in the fruit fly. P^{*}_{MR}, metabolic power (total flight costs) derived from the release of carbon dioxide during flight. In diptera the energy conversion factor is 21.4 J ml⁻¹ CO₂; P^{*}_{ind}, induced power; P^{*}_{pro}, wing profile power calculated using the drag coefficient of the robotic wing; P^{*}_{aero}, aerodynamic power; P^{*}_{acc}, inertial power; η_M, efficiency of the asynchronous flight muscle. Mean body weight of *Drosophila melanogaster* females is 1.05 ± 0.13 mg. Data are shown as means ± S.D. N= 27 flies. [†]= no flight force measurements were conducted in these experiments. [§]= assuming 100% elastic energy storage.

cost that is due to the motion of the wing *sensu stricto* (inertial power). Inertial energy at mid half stroke has two potential fates.¹³ In one case, the kinetic energy stored in the wing motion serves as a energy source while the wing is slowing down in the second half of each half stroke. This energy in turn may be used to overcome profile drag on the wing and to generate downward lift. Alternatively, the wing could store its kinetic energy elastically in the skeletal system of the flight motor, for instance in the highly elastic protein resilin that is spread throughout the wing and the thoracic cuticle,^{14,15} or in the elastic components of the asynchronous flight muscle. If the kinetic energy freed in the deceleration phase of each half stroke is lower than the combined profile and induced power requirements (aerodynamic power) no elastic energy recycling is required to minimize the mechanical power output of the flight muscle (Fig. 2B). Elastic energy recycling is beneficial for the flying insect only when inertial cost exceeds aerodynamic power requirements. In *Drosophila* this situation is given at flight forces below approximately 90% of the animal's body weight (Fig. 2A). In contrast, due to the high wing drag that is expected during elevated flight force production (flight forces that are equal and above body weight), calculations show that in the fruit fly inertial power is smaller than aerodynamic power. In this case, the elastic components in the entire flight system serve as springs that damp mechanical stress on both the skeletal structures and the myofilaments of the flight muscle rather than providing a mechanism to lower mechanical power output of the asynchronous flight muscles.

Behavioral Strategies

Flying insects may reduce their total energetic costs by increasing the efficiency with which chemical energy is turned into aerodynamic flight forces. Potentially, this can be achieved by at least three distinct mechanisms. First, the insect could increase the efficiency of chemical energy conversion into mechanical work by the filaments of the flight muscle or increase the efficiency of chemical energy production by the mitochondria (muscle efficiency). Second, the insect could increase the efficiency with which muscle mechanical power is turned into flight forces (aerodynamic efficiency). This requires an increase in the lift to drag ratio of the beating wings that can be achieved by a decrease in angle of attack during wing translation and by flapping wings with a high aspect ratio, which is the ratio between wing length and mean depth (chord). Third, insects may potentially decrease muscle mechanical power output at constant flight force production by changing the ratio between stroke amplitude and stroke frequency. In conventional aerodynamics, wing velocity (the product of amplitude and frequency) predominantly determines the magnitude of flight force production during the up and down stroke. As a consequence, an insect may produce the same flight force either at high stroke frequency and low stroke amplitude or by a low frequency and high amplitude.

In comparison, flight cost is minimal when the animal accelerate a large amount of air at low speed because in this case the kinetic energy ($=\text{fluid mass} \times \text{wake velocity squared}$) of the moving fluid is small. Since the volume of fluid that the wings accelerate downwards directly depends on stroke amplitude given at the angle between the dorsal and ventral excursion during wing flapping, the smallest muscle power output is required when the insect maximizes stroke amplitude while minimizing stroke frequency. This relationship implies that nervous activation of the muscle fibers by the thoracic ganglion, and thus muscle contraction dynamics, might be constrained primarily by the energetic cost to keep the animal airborne. However, measurements in a virtual flight simulator show that a tethered flying *Drosophila* produces maximum muscle mechanical power even at a flight force roughly equal to the animal's own body weight (hovering condition) that lies approximately 30% below the fly's maximum flight force. The additional power input at hovering flight conditions offers the fruit fly a broader range of different combinations between stroke amplitude and frequency for force production that should in turn enhance the animal's ability to control its flight force in free flight (Fig. 3B). Analytical models based on *Drosophila* kinematics show that the additional energetic expenses around hovering conditions due to high stroke frequency are relatively small and solely amount to approximately 10% of total induced power.¹⁶

