Characterization and Analysis of the Flight Dynamics of Fruit Flies

by

Emily M. Hilton

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Signature of Author..
Department of Mechanical Engineering
February 2, 2007

Certified by...
Dr. Triantaphyllos R. Akylas
Professor, Department of Mechanical Engineering
Thesis Supervisor

Accepted by..
Prof. John H. Lienhard V
Chairman, Undergraduate Thesis Committee
Department of Mechanical Engineering

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ABSTRACT

For centuries, the human race has been perplexed by the various complex physical manifestations in nature. Much of what we have seen in nature we have tried to recreate, from the migration tendencies and routes of sea creatures to the flight of birds and insects. The flight of the fly, in particular, is of interest because of their natural stabilization techniques. The works of two scientists, Steven Vogel and Michael Dickinson, were researched in order to find out how the flight dynamics of the fly worked. It was found that the fast horizontal wing beating of the fly as well as the body angle of the fly helped to generate lift and thrust within the fly. Equilibrium was achieved due to the haltere of the fly, a small stubby organ behind the forewing which detected Coriolis forces at the base of the wing and created counter-rotations. Both scientists used work done by earlier scientist J.W. Pringle, who modeled the haltere as a mass-dashpot-spring system using dynamics in order to analyze the oscillatory motion and how it affects flight. The research done by all three scientists can serve to one day be able to produce micro aerial vehicles, using the flight dynamics of the fly as the basis of the flight of these vehicles.

Thesis Supervisor: Dr. Triantaphyllos R. Akylas
Title: Professor, Department of Mechanical Engineering

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I would like to express my gratitude first to Professor Triantaphyllos R. Akylas for allowing me to undertake this research thesis under his supervision. This project allowed me to present a thesis in a field that I was interested in, as well as forced me to expand my existing knowledge of dynamics and to understand observational data and how it related to the neuromuscular system of insects. I have truly learned about the flight of flies and how it can relate to small-scale mechanical flying.

I would also like to thank Elliott Ortiz-Soto for helping me recover from an unfortunate situation which occurred recently and for his assistance in regaining important references and information which were relevant to this thesis. Without his help I probably would not have been able to find the will and courage to finish this thesis.

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CHAPTER 1

INTRODUCTION

For centuries, the human race has been perplexed by the various complex physical manifestations in nature. Much of what we have seen in nature we have tried to recreate, from the migration tendencies and routes of sea creatures to the flight of birds and insects. The realm of the sea has long been conquered, but it was not until the Wright brothers created the airplane in 1903 that we were able to fully understand and grasp the concept of flight through lift and drag and aerodynamics. When we looked to birds, we easily were able to come up with aerodynamic equations to find how lift and thrust were generated under its wings, and the airplane was made. However, when looking to insects, there are many more questions to be raised with their flight dynamics.

We look to the fly especially, because, unlike other insects, flies only have one pair of wings instead of two. When observing the *Drosophila virilis*, or the common fruit fly, it has been observed that they have two small rear club-shaped organs which seemed to have evolved from hind wings the fly may have had many years ago. This organ, the haltere, has long been researched by zoologists in order to find out its true role in the flight of the fly. Without them, the fly seems unable to stay balanced throughout flight, but how exactly they work to equilibrate the fly is still a mystery.

In order to find out how exactly these haltere aid in flight, I researched the works of several scientists and biologists interested in this field. The works of two scientists, in particular, were of interest since their research contradicted each other but still found many answers to the flight question of the fly. These scientists, Steven Vogel and Michael Dickinson, used the work of previous scientist J.W.S. Pringle and his model of the haltere of the fly and came to their own conclusions on what affected the flight of the fly. While Vogel experimented on the fly to find correlations between lift and thrust with respect to the body angle of the fly and stroke angle of the wing, Dickinson found a true purpose for the haltere of the fly. Dickinson found that the frictional damping of the air was not great enough to terminate the angular velocity of the fly during a rotation, and it therefore had to find other means to create a counter turn. Dickinson concluded that the haltere, in fact, was the cause of this counter-turn. By detecting Coriolis forces, the haltere send a signal to the wings and create such a counter-turn during a rotation. This can be seen more thoroughly throughout this thesis, which characterizes and analyzes the several components of the flight of the fly, and how it can be applied to robotic and mechanical applications for the future.

CHAPTER 2

THE FRUIT FLY (*DROSOPHILA VIRILIS*)

In order to implement findings in flight about small insects into real projects, such as small robotic flying vehicles, we need to fully understand the anatomy and the flight of insects. We look to the fly especially because unlike other insects, flies have only two wings instead of four. This makes it more comparable to flight that we are accustomed to, such as that of airplanes and birds. The flight of airplanes and birds can be explained through the theory of "steady-state aerodynamics," which states that the shape and angle of the wings of each causes air to travel faster over the top surface than the bottom. This decreases the pressure above the wing and generates lift beneath the wing. However, this theory does not hold when applied to flies, since it predicts that with the small wings and large body of the fly, the fly should never lift off the ground. ([3], p. 275)

2.1 Anatomy of the Fly

The anatomy of the fly plays a very important part in determining how it flies. As stated earlier, the flight of the fly would seem almost impossible due to its small, stubby wings and large body. We examine its anatomy and play close attention to a few of the organs of the fly. The following figure, Figure 1, shows the complete external anatomy of the fruit fly.

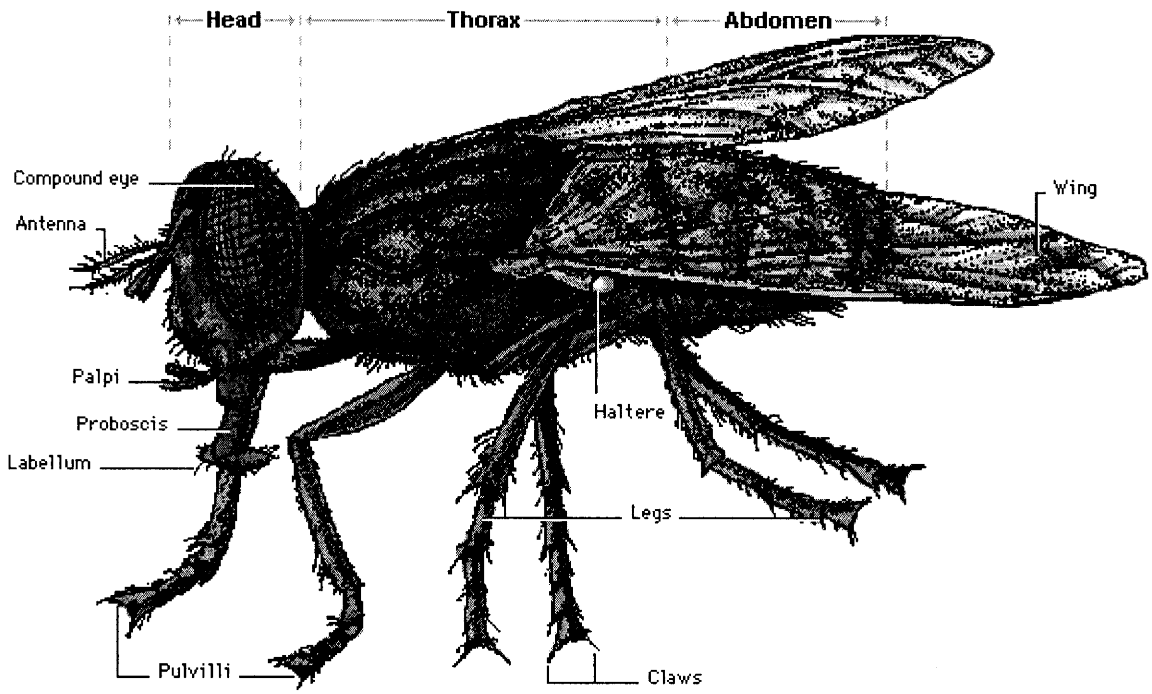

Figure 1 External Anatomy of the Fruit Fly taken from [4]

