WING AND MUSCLE OSCILLATIONS OF ASYNCHRONOUS FLIGHT MUSCLES

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Abstract

Intrigued by the delicate structure of the iridescent insect wings, I wanted to find out how much an insect's membranous wing weigh. Investigating the wing is important as the success of insects as terrestrial animals is due to their ability to fly. I approached the problem by reading studies done on insect flight, and came across a link between asynchronous muscle contractions and the wingbeat oscillations. Asynchronous muscles are unique, as each contraction is not dependent on a neural impulse; instead, they are controlled by the muscle itself which has the intrinsic ability to oscillate, the elasticity of the thorax, and wing oscillations. I calculated the wing mass of the bumblebee *Bombus terrestris* by modeling the asynchronous muscle and wing into a mass spring oscillator. The bumblebee wing mass was found to be 170 mg. This was not what I expected as wings are very light (<1mg), perhaps there was an error in approximation and calculation of the spring constant, k or the additional mass is due to the air mass the wing pushes around during flight.

Key words: asynchronous muscle, wing, spring, insect flight, *Bombus terrestris*.

Introduction

The wings of the more primitive insects such as grasshoppers, butterflies, and dragonflies are more extensive than the wings of more modern insects like the bees, flies, and mosquito. The primitive insects also use a different method of flight than the modern insects. In the flight muscles of the primitive insects, especially those with low wingbeat frequencies, each wing stroke is associated with an action potential. This type of flight is called synchronous because of the 1:1 correspondence between electrical and mechanical activity. On the other hand, in the more advanced insects, there is no direct correspondence between electrical and mechanical activity, hence the name asynchronous. These unique muscles contract in an oscillatory manner when it is attached to an appropriate resonant load such as the wing and the thoracic exoskeleton. This method of flight can facilitate wing-beat frequencies higher than, that of the action potentials. Previous experiments have shown the importance of the wing mass to asynchronous insects. Cutting a portion off the tips of the wings hence decreasing wing mass, increases the frequency of wingbeats; whereas, in synchronous insects, this has little effect on the frequency of wingbeats as it is controlled by neuronal input. In asynchronous insects, it is the oscillations of the wingbeats that causes the muscle to contract. This is an evolutionary advantage as a decreased wing surface produces less aerodynamic force per beat, so when the asynchronous insects increase the frequency of wingbeats it is compensating for the loss. The purpose of my study is to approach asynchronous flight muscles from a physics point of view and attempt to calculate the mass of the bumblebee *Bombus terrestris's* wings. My hypothesis is that the wing can be regarded as a 'mass-spring oscillator' which is being pulled upon by two asynchronous muscles whose mechanical properties are of a pair of stiff springs. If the 'mass-spring oscillator' is displaced and released, it will oscillate at a frequency which depends on the mass of the 'mass-spring oscillator' and the stiffness of the springs.

Materials and Methods

Animals

I chose the bumblebee *Bombus terrestris* as my test subjects.

Muscle cross-section area

From literature, I found the average length of the bumblebee *Bombus terrestris,* and from studying the anatomy of this bumble bee and using the law of proportions, I estimated the width and length of the cross-section area of the dorso-ventral muscle. Multiplying the width and length, and then subtracting the corners gave me the cross-section area of the muscle.

Muscle length

To calculate the muscle length I found the average body mass of the bumblebee, and put it in the regression equation provided by Josephson (1997) ($L = 1.12\ m_b^{\ 0.27}$, where L is the muscle length in mm and m_b is the body mass in mg). Josephson (1997) measured the length of muscle fibres using an ocular micrometer.

Wingbeat frequency

I measured the wingbeat frequency during flight by using the regression equation provided by Cooper (1993) ($f = 429.5\ m_b^{\ -0.17}$, where f is the wingbeat frequency in Hz and m_b is the body mass in mg). Cooper (1993) anaesthetized the bee with carbon dioxide, cemented a small wooden rod to the bee's sternum, and gave the bee a piece of paper to hold in its legs. Tethered flight is initiated by withdrawing the tissue paper from the animal legs and blowing across its head. Wing strokes are photographed with a video camera and then transferred to a computer for analysis.

Muscle stiffness

I calculated the stiffness of the muscle by calculating the slope of muscle stress against muscle strain for the data obtained in Josephson (1997). Josephson determined the muscle force during tetanic stimulation at a series of different length. The reference muscle length was set to a length close to the normal resting length. The muscle was stimulated tetanically for 0.5 s at 50 Hz and with a stimulus intensity 1.5-2 times that required for a maximal response. Immediately after the contraction, the muscle is shortened by 0.4-0.5 mm to the first test length and, after 2 minutes at the new length, stimulated again. In subsequent trials, the muscle test lengths were increased by either 0.09 or 0.18 mm per trial until the increased force upon stimulation becomes very small.