Power Constraints on Steering Capacity

Since the power output sustained by the flight muscles may directly constrain wing kinematics in the fruit fly at elevated power requirements for flight, it potentially lowers the ability of the insect to modulate wing kinematics at elevated aerodynamic performance and may thus limit flight maneuverability. High aerial maneuverability of an insect may be useful in a large variety of behavioural contexts including predator avoidance, prey catching, mating success, and male-male competition.^{17,18} Behavioral observation in the European beewolf *Philanthus triangulum* suggest a close correlation between flight maneuverability and mating success. The males of this species establish small territories near female nests and defend this territory against other males in air combats that require fast changes in wing motion and power requirements.¹⁹ Figure 3B shows that maximum mechanical power output of the asynchronous muscles constrains the kinematic envelope of *Drosophila* up to a unique combination of amplitude and frequency at maximum force production when stroke amplitude has reached its mechanical limit near 180 degs. Previous results have shown that fruit flies mainly control forces and moments by changing stroke amplitude of the two wings.^{20,21} A collapse in kinematic envelope during peak force production should thus attenuate greatly the maneuverability and stability of animals in free flight because stroke amplitude can not be modulated without a reduction in flight force production. The attenuation in steering performance can be demonstrated in

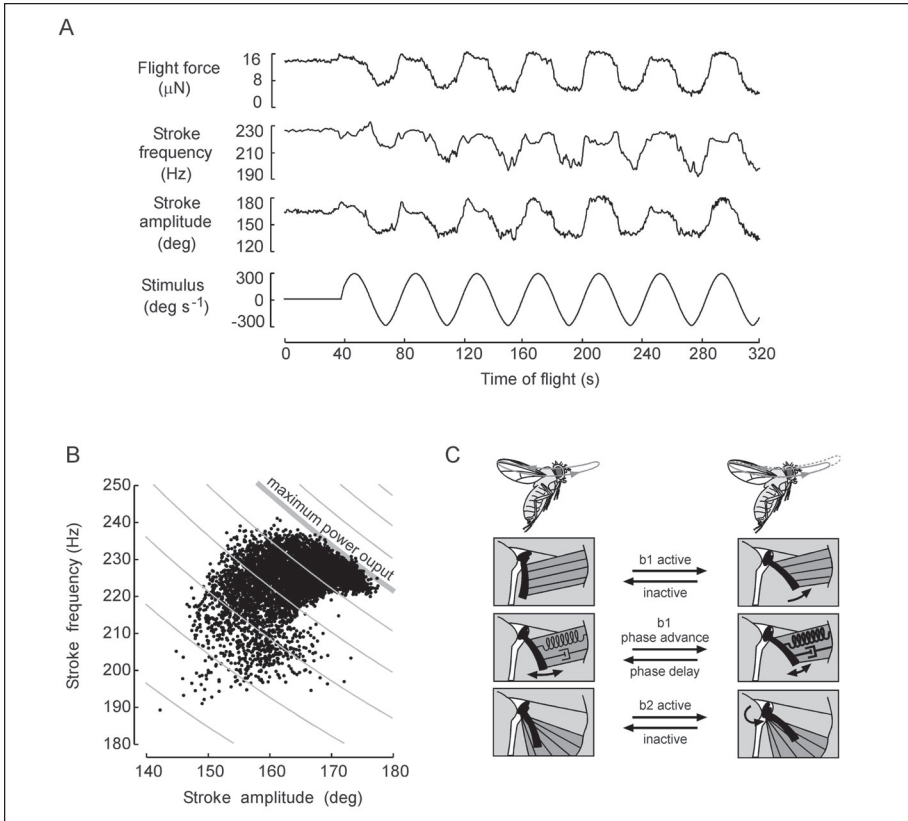


Figure 3. (A) Flight sequence of a tethered fruit fly during vertical oscillation of a visual lift stimulus (diagonal stripes) displayed in a virtual reality flight arena. In the attempt to stabilize the retinal slip of the visual pattern on the compound eye, the tethered flying *Drosophila* varies its production of total flight forces.⁵ This force modulation is accomplished by changes in stroke amplitude and stroke frequency due to alterations of spike activity in both the power muscles and at least two different sets of flight control muscles (basalar and axillar muscles). The rectification of stroke frequency when the fly generates highest forces indicates that the animal is producing maximum muscle mechanical power. (B) In vivo working range of the *Drosophila* flight motor. Flight kinematics is constrained by power availability and the morphological limit of stroke amplitude. The values are plotted as a function of instantaneous stroke amplitude during a flight sequence of a single fly such as shown in (A). The hyperbolic lines represent isolines at which flight muscle power is constant. Flight forces that are equal to the body weight of the animal are produced at a stroke amplitude approximately between 160 and 165 degs. The variance of possible amplitude and frequency combinations is decreasing from the left-hand side (low forces) to the right-hand side (high forces). At maximum flight force *Drosophila* is constrained to a unique combination between amplitude and frequency due to maximum power output of mean 171 W kg^{-1} muscle tissue. The restriction of wing kinematics at highest force lowers steering capacity and thus potentially attenuates maneuverability and stability in freely flying fruit flies. (C) Model of muscular mechanism of stroke amplitude control in the blow fly *Calliphora vicina*. The basalar 1 and 2 flight control muscles (b1 and b2) control the position of the basalar sclerite (black) that reconfigures