Of particular interest in this thesis is the thorax of the fly, which externally consists of the wings, the legs and the halteres. On a normal fly of the class *Diptera*, you will find two wings, six legs, and two halteres. [8] The wings serve the obvious purpose as primary factor in flight. The exact flight dynamics of the wings will be discussed more thoroughly in Section 2.2, but for now, the wings beat back and forth in the horizontal plane instead of up and down, like birds. The legs somewhat serve a purpose in the flight of the fruit fly, but for the most part, in pulling the four hind legs closer to the body, the fly achieves a more aerodynamic and stable flight. The halteres are small stubby organs, shaped somewhat like dumbbells, which somehow aid the wings in flight. These halteres, found on either side of the fly's body beneath the wings, evolved from the third and fourth hind wings the fly used to have thousands of years ago. ([2], p. 904) The following figure, Figure 2, shows a close-up of this organ next to the wings.

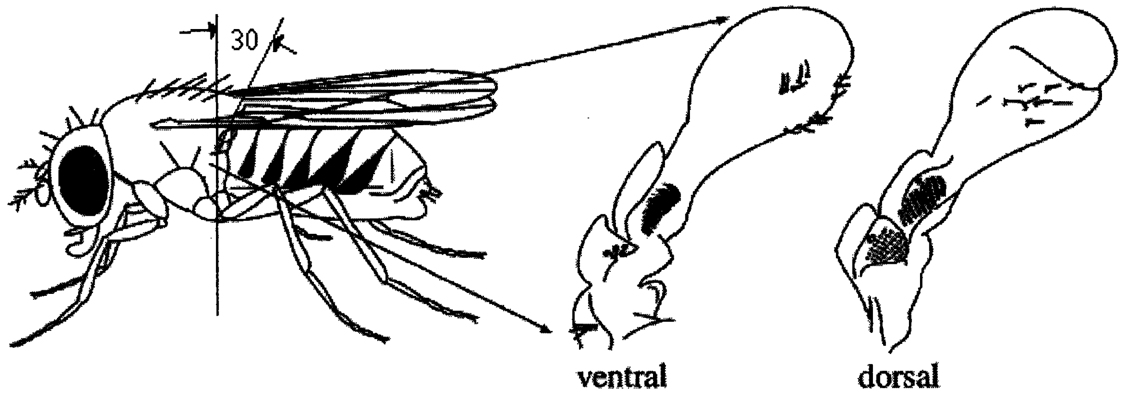

Figure 2 Position of Haltere on Body of Fruit Fly and Close-up of Halteres taken from ([2], p.904)

As you can see, the evolution of the hind wings into these small club-shaped organs on the fly has been great. Not only are they much smaller than the fore wings, their shape too seems to have an effect on their purpose and role in the flight of the fly. When at rest, the haltere of the fly are at a 30-degree angle to the vertical. More on how these halteres aid the wings in flight will be discussed more thoroughly in Section 2.2 and Section 3.1.

2.2 Flight of the Fly

The fly controls its flight about three axes, the yaw axis, pitch axis, and roll axis. The following figure, Figure 3, shows the exact configuration of these axes with respect to the fly's body, which is the moving frame of reference.

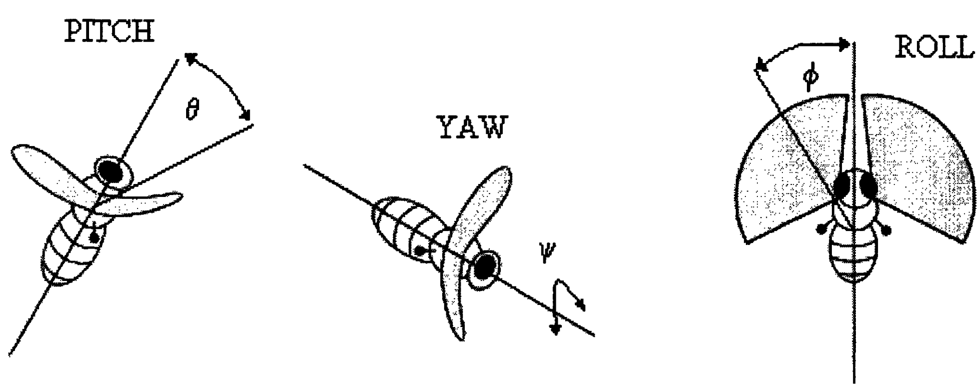

Figure 3 Yaw, Pitch and Roll Axes with Respect to the Fruit Fly

The inertial frame of reference, or the environment, also has a yaw, pitch and roll axis, but in order to simplify the complicated flight of the fly, we will only be discussing these axes with respect to the body of the fly. The fly changes its movements in these axes through small angular changes in their wing flapping. $\theta, \phi, and \psi$ are the angles by which the fly controls its pitch, yaw, and roll. ([2], p.907) As said earlier, flies do not flap their wings up and down, since this would be almost useless for their body size and short stubby wings. Instead, flies flap their wings back and forth, in the horizontal plane. Each back and forth movement of the fly's wings is called the upstroke and downstroke of the wing. ([3], p. 276) As the wing goes downstroke, the wing is slightly angled so that it pushes air upwards or downwards, depending on the direction it chooses to hover in. At the end of the stroke, the wing flips over so that the upstroke is also slightly angled in the same vertical direction of the downstroke. A schematic of this movement can be seen in Figure 4 below.

Figure 4 Wing Movement of Fly during Upstroke and Downstroke taken from ([3], p.276)

Notice in Figure 4 the arrows at the front center of the "fly." These arrows show the direction of thrust that the fly is generating during each stroke, i.e. the fly moves backward during an upstroke and forward during a downstroke. This causes hovering in the fly instead of movement forward, since the amount of horizontal, or forward, force the fly produces in its downstroke is almost equal and opposite to the amount of horizontal force produced in the upstroke. During flight, the halteres beat in anti-phase to the wings, meaning they beat up and down while the wings beat back and forth. The wings of a fly beat at about 100 to 150 *Hz*, causing maneuvers to occur quickly and effectively while in flight.. During flight, the halteres beat in anti-phase to the wings, beating up and down while the wings beat back and forth. ([3], p. 277)

In order to move forward, backward, left or right, the fly changes its angle of attack, or the angle the fly makes with respect to each of its three axes. For example, by pitching itself downward, the fly thrusts forward, much like a helicopter does in order to generate more forward thrust. There is, however, a unique reaction of the fly that does not solely depend on the pitch, yaw, or roll angle. ([3], p. 274) Depending on what they encounter during flight and where they would like to continue, the fly creates a rapid change in angle and wing flap in order to change its direction and position. This is referred to as the saccade of the fly, which will be discussed more thoroughly in Section 2.3.