Results

Table 1

Muscle cross-section area	**1.2×10^{-6} m^2**
Muscle length	5.0×10^{-3} m^2
Wingbeat frequency	170 Hz
Muscle stiffness	800 kN m^{-2}
Muscle spring constant	192 Nm^{-1}
Wing mass	170 mg

Muscle cross-section area

The average length of the bumblebee *Bombus terrestris* is approximately 17mm. I estimated the cross-section area of the dorso-ventral muscle to be approximately **1.2×10^{-6} m^2.**

A = (width x length) - corners
= 1.7mm x 0.9mm – $0.3mm^2$
= 1.2 mm^2 ≈ 1.2×10^{-6} m^2

Muscle length

The average body mass of bumblebee *Bombus terrestris* is 248mg. From the regression equation provided by Josephson (1997) ($L = 1.12\ m_b^{\ 0.27}$) (Fig.1), I calculated the length of the muscle to be **5.0×10^{-3} m**.

$L = 1.12\ m_b^{\ 0.27}$
$= 1.12\ (248mg)^{0.27}$
= 5.0 mm ≈ 5.0×10^{-3} m^2

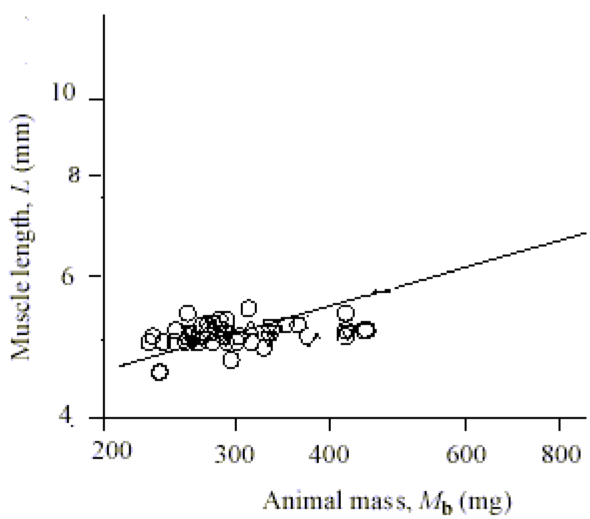


Fig. 1. Relationship between bumblebee muscle length and body mass

Wingbeat frequency

I calculated the wingbeat frequency during flight by using the regression equation provided by Cooper (1993) ($f = 429.5\ m_b^{-0.17}$) to be **170 Hz**.

$$f = 429.5\ m_b^{-0.17}$$
$$= 429.5\ (248\text{mg})^{-0.17}$$
$$= 170\ \text{Hz}$$

Muscle stiffness

One of the characteristics of asynchronous muscles is that they are very stiff; in other words, the muscle is quite resistant to stretch. Passive force rises rapidly with elongation, but it plateaus at extensions of 10% above reference length. To find the stiffness of the bumblebee's muscle, I calculated the slope of muscle stress against strain from Josephson (1997) data (Fig. 2), which turns out to be **800 kN m^{-2}.**

slope = rise / run

$$= \frac{70\ \text{kN m}^{-2} - 30\ \text{kN m}^{-2}}{103\% - 98\%} \times 100\%$$
$$= 800\ \text{kN m}^{-2}$$

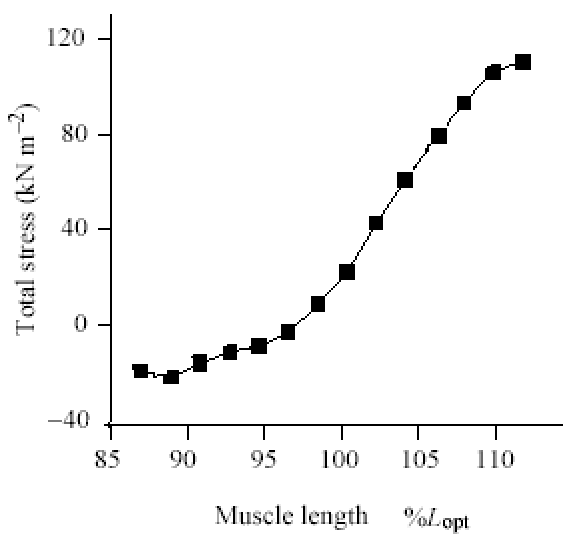


Fig. 2. Relationship between muscle stress and strain

Muscle spring constant

Assuming that asynchronous muscles behave like a spring (Fig. 3), I calculated the muscle spring constant to be **192 Nm^{-1}.**