the wing hinge by a long tendon. During flight b1 typically fires one spike in each stroke cycle to maintain a tonic tension on the basalar sclerite. The timing of b1 spike initiation phase within the stroke cycle alters the position of the basalare by either increasing muscle tension (spike phase advanced) or decreasing muscle tension (spike phase delayed). The mechanical muscle properties are indicated as a dashpot and a spring. Higher muscle tension correlates with an increase in stroke amplitude when a higher flight force is required as shown in (A). Activation of b2 produces similar changes in the basalare motion. However, in contrast to b1, the b2 is typically inactive during flight and only becomes active during turns. Figure 3C is redrawn partly from Tu and Dickinson.²⁶

tethered flies flying in a flight simulator, in which the animal is stabilizing actively the angular velocity of a visual pattern (black bar) displayed in the arena by controlling the bilateral difference between left and right stroke amplitude. When flight force increases, the animal's steering capacity decreases indicating that the ability of the fly to control yaw moments around its vertical body axis and flight direction is impaired.²² Although the constraint of mechanical power output on wing kinematics might be small in an unloaded animal, the limited power output of the flight muscles may significantly lower maneuverability and stability when the insect is carrying prey or additional loads, leaving the animal susceptible to a higher risk of predation.²³

Balancing Power and Control

Kinematic Changes

In many insect species, flight is not solely a mode of transport but also a means of prey capture, mating display and territorial maintenance—behaviors that can demand rapid and elaborate maneuvers. For a moth darting away from an attacking bat or a mosquito trying to escape from an attacking dragonfly, the ability to rapidly *change* power output may represent as important a selectional criterion for the insect flight motor as the absolute level of power production.^{24,25} In contrast to insects with synchronous flight muscles, electrophysiological evidence indicates that in diptera small control muscles adjust the amplitude, angle of attack, rotational timing at the stroke reversals, and wing trajectory during the up and down stroke (for a more detailed description of control muscle function see Fig. 4). In comparison to the 'big and dumb' asynchronous flight muscles, the 14 pairs of flight control muscles offer the fly's nervous system a means of rapidly controlling wing kinematics and power output of the flight motor. There are two pairs of control muscles that are responsible for alteration in stroke frequency by changing the stiffness of the resonating thoracic box: the pleurosternal muscles one and two. In contrast, stroke amplitude is modulated by at least the first and second basalar muscle (b1 and b2) and the first control muscle of the pterale (I1). Direct electrical activation of b1 and b2 in a flying fly results in an increase in stroke amplitude during flight whereas activation of the I1 control muscle induces a collapse of stroke amplitude.²⁶⁻²⁸ When no flight power is required for wing motion such as during cleaning behaviour and courtship song production, some control muscles are powerful enough to move the wing to the appropriate position for cleaning or to vibrate the wings with a low stroke amplitude.^{29,30} Control muscles, however, are too small to generate enough power to accommodate directly the changes in wing kinematics occurring in a flying animal.