2.3 The Saccade

The saccade in the flight of flies is a term that describes how a fly alters its flight direction by generating rapid, repeated turns during its path of straight flight. Usually the saccade results as a reaction to an obstacle or a hindrance that the fly visually encounters while flying, or while the fly is in search of food. Instead of making complete turns (180 degree rotations), the fly chooses to turn 90 degrees either left or right. ([3], p. 274) The wings of the fly move in perfect symmetry when moving back and forth. In order to generate saccades, flies use very small alterations in their wing motion. In fact, the forces that the fly generates with respect to the yaw, pitch and roll axes change very little through the saccade. By changing the orientation of its body, the fly can increase lift and thrust during the saccade. In order to rotate in each direction, the fly must overcome its moment of inertia as well as frictional damping. ([3], p.278) For example, in order to rotate in the yaw axis, the fly must generate enough torque to overcome both of these factors. The torque required to do so, T_ϕ, can be approximated by equation (1),

$$T_\phi = I_\phi \frac{d^2\phi}{dt^2} + C_\phi \frac{d\phi}{dt}$$ **(1) taken from ([3], p.278)**

where I_ϕ and C_ϕ are the moment of inertia and frictional damping about the yaw axis of the fly, and ϕ is the yaw position, stated earlier. It has been measured by Professor Michael H. Dickinson and his team at the Dickinson Laboratory at the California Institute of Technology, who will be discussed more thoroughly in Chapter 3, that the dynamics of flight of this insect are dominated by body inertia and not frictional damping. Since the viscosity of air does not dominate the dynamics of rotation, the fly does not reach terminal angular velocity (i.e. angular velocity does not reach zero) during a saccade, and the fly is unable to stop its motion at the end of a turn. ([3], p.279) In order for stopping to occur, the fly creates a counter-turn in the opposite direction using the halteres as sensory organs to initiate the counter-turn and to end the saccade movement. The following figure, Figure 4, shows a fly's saccade in detail.

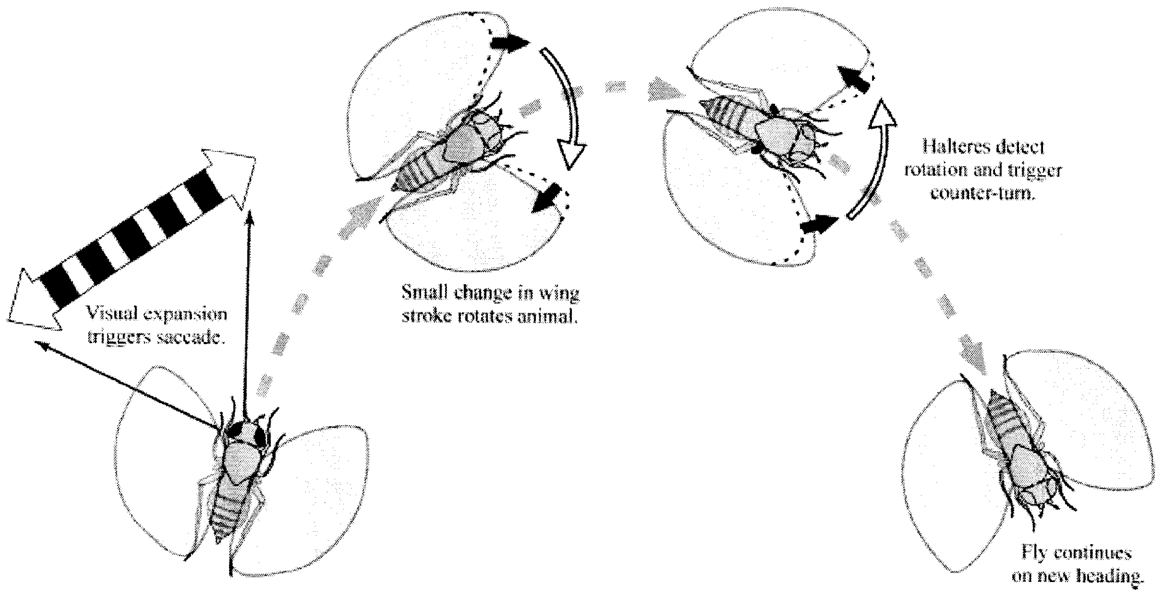

Figure 5 Schematic Model of the Saccade taken from ([3], p.280)

The steps in this figure, and to summarize what has been said about the saccade in the earlier paragraphs, show that the fly first initiates the saccade due to a visual stimulus or in order to find food to eat. After seeing this obstacle in its flight or in not finding food along its path, the fly begins to make small alterations in its wing flapping, often changing direction by elongating the upstroke and downstroke on one side while shortening the strokes on its opposite side. As stated earlier, since the viscosity of air is not enough to stop the turn, the fly must use internal means in order to keep its intended direction. The halteres sense the intended rotation and send a signal to the rest of the body to create a small counterturn with the wings, making the fly slow itself down until it is flying straight onto its intended path. ([3], p.280)

CHAPTER 3

FLIGHT AND EXPERIMENTATION

This chapter on flight and experimentation deals exclusively with the early analysis of a biologist named Steven Vogel, who in the 1960s was a graduate student at Harvard, and with the more recent findings and models of Michael H. Dickinson, a biology professor and researcher at the California Institute of Technology. The early findings of Steven Vogel involved research on the aerodynamics of the fly wings found through observations on tethered flies inside an experimental apparatus he devised. However, he refutes the halteres having any effect on the flight of the fly due to their small size, an idea that Michael H. Dickinson along with others now disprove. Using J.W.S. Pringle's model of the haltere, both scientists came to find useful information about the flight of the fly while having different purposes for the haltere during that flight. Dickinson's models show that without the haltere, the flies cannot stabilize themselves and soon crash into the ground rather than flying correctly, while Vogel shows the proportionality between body angle and lift generated during flight.

3.1 Pringle's Model of the Haltere

J.W.S. Pringle was a scientist in the early 1940s and 1950s who was very interested in the flight dynamics of the fly. By studying the haltere extensively, he came up with a mechanical model of the fly which he used to create. The following figure, Figure 6, shows his drawings of the haltere which can be compared to this mechanical model of the haltere using a mass-dashpot-spring system seen in Figure 7.

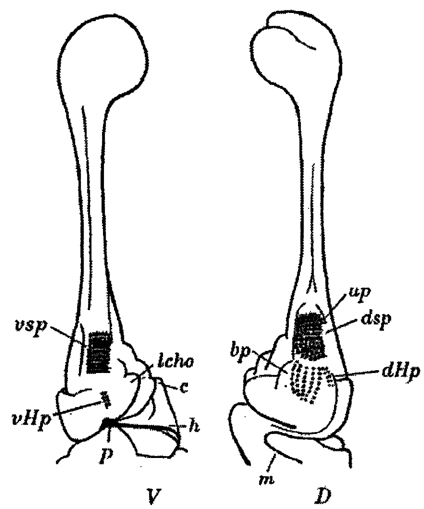

Figure 6 Pringle's Drawings of the Ventral and Dorsal side of the Haltere taken from ([5], p.350)

Above Pringle is showing the top view and bottom view of the left haltere of a fly. Pringle's drawings showed in detail the different biological parts of the haltere, but the main ones we are concerned with in this thesis are the following (using Pringle's lettering in Figure 6): *h*, main hinge line, *P*, strong point in the articulation at the intersection of the main hinge and secondary fold, *m*, point of attachment of muscle, and *bp*, basal plate. ([5], p.350) We are concerned with only these four biological parts of the haltere because we can compare them to the simplified parts of the mechanical system shown in Figure 7. The basal plate consists of fluid and other small sensory organs that aid in the movement of the haltere about the main hinge line. In Figure 7, the basal plate has been simplified to a system consisting of a dashpot *H*. The hinge line, *h*, is now represented by the bearings through *AA* with an elasticity of the hinge being represented by the spring *S*, a torsional spring which connects into the bearings. The point of articulation, *P*, is about the same point P we can find in Figure 7. Finally, the point of attachment of the muscle, *m*, is now represented by *M*. ([5], p.352)