Stress (σ) is defined as:

$$\sigma = \frac{F_{tension}}{\text{cross-section area}} = \frac{F_t}{A} \qquad \text{(Eq. 1)}$$

Young's modulus (Y) equation:

$$Y = \frac{\text{stress}}{\text{strain}} = \frac{F / A}{\Delta L / L} \qquad \text{(Eq. 2)}$$

Rearranging it gives:

$$\sigma = Y \bullet \frac{\Delta L}{L} \qquad \text{(Eq. 3)}$$

Combining Eq. 1. and Eq. 2. yields:

$$\frac{F}{A} = Y \bullet \frac{\Delta L}{L}$$

$$F = A \bullet Y \bullet \frac{\Delta L}{L} \qquad \text{(Eq. 4)}$$

Hooke's Law of springs:

$$F_{spring} = k \bullet \Delta L \qquad \text{(Eq. 5)}$$

Combining Eq. 4. and eq. yields:

$$k = A \bullet \frac{Y}{L} \qquad \text{(Eq. 6)}$$

$$= 1.2 \times 10^{-6}\ m^2 \bullet \frac{800\ kNm^{-2}}{5.0 \times 10^{-3}\ m}$$

$$= \mathbf{192\ Nm^{-1}}$$

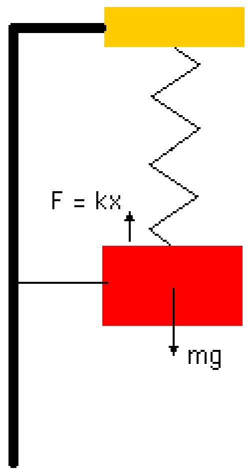


Fig. 3. Free body diagram of mass-spring oscillator

Wing mass

Assuming that the wing and muscle oscillates in a harmonic motion, I calculated the wing mass to be **170 mg.**

a 'mass-spring oscillator' has period (T):

$$T = 2\pi \sqrt{m/k} \qquad \text{(Eq. 7)}$$

Since frequency (f) is the inverse of period:

$$f = 1/(2\pi) \cdot \sqrt{k/m} \qquad \text{(Eq. 8)}$$

To find the mass of the wings:

$$m = \frac{k}{(f \cdot 2\pi)^2} \qquad \text{(Eq. 9)}$$

$$= \frac{192\ \text{Nm}^{-1}}{(170\ \text{Hz} \cdot 2\pi)^2}$$

$$= 1.7 \times 10^{-4}\ \text{kg} \approx \mathbf{170\ mg}$$

Discussion

In my experiment, I found the wing mass to be 170 mg. This was not what I have expected. From my observations of bumblebee's wings, I predicted the mass of their membranous wings to be less than 1 mg. My hypothesis for the experiment is that the wing of the wing of a bumblebee can be modeled as a 'mass-spring oscillator' which is pulled upon by antagonistic muscles whose properties are largely those of a pair of stiff springs (Fig. 4). If the 'mass-spring oscillator' is displaced and released, it will oscillate at a frequency which depends on the mass of the 'mass-spring oscillator' and the stiffness of the springs ($f = 1/(2\pi) \cdot \sqrt{k/m}$). During oscillation, each of the springs will be alternately stretched beyond and allowed to shorten below the equilibrium position.

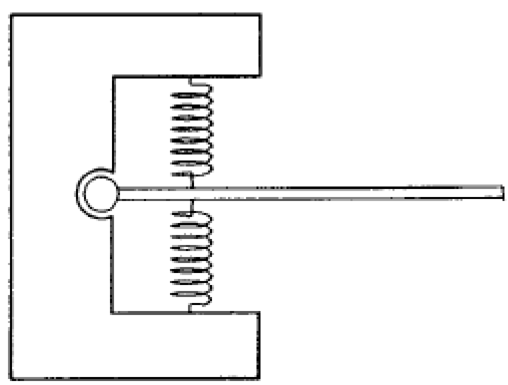


Fig. 4. A physics model of asynchronous muscle (springs) and wing (pivoting rod)

Prior to defending the discrepancy of my result, I am going to provide a cellular explanation of how the asynchronous muscle oscillates and the mechanical arrangement that shows how the asynchronous muscle contraction is linked to wing strokes, which supports my model assumption.