Negative Work of Control Muscles

In order to function for steering in a flying insect, it is not necessary that flight control muscles generate a large amount of muscle power. Since most control muscles in diptera insert directly onto the sclerites of the wing hinge, they function by reconfiguring the motion of the wing hinge within the up and down stroke. These modifications in the wing gear mechanisms thus may alter the transmission of muscle power from the asynchronous flight muscles to the moving wings. This biomechanical arrangement consisting of fast responding muscle actuators and mechanical gear components allows the fly to conduct modifications of wing motion (such as stroke amplitude, Fig. 3A and C) within a few stroke cycles although the neural activation of the power muscles could not instantaneously support the associated changes in power requirements. Nevertheless, the nervous system of *Drosophila* is not simply switching the power muscles on and off during flight, but rather changing the frequency of muscle spikes in accordance with the mean power requirements of the entire flight system (Fig. 5).

The reconfiguration of the wing hinge is not necessarily requiring that control muscles are doing positive work during contraction. In the one case in which a work-loop analysis was performed on a steering muscle (b1 muscle), the high strain frequency ranging from 100 to 200 Hz and the typical low content of contractile filaments makes the b1 muscle fiber

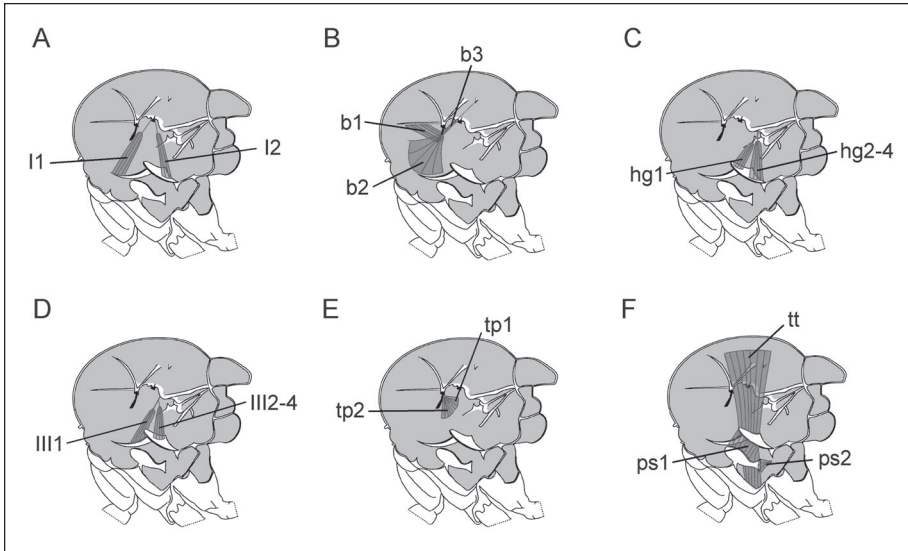


Figure 4. Morphology and function of the 14 flight control muscles in flies. (A) The muscles of the first pterale: I1 and I2. Activity of I1 and I2 is correlated with a decrease in stroke amplitude during flight. (B) The muscles of the basalare: b1, b2 and b3. Muscle b1 typically fires a single action potential in every stroke cycle whereas b2 is only active during turning maneuvers in (tethered) flying animals. Both muscles increase stroke amplitude by rotating the basalar apodeme forward. Spikes of control muscles occur in a narrow phase band of the wing beat cycle that determines their efficacy on wing kinematics. In *Drosophila* electrical stimulation of b2 at different phase bands indicates that the phasic effect of muscle contraction amounts to a approximately 10% modulation of the tonic effect on stroke amplitude. The b2 also controls the rotational speed of wing rotation at the end of each stroke cycle. The b3 is counter balancing force generation of b1 and b2. See (Fig. 3C) for more details. (C) The muscles of the posterior notal wing process: hg1 and hg2-4. During turning behavior the hg3 is active on the outer side of the turn and inactive on the contralateral side. (D) The muscles of the third pterale: III1 and III2-4. The III1 pulls the wing back when active but also increases stroke amplitude during flight turns. The III2-4 are likely to act similar to III1. (E) The indirect tergopleural muscles: tp1 and tp2. These muscles are likely to control angle of attack during wing stroke. (F) The indirect control muscles: tergotrochanter (tt) and pleurosternal muscles ps1 and ps2. The tergotrochanter muscle inserts on the inner side of the scutum and connects via a long apodeme to the trochanter of the mesothoracic leg. It is activated during take-off and straightens the middle leg to elicit a 'jump' start of the fly. In *Calliphora* and the house fly *Musca* stroke frequency increases when spike frequency of ps muscle increases supposedly due to alterations in tension between sclerites within the wing hinge. Results are taken from various authors.^{26,27,44-52} Figures are redrawn from Dickinson and Tu.⁵³