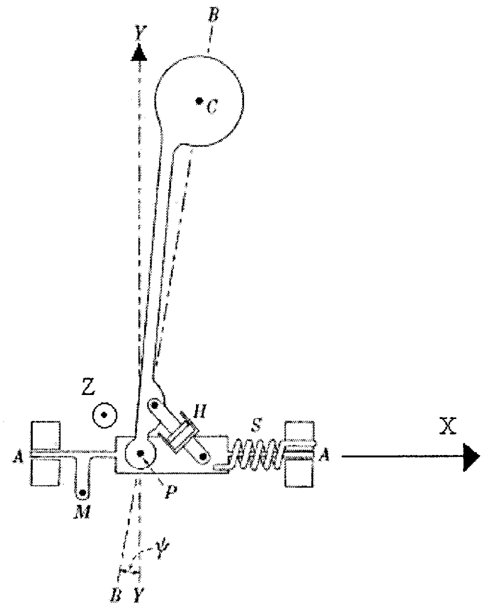

Figure 7 Diagram Illustrating Mechanics of Haltere Oscillations taken from ([5], p.352)

As stated earlier in this thesis, when the haltere is at rest, it makes an angle with the vertical which has been found to be close to 30 degrees. (For Pringle's calculations, we will leave this angle simply as ψ.) The center of mass of the haltere's end lies on the line *PB*, which makes the angle ψ mentioned earlier. Pringle then used the following given values for the mechanical system described in Figure 7: m as the mass of the moving portion acting at *C*, l as the distance from point *P* to point *C*, ψ as the angle between the lines *PY* and *PB*, and ω as the maximum angular velocity about *AA*. ([5], p.381) Oscillations occur about bearings *AA* due to the muscle at point *M* pulling the end of the haltere down from rest and the elastic force of the muscle restoring the haltere to its initial position.

The mechanical system seen in Figure 7 is still a very complex system to solve. In order to simplify the problem, Pringle first assumed that these oscillations were simple harmonic motions, the system moves rigidly, and the mass of the entire system is concentrated at one point. Using these assumptions, dynamics can be used to determine the properties of the mechanical system described in Figure 7. Now instead of looking at the entire mechanical system shown in Figure 7, we can assume that a point mass is moving in one direction along an arc. In general, simplifying the system like this led to Pringle concluding that apart from the primary torque of the fly caused by the fly changing in direction, there were also secondary torques at the base of the haltere in the yaw, pitch and roll axes. The complete solution of the dynamics can be found in the Appendix of this Thesis.

In applying equations (10),(11),(12), and (13) found in the Appendix to the generalized mass and size of the fly which we state in the table below, we find that the secondary gyroscopic torques in the yaw, pitch, and roll axes.

Table 1 Standardized Values Used to find Resultant Torques on Fly's Haltere taken from ([5], p.358)
{N.B. 1 dyne is defined as $10^{-5}N$, $\omega_1 \omega_2 \omega_3$ are taken from Appendix as constant rotations about x-, y-, and z-axes.}

Mass of Fly	2.3×10^{-2} g
Mass of Haltere	4.75×10^{-6} g
Length of Haltere	$0.07cm$
Frequency of Oscillation	$150Hz$
Half-Amplitude of Oscillation	75°
Primary Torque	2.7×10^{-2} dyne-cm
Gyroscopic Torque: Yaw	$3.7\times10^{-5}\omega_3$ dyne-cm
Gyroscopic Torque: Pitch	$4.9\times10^{-5}\omega_2$ dyne-cm
Gyroscopic Torque: Roll	$2.8\times10^{-5}\omega_1$ dyne-cm

The gyroscopic torques are much smaller than the primary torque. The values given above are the maximum torques found by simplifying the haltere as a light rod with a point mass at the end. If the fly were to rotate with a rotational velocity of 1 rev per sec, then the gyroscopic torques are about 1/100th of those due to the primary rotation. Since the torques produced by the haltere's end on the base are very small, they have little to no gyroscopic effect on the primary torque of the whole fly itself.

We continue on to the next section, Section 3.2, to find out how biologists Steven Vogel and Michael Dickinson used experiments to find out how halteres affect the flight of the fly, and the overall purpose of the haltere in flight.

3.2 Experiments by Vogel and Dickinson

The experiments done by Vogel and Dickinson help us better understand how the fly flies. Vogel creates an experiment which looks for a correlation between the lift and thrust of the fly with respect to the body angle of the fly as well as the stroke angle of the wing. Dickinson finds a true purpose for the haltere, which we found out in the previous section to not have a true gyroscopic effect on the whole fly. Instead, the haltere aid the wings of the fly by other means, namely, through the sensory organs located on the basal plate of the haltere.

3.2.1 Early Flight Experiment by Vogel, Haltere not considered

Steven Vogel's early analysis of the fruit fly stemmed from earlier work done by Weis-Fogh on four-winged locusts. Instead of doing any theoretical analysis like Pringle, Vogel analyzed and concluded his theory on the flight of flies based on empirical and experimental investigations. ([6], p.567) Using anesthetized *Drosophila virilis* specimens, Vogel tethered them in a pressurized tunnel, while taking pictures of the flies with a strobe light. The following figure, Figure 5, shows the arrangement of his experiment.

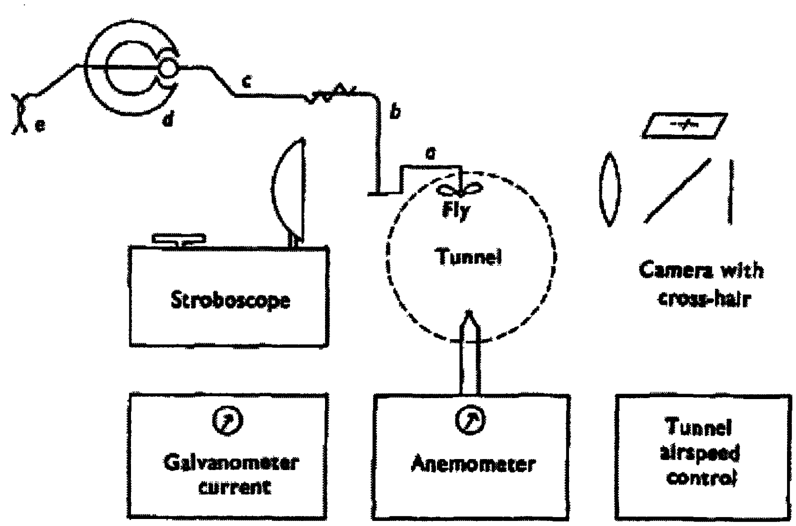

Figure 8 Arrangement of components in Vogel Performance Experiments taken from ([6], p.568)

The fly is tethered to a wire which in turn is attached to a pendulum with counterweights in order to keep the fly centered in the tunnel. By applying bursts of air to the tethered fly and then observing the fly's wing movements through the strobe light, Vogel was able to theorize about the flight of the flies and approximate the amount of lift that the flies would need in order to fly. Also, he found a proportional correlation with the body or pitch angle (θ) and the lift. At a certain pitch angle, the fly generated almost 100% lift, meaning there was little to no drag, and the amount of lift the fly produced was proportional to the varying pitch angle with respect to incoming bursts of air in the tunnel. ([6], p.575)