Muscle physiology

'Delayed stretch activation' and 'delayed shortening deactivation' are two unique properties found in asynchronous muscle that supply the energy needed to maintain oscillatory contraction. The relationship of changes in length and force against time (Fig. 5a) shows that force falls during shortening (a) and continues to fall, because of 'delayed shortening deactivation,' during the interval at which length is constant (b). Then force rises during the subsequent stretch (c) and because of 'delayed stretch activation,' rises further to a peak even though length is constant (d). A plot of the muscle stress against strain to forms a work loop (Fig. 5b). The difference between the work of shortening and the work of lengthening (area of the work loop) is the net work done over the cycle. The work loop of an asynchronous muscle is traversed in a counterclockwise direction; force is higher during shortening than during lengthening, which means there is net work output by the muscle. The of net work output in the asynchronous flight muscle of bumblebees *Bombus terrestris* is 0.63 J kg^{-1} (Josephson, 1997). Comparing this muscle with synchronous muscle, which has a work loop that is traversed in a clockwise direction, meaning, it absorbs work for each cycle.

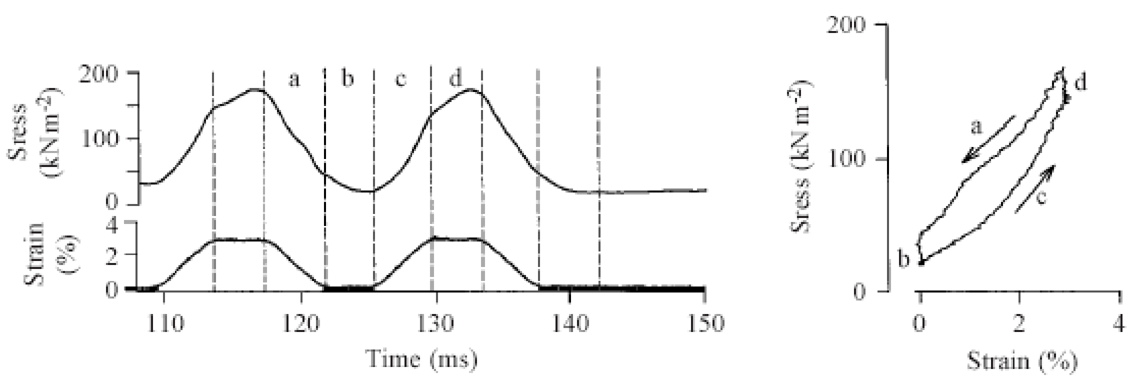


Fig. 5. a) Strain and stress changes against time during stretch and release. b) work loop of an asynchronous muscle

Muscle mechanics

The mechanics of asynchronous flight muscle differs from the synchronous flight muscle. Instead of having the flight muscles attached to the wing, the two sets of asynchronous muscles are arranged perpendicularly to one another filling the thorax, change the shape of the thorax to elevate and depress wings. Contraction of the dorso-ventral muscle flattens the thorax dorso ventrally and lengthens it, this change in the shape of the thorax acts through hinges to move wing up with the sides of the exoskeleton acting as a fulcrum. At the same time, the lengthening of the thorax stretches and activates dorsal longitudinal muscle. As the longitudinal muscle contracts, the thorax is pulled shorter and causes the notum to bow or bulge, and this change of shape act through the hinges to move wing downward. The shortened thorax stretches and activates dorso-ventral muscle, and the process repeats (Fig. 6). In asynchronous insects, the movement of wings involves the muscles as well as the elasticity of the thorax.