incapable of generating positive work during flight. In other words, regardless of its nervous activation, the b1 muscle is stretched throughout the stroke due to the relative changes in distance between the basalar sclerite of the scutum and the wing hinge (Fig. 3C). The power required for lengthening the muscle in turn comes from the power muscles. As a consequence, the b1 muscle does not produce positive work on the wing hinge; it functions more as an active spring than a force producing element.³¹ This concept in control of muscle power and wing kinematics allows the animal to exert a rather constant tension on the complex wing hinge throughout the entire stroke cycle which is likely to facilitate the control performance of the mechanical thoracic resonator. Moreover, through their influence on stroke parameters such as amplitude and frequency, the nervous activity in flight control muscles is critical in regulating the power output of the much larger asynchronous muscle fibers.

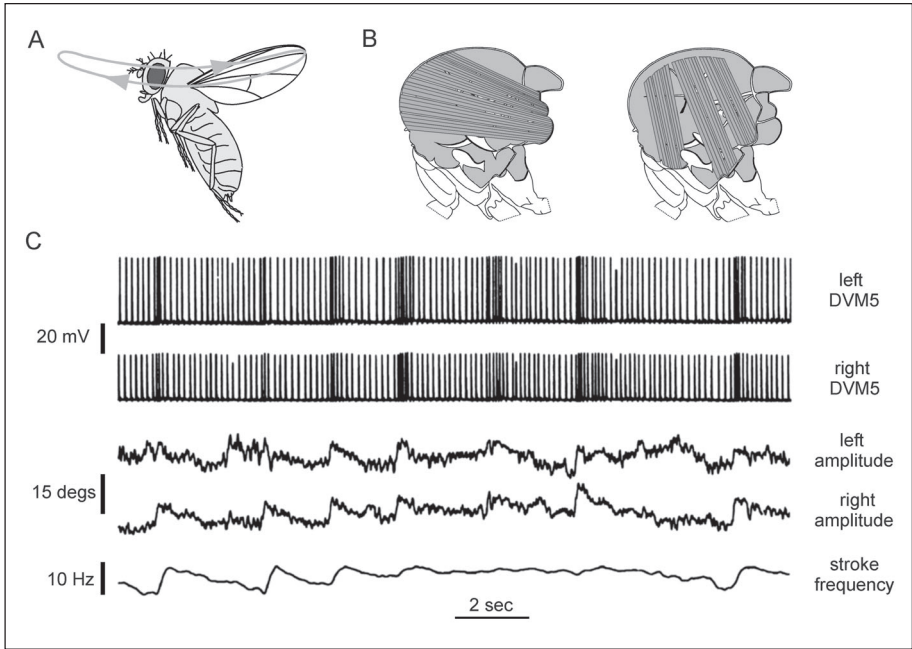


Figure 5. (A) Hovering posture of a freely flying fruit fly. The main stroke plane is oriented approximately horizontally indicating that the lift vector produced by the beating wings is oriented perpendicular to the stroke plane. There are 4 stroke phases: 2 translational phases (up and down stroke) and 2 rotational phases at the end of each half stroke in which the wings are quickly rotated around the longitudinal wing axis. (B) Generalized morphology of the indirect power muscles in flies. The 6 dorsal longitudinal muscles fibers (DLM, left), and 7 dorso-ventral fibers (DVM, right) are seen from the medial section of the right side. Indirect power muscles do not insert directly on or near the wing hinge but are attached throughout the thoracic cuticle. Their contractions generate distortions of the thoracic exoskeleton which an elaborate hinge transforms into the up and down wing motion. (C) Neural drive of the asynchronous muscle increases during flight maneuvers of *Drosophila*. The top two traces show intracellular recordings from a bilateral pair of DVM. The firing rate of these muscles correlate with changes in stroke amplitude and stroke frequency during flight. According to conventional aerodynamic theory a simultaneous increase in both amplitude and frequency results in an increase in flight force production and *vice versa*. Wing kinematic responses were elicited using a moving visual stimulus in front of the fly. The increase in spike firing rate is assumed to be linked to an increase in free intracellular calcium concentration that in turn facilitates mechanical power output of flight muscle fibers due to an increase in recruitment/activation of myofibrils during stretch activation.