Unlike four-winged insects, Vogel found that lift and pitch angle with respect to the air speed were dependent of each other, in contrast to Weis-Fogh experiments on locusts in 1956. ([6], p.575) Weis-Fogh had concluded in his earlier findings that the body angle and lift of locusts were completely independent parameters of each other, and there was no reason to believe that one affected the other. Steven Vogel, however, found that in the observation of tethered flies the same did not hold true. Using standardized numerical values for parameters in a "standard performance" of a fly, he found that because of the small size of the body of the fly, changing the pitch angle of the fly did not increase the drag as much as it did with the much longer locusts. For the fly, drag did not greatly decrease the amount of lift produced when varying body angle, and therefore Vogel could come up with the following almost linear correlation between drag (and lift) and the body angle of the fly. ([6], p. 576)

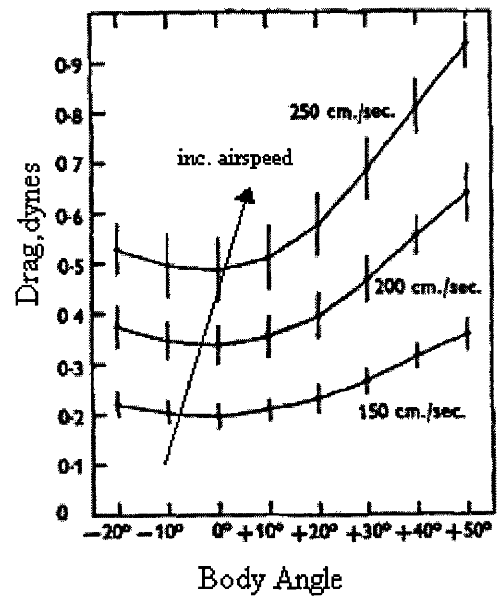

Figure 9 Drag versus Body Angle and Airspeed of Fly, Standard Deviations indicated by Vertical Lines taken from ([6], p.573)

When the fly had 0-degree pitch angle with the wind, it had the minimum drag force for each airspeed. As the body angle was increased or decreased from the zero point, the drag increased almost linearly. The drag increased faster with increasing airspeed, but this is expected since the faster the air travels on a body, the more drag it will produce.

Steven Vogel also was able to determine how other parameters, while pitch angle was fixed, affected speed, lift, and thrust. Vogel found how varying stroke angle, or the angle the wings of the fly make in an upstroke or downstroke with respect to the pitch axis of the fly, affects lift and thrust. While flies were held at a constant body angle of 12°, Vogel found a close to linear correlation between lift and thrust and stroke angle in his experimental data. ([7], p.387) The following figure, Figure 7, shows the correlation he finds between lift and thrust and stroke angle.

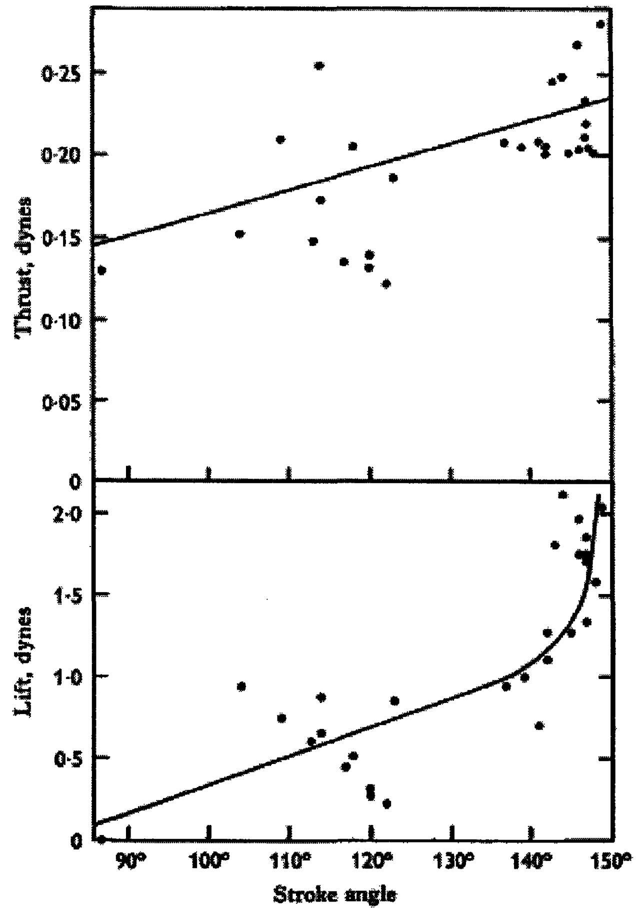

Figure 10 Variations of Thrust and Lift with varying Stroke Angle at Fixed Body Angle of 12 degrees taken from ([7], p.387)

As you can see, there is a linear correlation between lift and thrust and the varying stroke angle. However, the lift increases unstably at very high stroke angles. Vogel attributes this anomaly to a shift in the plane of stroke and the fly flying at a nearly vertical position, thereby generating much more lift under its wings. ([7], p.385)

Vogel concludes that the body angle is the primary regulator in determining the ratio of lift to thrust and that the stroke angle regulates the magnitude of the output stroke force (the force generated during a stroke). However, Vogel determines that the fly adjusts its body angle using an aerodynamic mechanism which changes as a result of the force the wings exert on the body. This aerodynamic mechanism must produce a moment about the fly's center of mass. Vogel does state that this is easy for four-winged insects because they can produce the necessary torque by controlling both pairs of wings. He does, however, assume that the mass of the haltere of the fly is much too small, a reference to Pringle's earlier work, and therefore they cannot produce the necessary counter-torque needed to control its body angle. We now know that although the haltere do not create the gyroscopic torques necessary to create counter-turns on their own, the haltere do indeed serve a purpose in flight when rotating. The next subsection, Section 3.2.2, deals with a latter scientist, Michael H. Dickinson, and his most relevant experiment to this thesis which proves that the haltere has an effect on the control of the body angle and equilibrium of the fly.

3.2.2 Dickinson's Experiment for Equilibrium Reflexes in Fruit Flies

Michael H. Dickinson's more advanced experiments prove that the halteres do indeed aid in the rotation and control of a fly's body. Much of what he has proven has been said earlier in this thesis, but what we are concerned about now is how he came up with these results which we now deem as facts in the flight of the fly. Dickinson, like Vogel, also analyzed the flight of flies through the use of experiments on tethered flies in an environment. His experiment, which we see below in Figure 8, consisted of a rotating chamber with an internal virtual reality environment for the fly.

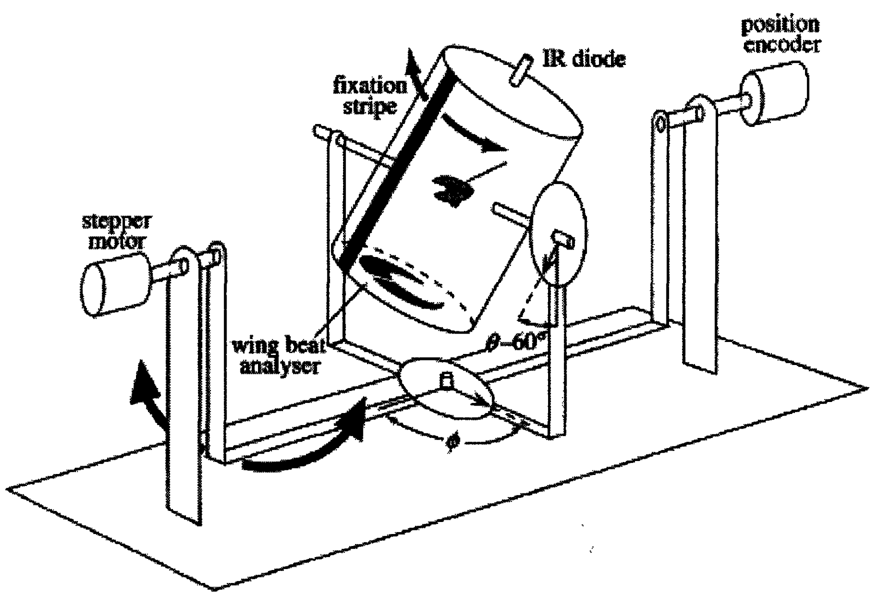

Figure 11 Model of Virtual Reality Chamber and Setup for Experimentation on Equilibrium-Reflexes of the Fly taken from ([2], p.904)

The chamber is a mechanically controlled gimble which also has a wing beat analyzer which found the frequency and movement of the wings as the virtual environment changed. As the gimble rotated in the pitch and roll axes of the inertial frame of reference, the fly, feeling such movements as its own, adjusted the beating of its wings in order to adjust to stay level within the frame of reference. The following figure, Figure 9, shows the data picked up from the analyzer. In this figure you can see exactly how the fly changed its wing beating and pattern in order to remain in equilibrium as the gimble rotated.