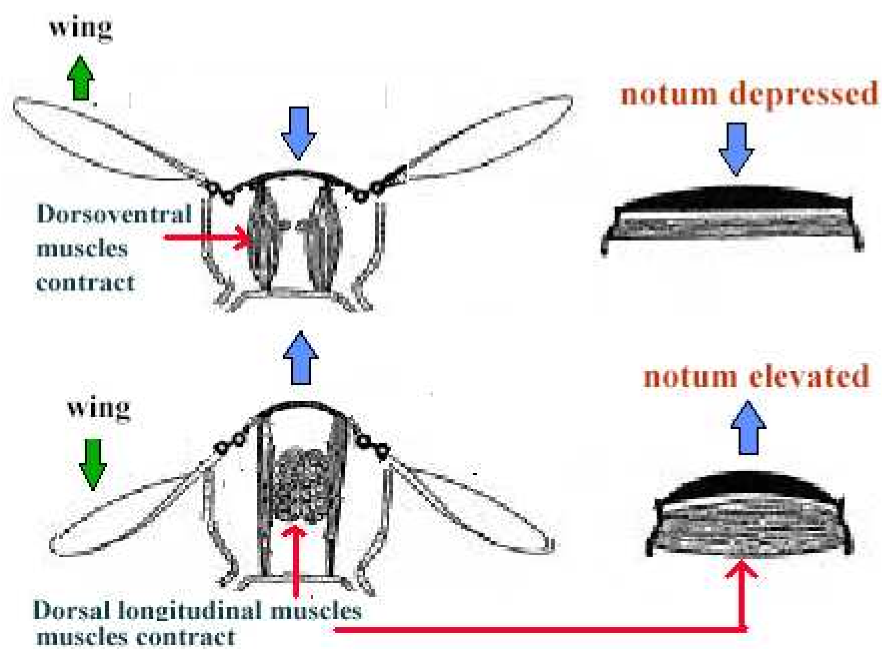


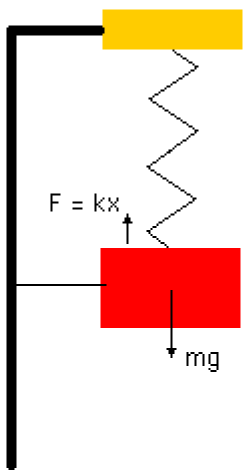
Fig. 6. a) Cross-section of asynchronous muscle. b) side view

Although the wings of bumblebees is light, the wings push air around (added mass) to create a lift force F_L(Fig. 7). In order to keep the insect in the air, the average vertical component of the lift force must equal the insect's weight.

$$F_L \approx \text{weight of bee}$$

The air mass should be approximately $M_{bee} \approx 248$ mg

Therefore the mass of the oscillator or the wing should be $\approx M_{bee}$



$k = 192\ \text{Nm}^{-1}$

f = 170 Hz = $1 / (2\pi) \sqrt{(k/m)}$

m = 170 mg

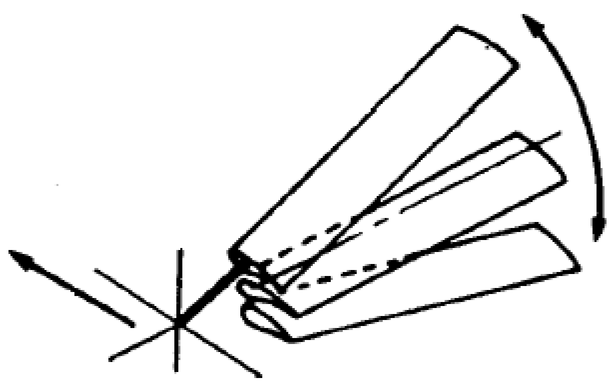


Fig. 7. Air mass moved as a result of wing stroke

Other experiments reconfirmed my calculated wingbeat frequency for bumblebee Bombus terrestris. Perhaps my calculation of spring constant is not complete as I did not factor in the stiffness of the notum, which is the top exoskeleton of the insect that bulges up during dorsal longitudinal muscle contraction. It is made up of cuticle, whose stiffness can be compared to copper! It bows up and down like a stiff saw during asynchronous insect flight. However, from the equation based on my simplified model, the spring constant should be lower for the mass to be less.

$$m = \frac{k}{(f \cdot 2\pi)^2}$$

In conclusion, the test result of wing mass, 170mg, is still a little high. Some of this additional mass can be accounted for by the air mass the wings carry along when it flaps down to generate lift force. Some of the mass is from the blood veins in the wings.

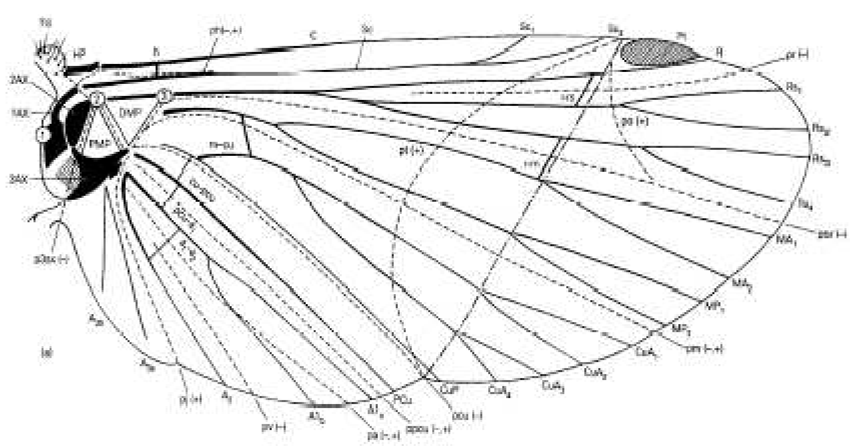


Fig. 8. Structure of an insect wing

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