Changes in Muscle Efficiency in Vivo

The changing power requirements for flight demands alter the mechanical power requirements that face the asynchronous flight muscles to rapidly commit additional mechanical power during flight maneuvers. In the fruit fly, spike frequency in the indirect flight muscles increases when the wings undergo larger stroke angles due to an activation of basalar control muscles which is correlated with an increase in flight force production.³² This increase in neural input might raise the release of calcium from internal stores, although fibrillar muscle contains only a small fraction of sarcoplasmic reticulum. An alternative explanation that is consistent with the presence of calcium currents in the asynchronous fibers is that calcium enters the muscle from outside through voltage gated calcium channels.^{33,34} Although the steady-state calcium activation curve is steep,³⁵ the calcium influx from a burst in spikes of the DLM and DVM

could function to recruit cross bridges into force production. As a consequence, the fuel consumption of the muscle fibers increases. The benefit of nervous muscle activation for providing a higher level of mechanical power, however, depends on muscle efficiency. Although typically assumed constant, muscle efficiency might also vary during flight force production, helping to assuage the increased metabolic demands resulting from elevated force production.

Muscle efficiency can be estimated by deriving at least two of the three factors: total metabolic rate, metabolic heat production and muscle mechanical power output. Because it is difficult to record exact measures of heat production in small insects, biologists derive muscle efficiency from the ratio between simultaneous measurements of carbon dioxide release and the mechanical work done by the muscle fibers. Strain-stress measurements in vitro of isolated muscles fibers are done in a muscle rig in which the isolated fibers undergo cyclic oscillations at a rate that would occur during flight in the intact animal. However, in many instances the mechanical power output estimated from these experiments is significantly lower than those predicted in the behaving animal.³⁶ Alternatively, muscle power can be derived from the power requirements for flight by simultaneously measuring stroke amplitude, stroke frequency and total flight force. To modulate wing kinematics and thus power requirements in flight, fruit flies are flown in a virtual flight simulator and stimulated with visual patterns moving vertically around the fly.⁵ *Drosophila* responds robustly to this moving pattern by modulating the production of flight forces and thus power requirements in flight (Fig. 3A). These experiments are roughly analogous to electronically changing the weight of the animal and allow modulation of muscle power output in the intact animal. Muscle efficiency in *Drosophila* is lowest (5.6%) when the animal produces small flight forces and rises to a maximum (23.5%) during maximum force production (Table 1, Fig. 2C). The increase in muscle efficiency reflects the steep increase in profile power requirements with rising flight force, while the animal produces carbon dioxide at moderate rates even at elevated locomotor activity. The different slopes in metabolic rate and aerodynamic power requirements for flight help the fruit fly satisfy the increased energetic demands resulting from elevated flight force production when carrying loads and when performing flight maneuvers.

Concluding Remarks

Like all flying insects, the fruit fly *Drosophila* must regulate the amount of power that is generated by the flight musculature to match the changing demands of the locomotory output. The control of power output results from two separate effects: the changes in the asynchronous muscle's own neural drive as well as the activation of smaller, less powerful control muscles. Through their action on the stiffness of the thoracic box and the wing hinge, control muscles can alter the strain rate of power muscles by changing stroke amplitude and the frequency of the mechanical resonator, thereby changing both the power output and eventually flight force. Although the flight motor of flies differs from muscle systems design in other insects with synchronous power muscles, it reveals the trade-off between power generation and control in flapping flight which may potentially limit flight performance and thus aerial maneuverability in many flying insects.

References

1. Ellington CP. Limitations on animal flight performance. *J Exp Biol* 1991; 160:71-91.
2. Josephson RK. Contraction dynamics and power output of skeletal muscle. *Ann Rev Physiol* 1993; 55:527-546.
3. Josephson RK, Stevenson RD. The efficiency of a flight muscle from the locust, *Schistocerca americana*. *Journal of Physiology* 1991; 442:413-429.
4. Stevenson RD, Josephson RK. Effects of operating frequency and temperature on mechanical power output from moth flight muscle. *J Exp Biol* 1990; 149:61-78.
5. Lehmann F-O, Dickinson MH. The changes in power requirements and muscle efficiency during elevated force production in the fruit fly, *Drosophila melanogaster*. *J Exp Biol* 1997; 200:1133-1143.
6. Casey TM. A comparison of mechanical and energetic estimates of flight cost for hovering sphinx moths. *J Exp Biol* 1981; 91:117-129.