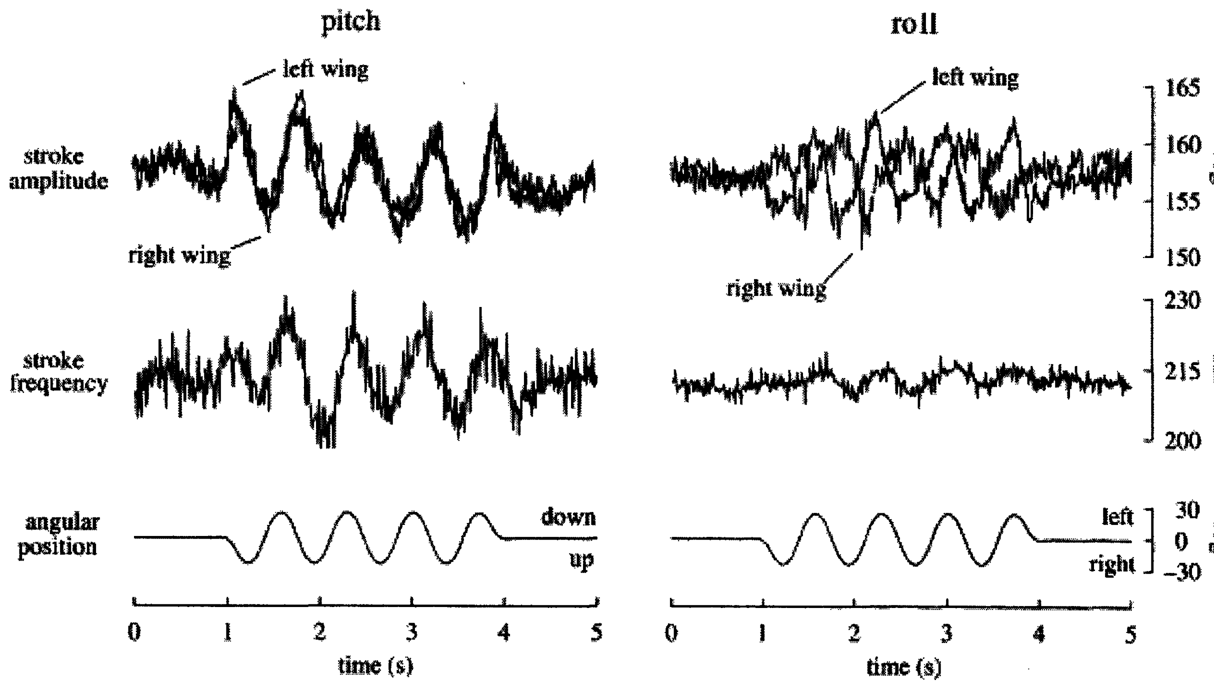

Figure 12 Equilibrium Reflexes in Response to Oscillations about the Pitch and Roll Axes taken from ([2], p.905)

A positive angular position signified that the fly was heading down or left with respect to the pitch and roll axes respectively. With changes in the pitch angle, θ, the fly tended to beat the wings the same, as would be expected with changes in this axis. However, with changes in the roll angle, φ, the wings tend to beat a bit offset and sometimes anti-phase in order to readjust to an equilibrium position. The stroke frequency for changes in pitch angle tends to vary greatly between 200 and 230 Hz, since changes in the fly's vertical position means the fly must equilibrate itself by beating its wings more or less. Stroke frequency for changes in roll angle didn't vary greatly, since the beating of the wings does not affect its position as much as beating them at offset upstrokes and downstrokes. ([2], p.905)

Moreover, Dickinson then performed experiments on flies inside the same rotational gimble setup which had either none, one or both halteres removed. This proved that halteres indeed have an effect on the beating of the wings as well as the equilibrium of the fly. The following figure, Figure 10, shows the results of Dickinson's experiment.

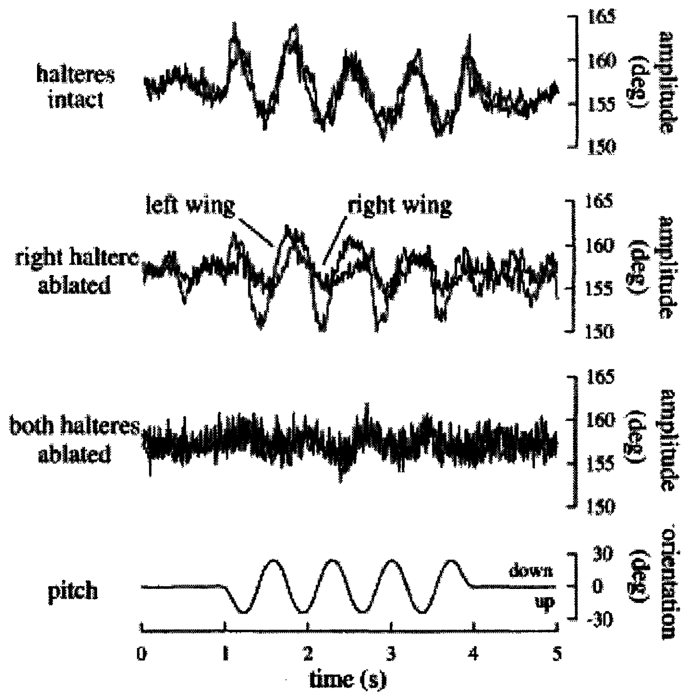

Figure 13 Wing Response of Fly during Rotation of Apparatus with None, One, and Both Haltere Removed taken from ([2], p.908)

With the halteres intact, the wings of the fly beat symmetrically, oscillating back and forth with the same stroke length on either side while the gimble is rotating, much like the results seen in Figure 10 for the pitch stroke amplitude. When the right haltere was removed from the fly, the left wing continued with the normal oscillations as it used to with both halteres intact, but the right wing seemed to have no response-mechanism whatsoever. The right wing did little to correct its position since it could no longer detect rotations on that side of its body. Finally, with both halteres removed, the fly had no response-mechanism to the rotating gimble, and therefore it could not readjust to find its equilibrium within the rotating frame of reference. ([2], p.908)

CHAPTER

4

RESULTS AND APPLICATIONS

This chapter discusses the experiments from the previous chapter and concludes how the haltere aid in flight. Applications of the flight of the fly are also introduced and their relation to the previous experiments is also discussed.

4.1 Importance of Haltere in Flight

Michael Dickinson's experiments found an immediate role for the haltere, which is to provide feedback to the wing-steering muscles in order to stabilize the moments resulting from aerodynamic forces. ([2], p.905) This feedback provided by the haltere alters the stroke frequency seen above in Figure 9 as well as the wing rotation. Dickinson, using Pringle's earlier work as a foundation for his biological findings, found that the haltere function by detecting Coriolis forces, the inertial forces acting on a moving object in a rotating frame of reference. In order to find the magnitude and direction of the Coriolis force, the cross-product of the haltere's linear velocity with the angular velocity of the fly's thorax and the mass distribution of the haltere is taken. ([2], p.904) This can be summarized by Equation (2):

$$F_C = m_h(v_h \times \omega_{fly}) \tag{2}$$

where F_C is the Coriolis force, v_h is the linear velocity of the haltere, m_h is the mass distribution of the haltere and ω_{fly} is the angular velocity of the fly's thorax. The expression $v_h \times \omega_{fly}$ is seen again in the Appendix, when finding the acceleration of the mass *m* which acts in direction *ob*. This expression is the Coriolis acceleration within a rotating frame of reference. Inside a rotating frame, the fly may move in a straight line, but to an outside observer, the fly takes a considerably different path.

Even though the haltere do serve a purpose in the stabilization of the fly, it isn't a direct gyroscopic one. Vogel's conclusion that the mass of the haltere are much too small to affect the rotational movements of the fly are indeed correct, however Dickinson's experiments prove that the fly does need the haltere in order to stabilize itself. As mentioned before, Dickinson's experiments showed that without one or both of the haltere, wing functionality tended to decrease immensely, and the fly no longer knew how to equilibrate itself using its wings. Using the sensory organs at its base, the haltere sense changes in the forces due to the environment upon the fly, like the Coriolis force mentioned before. The role of the haltere is not a physiological one but a neuromuscular one which sends signals to the brain in order for it to change its stroke frequency or body angle.

4.2 Application of Results into Mechanical Systems

One of the more important reasons why we are interested in the flight of flies is that with smaller-scale flying objects, it is hard to try to implement the same aerodynamic designs we find in airplanes and birds. Many hopeful mechanical projects for the future include robot "seekers" at a small scale, almost to the size of insects. These robotic seekers would imitate the flight of flies and be able to creep into small places in order to find things or people. Already, micro aerial vehicles, or MAVs, are being modeled after the flight of flies. These robotic insects are electromechanical devices propelled by a pair of independent flapping wings to achieve sustained autonomous flight. ([1], p.1) The following figure, Figure 11, shows such a model of a Micromechanical Flying Insect, or MFI, that is being modeled at the University of California at Berkeley.

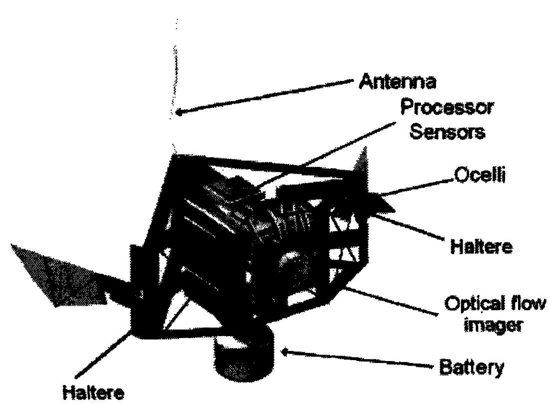

Figure 14 Model of a Micromechanical Flying Insect Based on a Blow Fly taken from ([1], p.1)

As you can see, there are various similarities between this model and that of the anatomy of the fly. The model shown above would be about ten times the size of a regular house fly, have a mass of only 100 *mg*, and wing beat frequency of 150*Hz*. Earlier micro aerial vehicles designed after birds are great for long ranges and fast speed flight, but they do not have the ability to hover or maneuver well, which is necessary in urban or indoor environments.

When designing these robotic vehicles, it is known that the flight of the fly is difficult to comprehend and model. Since most of the experiments done on the fly, like those done by Vogel and Dickinson, were done on tethered flies, modeling the free flight of the fly tends to be trickier. In order to do so, researchers use mathematical modeling to obtain optimization values for the wing aerodynamics, body dynamics, actuator dynamics, sensors, external environment and flight control algorithms. ([1],1) The mathematical modeling is done computationally in a complete program simulator called the Virtual Insect Flight Simulator (VIFS). This simulator combines all the different important parts of flying and gives a realistic analysis and ways to improve the design of the sensors and flight control algorithms. ([1], p.2) The following figure shows a block diagram of how the VIFS inputs values given in order to find the position, orientation and velocity of the fly.

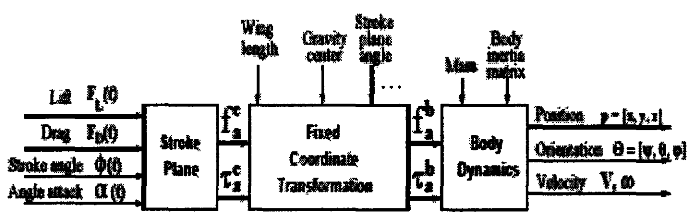

Figure 15 Body Dynamics Block Diagram for Virtual Insect Flight Simulator taken from ([1], p.6)

The inputs are the same parameters we found throughout Vogel's experiments: lift, drag, stroke angle and angle attack (body angle in Vogel's experiments). The correlation between lift and both of these angles found by Vogel is once again found through mathematical modeling and input into the VIFS in order to find the six degrees of freedom associated with the position and orientation of the fly in the x-,y-, and z-axes as well as the yaw, pitch, and roll axes. ([1], p.6)

It is curious to note that the model being produced above in Figure 14 for the micromechanical flying insect does include the haltere as part of the body structure. However, since we know that the haltere do not produce a significant gyroscopic torque onto the fly – and the researchers know this too – we find it difficult to see a physical purpose as part of the fly. Yet, the researchers include the haltere as one of many sensors that can detect complex sets of forces during flight, namely the gravitational, inertial, angular acceleration, centrifugal and Coriolis forces. ([1], p.9) The following block diagram represents the haltere kinematics in the robotic insect.

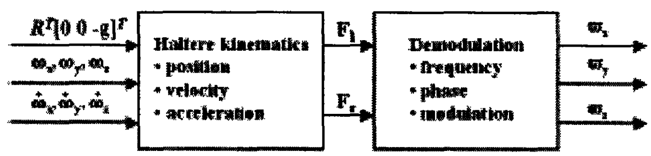

Figure 16 Block Diagram Representation of Haltere Kinematics taken from ([1], p.9)

This block diagram inputs a rotational matrix for the haltere as well as angular velocities and accelerations affecting the haltere to modify the true angular velocities and orientation of the robotic fly. ([1], p.9)

Although much mathematical modeling has brought together the experiments done on tethered flies with the models of robotic insects, there is still much to learn about the flight of insects. The mathematical models presented for the robotic insects are only theoretical models, with prototypes still being built out of appropriate materials, and sensors still being programmed in order to produce adequate results in the field of biomimetic insects. For future progress, scientists hope to expand on the prototypes and the Virtual Insect Flight Simulator as better modeling and understanding of the flight of insects becomes more available. ([1], p.11)

CHAPTER 5
CONCLUSION

Although humans have been able to understand the flight of birds and have thus implemented that into airplanes and large flying objects for over a century, the new surge of nanotechnology makes it urgent to understand how the flight of smaller living creatures, namely insects, works. Using observations and experiments, two biologists, Steven Vogel and Michael Dickinson, both during different decades, tried to determine how flies fly, since unlike other insects, flies only have two wings instead of four, making them like the bird but more difficult to understand. Due to the small wing size of the fly and the relatively large body size, it seems almost impossible based on aerodynamics of birds for the flies to fly.