7. Tucker VA. Bird metabolism during flight: Evaluation of theory. *J Exp Biol* 1973; 58:689-709.
8. Ellington CP. The aerodynamics of insect flight. VI. Lift and power requirements. *Phil Trans R Soc Lond B* 1984; 305:145-181.
9. Pennycuik CJ. Power requirements for horizontal flight in the pigeon *Columba livia*. *J Exp Biol* 1968; 49:527-555.
10. Pennycuik CJ. Mechanics of flight. In: Farner DS, King JR, eds. *Avian Biology*. London: Academic Press, 1975:1-75.
11. Lehmann F-O. The constraints of body size on aerodynamics and energetics in flying fruit flies: An integrative view. *Zoology* 2002; 105:287-295.
12. Dickinson MH, Lehmann F-O, Sane S. Wing rotation and the aerodynamic basis of insect flight. *Science* 1999; 284:1954-1960.
13. Dickinson MH, Lighton JRB. Muscle efficiency and elastic storage in the flight motor of *Drosophila*. *Science* 1995; 268:87-89.
14. Gorb SN. Serial elastic elements in the damselfly wing: Mobile vein joints contain resilin. *Naturwissenschaften* 1999; 552-555.
15. Ardell DH, Andersen SO. Tentative identification of a resilin gene in *Drosophila melanogaster*. *Insect Biochemistry and Molecular Biology* 2001; 31:965-970.
16. Lehmann F-O. The efficiency of aerodynamic force production in *Drosophila*. *Comparative Biochemistry & Physiology. Part A, Molecular & Integrative Physiology* 2001; 131:77-88.
17. Roeder KD, Treat AE. The detection and evasion of bats by moths. *Am Sci* 1961; 49:135-148.
18. Currie RW. The biology and behavior of drones. *Bee World* 1987; 68:129-143.
19. Strohm E, Lechner K. Male size does not affect territorial behaviour and life history traits in a sphecid wasp. *Anim. Behav* 2000; 59:183-191.
20. Götz KG, Wehrhan C. Optomotor control of the force of flight in *Drosophila* and *Musca* I. Homology of wingbeat-inhibiting movement detectors. *Biol Cybernetics* 1984; 51:129-134.
21. Götz KG. Bewegungsschen und Flugsteuerung bei der Fliege *Drosophila*. In: Nachtigall W, ed. *BIONA- report 2*. Stuttgart: Fischer, 1983:21-34.
22. Lehmann F-O, Dickinson MH. The production of elevated flight force compromises flight stability in the fruit fly *Drosophila*. *J Exp Biol* 2001; 204:627-635.
23. Marden JH. Bodybuilding dragonflies: Costs and benefits of maximizing flight muscle. *Physiol Zool* 1989; 62:505-521.
24. Marden JH, Waage JK. Escalated damselfly territorial contests are energetic wars of attrition. *Anim Behav* 1990; 39:954-959.
25. Marden JH, Rollins RA. Assessment of energy reserves by damselflies engaged in aerial contests for mating territories. *Anim Behav* 1994; 48:1023-1030.
26. Tu MS, Dickinson MH. The control of wing kinematics by two steering muscles of the blowfly, *Calliphora vicina*. *J Comp Physiol A* 1996; 178:813-830.
27. Lehmann F-O, Götz KG. Activation phase ensures kinematic efficacy in flight-steering muscles of *Drosophila melanogaster*. *J Comp Physiol* 1996; 179:311-322.
28. Lehmann F-O. Aerodynamische, kinematische und electrophysiologische Aspekte der Flugkraftzeugung und Flugkraftsteuerung bei der Tauflye *Drosophila melanogaster*. Max-Planck-Institute for biological Cybernetics. Tübingen: Thesis, University of Tübingen, 1994:131.
29. Ewing AW. The neuromuscular basis of courtship song in *Drosophila*: The role of direct and axillary wing muscles. *J Comp Physiol* 1979; 130:87-93.
30. Benner-Clark HC, Ewing AW. The wing mechanism involved in the courtship of *Drosophila*. *J Exp Biol* 1968; 49:117-128.
31. Tu MS, Dickinson MH. Modulation of negative work output from a steering muscle of the blowfly *Calliphora vicina*. *J Exp Biol* 1994; 192:207-224.
32. Heide G, Spüler M, Götz KG et al. Neural control of asynchronous flight muscles in flies during induced flight manoeuvres. In: Wendler G, ed. *Insect Locomotion*. Berlin: Paul Parey, 1985:215-222.
33. Patlak J. The ionic basis for the action potential in the flight muscle of the fly, *Sarcophaga bullata*. *J Comp Physiol* 1977; 107:1-11.
34. Salkoff L, Wyman R. Ionic currents in *Drosophila* flight muscle. *J Physiol* 1983; 337:687-709.
35. Peckham M, Molloy JE, Sparrow JC et al. Physiological properties of the dorsal longitudinal flight muscle and the tergal depressor of the trochanter muscle of *Drosophila melanogaster*. *J Muscle Res Cell Motil* 1990; 11:203-215.
36. Tohtong R, Yamashita H, Graham M et al. Impairment of muscle function caused by mutations of phosphorylation sites in myosin regulatory light chain. *Nature* 1995; 374:650-653.
37. Chan WP, Dickinson MH. In vivo length oscillations of indirect flight muscles in the fruit fly *Drosophila virilis*. *J Exp Biol* 1996; 199:2767-2774.