However, the dynamics of the wings of the flies is much different to that of birds. Unlike other insects and birds, the fly also has a separate organ which controls its equilibrium called the haltere. Although the haltere was found by J.W.S. Pringle to have no direct gyroscopic effect on the fly, it did serve a purpose in the stabilization of flight. Dickinson found that the haltere had a great effect on the flight of the fly, not only on the stroke amplitude of the wing beating but also on the rotational equilibrium of the fly. In order to be able to complete full turns in a saccade, the fly had to create a counter-turn, and the haltere detected the Coriolis effects of the turn in order to do so. Both Vogel and Dickinson found specific parameters important in the analysis of the flight of the fly, and how these parameters could serve to be useful for other purposes, like mechanical systems and robotic flight.

Much of the research these scientists have done has served to fully understand the flight of the fly, which is needed in order to apply these dynamics to small-scale robotic flight. Using the known parameters involved in the flight dynamics of tethered flies – seen in experiments by Vogel and Dickinson, mathematical models are being explored to find true optimal values for wing size and shape in a robotic insect. Since there is still much to explore in the flight of insects, what is found now is just modeling of robotic flight. There is still much needed in order to compare such theoretical models with real experimental prototypes of free-flying robots. It is projects like these that can lead to future development in the modeling of biomimetic vehicles, or vehicles that imitate nature.

APPENDIX

Using the figure below as the simplification of the mechanism in Figure 7, dynamics could be used to find the torques created. A mass *m* supported on a light rod of length *l*, oscillates within plane *zoa*. The rod makes angle ϕ at any instant with the horizontal plane, and plane *zoa* is inclined at constant angle to axis *oy*. The whole object is subject to constant rotations with magnitude $\omega_1, \omega_2, \omega_3$ about the x, y, and z axes respectively ([5], p.381)

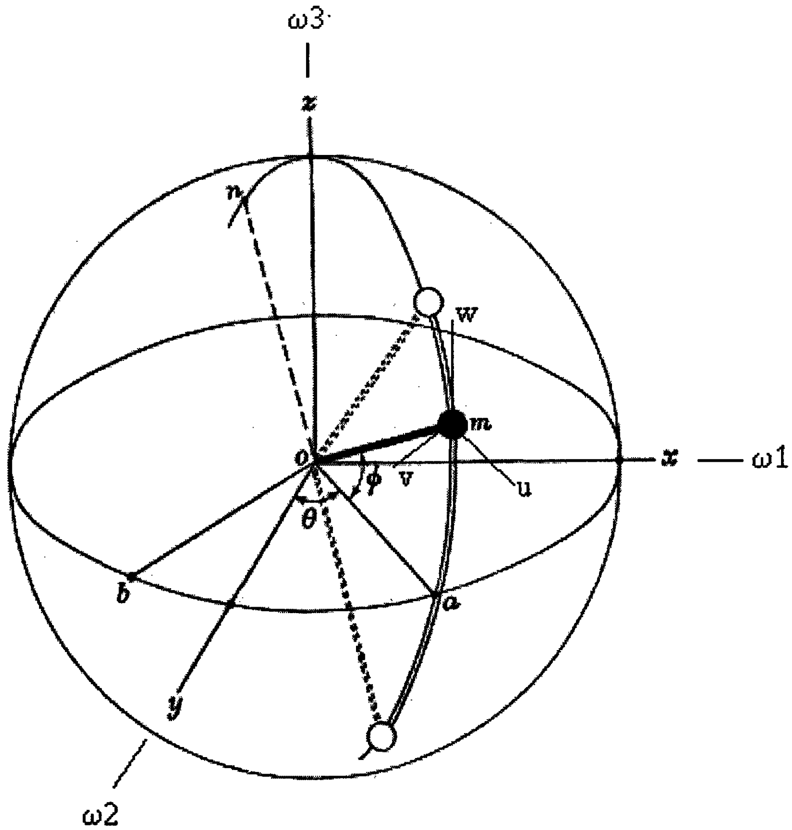

Figure 17 Simplification of Mechanism in Figure 7 taken from ([5], p.381)

If we let ω_a and ω_b be the components of rotation about the horizontal axes *oa* and *ob* respectively, we find that in terms of the constant rotations $\omega_1, \omega_2, \omega_3$, ω_a and ω_b are:

$$\omega_a = \omega_1 \sin\theta + \omega_2 \cos\theta \qquad (1)$$

$$\omega_b = -\omega_1 \cos\theta + \omega_2 \sin\theta \qquad (2)$$

The components *u, v* and *w* of the velocity of *m* in directions *oa, ob,* and *oz* are found using the expression for velocity $v = r \times \omega$. The following velocities were found:

$$u = l\sin\phi\omega_b - l\sin\phi\, d\phi/dt \qquad (3)$$
$$v = l\cos\phi\omega_3 - l\sin\phi\omega_a \qquad (4)$$
$$w = -l\cos\phi\omega_b + l\cos\phi\, d\phi/dt \qquad (5)$$

In order to find the acceleration of *m* in direction *ob*, the same expression can be applied to find the acceleration $a = v \times \omega$. Since the velocity has three components and the angular velocity does also, the acceleration in direction *ob* also has three components:

$$\begin{aligned}\dot{v} &= dv/dt + \omega_3 u - \omega_a w \\ &= -l\sin\phi\, d\phi/dt\, \omega_3 - l\cos\phi\, d\phi/dt\, \omega_a + l\sin\phi\omega_b\omega_3 - l\cos\phi\omega_b\omega_a - l\cos\phi\, d\phi/dt\, \omega_a \\ &= -2l\sin\phi\, d\phi/dt\, \omega_3 - 2l\cos\phi\, d\phi/dt\, \omega_a + l\omega_b(\omega_3\sin\phi - \omega_a\cos\phi).\end{aligned}$$

The angular velocity of *om* is large in comparison to any other velocities, so we can neglect the terms not containing $d\phi/dt$. Substituting equation (1) into $\dot{v}$ and neglecting other terms, we find the acceleration of *m* in direction *ob* to be:

$$\dot{v} = -2l\sin\phi d\phi/dt\omega_3 - 2l\cos\phi d\phi/dt\omega_1\sin\theta - 2l\cos\phi d\phi/dt\omega_2\cos\theta \qquad (6)$$

In reference to the origin, this represents a torque about the axis *on* at right angles to *om* in the plane of oscillation *zoa*. The magnitude of the torques are found to be

$$-2ml^2\omega_3 d\phi/dt\sin\phi \qquad (7)$$
$$-2ml^2\omega_2 d\phi/dt\cos\phi\cos\theta \qquad (8)$$
$$-2ml^2\omega_1 d\phi/dt\cos\phi\sin\theta \qquad (9)$$

which are in the yaw, pitch and roll axes respectively.

The accelerations in directions *oa* and *oz* can be found in the same way, but first they are combined into one acceleration perpendicular to *om* in the *zoa* plane. By applying the same expressions used above and neglecting all other terms, we find this acceleration to be $-ld^2\phi/dt^2$ with a resulting torque on the origin to be $-ml^2d^2\phi/dt^2$, which is the primary torque maintaining oscillations. If we consider the oscillation to be harmonic, then ϕ can be expressed as $\phi = \phi\sin 2\pi nt$, where *n* is the frequency. Finally, the maximum values for all torques affecting rotations can be expressed as follows: ([5], p.382)

Primary Torque	$4ml^2\pi^2n^2\phi_0$	(10)
Yaw	$2ml^2\pi n\phi_0^2\omega_3(approx.)$	(11)
Pitch	$4ml^2\pi n\phi_0\cos\theta\omega_2$	(12)
Roll	$4ml^2\pi n\phi_0\sin\theta\omega_1$	(13)

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