38. Casey TM, Ellington CP. Energetics of insect flight. In: Wieser W, Gnaiger E, eds. *Energy Transformations in Cells and Organisms*. Stuttgart: Thieme Verlag, 1989:200-210.
39. Dickinson MH, Hyatt CJ, Lehmann F-O et al. Phosphorylation-dependent power output of transgenic flies: An integrated study. *Biophys J* 1997; 7:3122-3134.
40. Wakeling JM, Ellington CP. Dragonfly flight III. Lift and power requirements. *J Exp Biol* 1997; 200:583-600.
41. Josephson RK. Temperature and the mechanical performance of insect muscle. In: Heinrich B, ed. *Insect thermoregulation*. New York: John Wiley & Sons, 1981:19-44.
42. Heinrich B. Temperature regulation of the sphinx moth, *Manduca sexta*. I. Flight energetics and body temperature during free and tethered flight. *J Exp Biol* 1971; 43:141-152.
43. Lehmann F-O. Ambient temperature affects free-flight performance in the fruit fly *Drosophila melanogaster*. *J Comp Physiol B* 1999; 169:165-171.
44. Nachtigall W, Wilson DM. Neuro-muscular control of dipteran flight. *J Exp Biol* 1967; 47:77-97.
45. Heide G. Die Funktion der nicht-fibrillären Flugmuskeln bei der Schmeißfliege *Calliphora*. Teil I: Lage, Insertionsstellen und Innervierungsmuster der Muskeln. *Zool Jb Physiol* 1971; 76:87-98.
46. Heide G. Die Funktion der nicht-fibrillären Flugmuskeln bei der Schmeißfliege *Calliphora*. Teil II: Muskuläre Mechanismen der Flugssteuerung und ihre nervöse Kontrolle. *Zool Jb Physiol* 1971; 76:99-137.
47. Heide G, Götz KG. Optomotor control of course and altitude in *Drosophila* is achieved by at least three pairs of flight steering muscles. *J Exp Biol* 1996; 199:1711-1726.
48. Egelhaaf M. Visual afferences to flight steering muscles controlling optomotor responses of the fly. *J Comp Physiol A* 1989; 165:719-730.
49. Kutsch W, Hug W. Dipteran flight motor pattern: Invariabilities and changes during postlarval development. *J Neurobiol* 1981; 12:1-14.
50. Wisser A. Mechanisms of wing rotating regulation in *Calliphora erythrocephala* (Insecta, Diptera). *Zoomorphol* 1987; 106:261-268.
51. Wisser A, Nachtigall W. Functional-morphological investigations on the flight muscles and their insertion points in the blowfly *Calliphora erythrocephala* (Insecta, Diptera). *Zoomorphol* 1984; 104:188-195.
52. Pfau HK. Funktion einiger direkter tonischer Flügelmuskeln von *Calliphora erythrocephala* Meigen. *Verh Dtsch Zool Ges* 1977; 70:275.
53. Dickinson MH, Tu MS. The function of Dipteran flight muscle. *Comp Biochem Physiol A* 1997; 116A:223-238.