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# Emergent wingstroke in asynchronous insects and robots is governed by time-delayed strain rate feedback

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## 1 Introduction

The wing motion of many flying insects are generated by pairs of antagonistic power muscles that apply force to the elastic exoskeleton which transmits motion to rotational wing hinges. Insect flight muscle is typically characterized as either synchronous or asynchronous. Asynchronous muscle is a specialized type that experiences a delayed increase in tension in response to an increase in strain, a phenomenon known as delayed stretch-activation (dSA) [1]. When arranged antagonistically, asynchronous muscles self-oscillate, enabling high-frequency wingbeats in flies, bees, and other insects. While the physiology of dSA muscle in isolation has been studied extensively, the interaction of body elasticity, asynchronous muscle, and aerodynamic loading in a complete “spring-wing” system has not been examined.

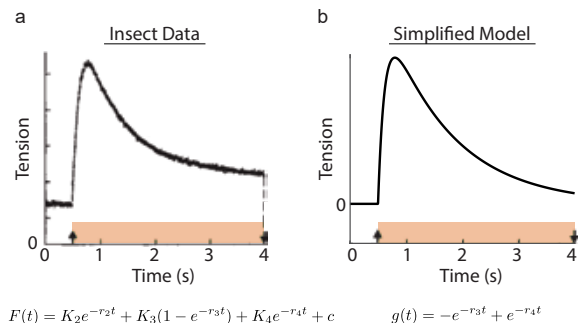
We present a newly adapted model of the dSA response which characterizes it as a 2nd-order filter on the strain rate of the muscle. This model enables us to study the emergence of oscillations in the dynamics of self-excited asynchronous systems via a model of the flapping dynamics including elastic energy storage. We then implement the feedback model on a recently-developed dynamically-scaled robophysical system [2] as a proof of concept and compare the experimental results to results from muscle physiology literature.

## 2 The spring-wing equations of motion

Despite the true complexity of the insect flight system, a simplified model based on a harmonic oscillator with nonlinear damping has proven useful to capture relevant wingstroke dynamics. We model the wingstroke of an asynchronous insect using a “spring-wing” equation

$$I\ddot{\theta} + k\theta + \Gamma\dot{\theta}|\dot{\theta}| = \tau_{async}(\theta, \dot{\theta}) \quad (1)$$

The rotational inertia,  $I$ , is the combination of wing inertia and added-mass inertia from the surrounding fluid. The spring constant  $k$  represents the elastic restoring torque present in insect exoskeletons [3, 4]. However, an important feature of  $k$  recently observed is that it contains both



**Figure 1:** a) Transient tension response from the giant waterbug *L. indicus* (Data and equation from [5]). The arrows and orange region indicate the duration of the stretch-and-hold test. b) A plot of the simplified model with parameters chosen to match the data in (a).

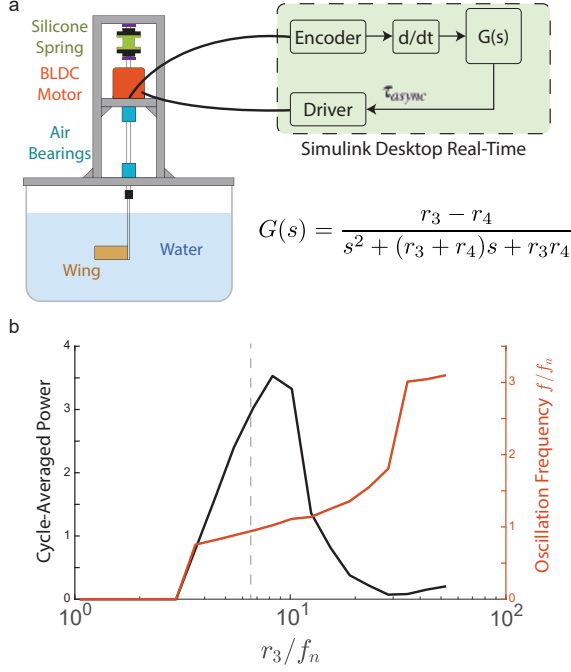
a real and imaginary component,  $k = k_0(1 + i\gamma)$ . The real component represents the linearized elasticity and the imaginary component represents a structural damping which is a frequency-independent force observed in some insects [4]. The aerodynamic torque is modeled by a time-averaged torque coefficient  $\Gamma$  and is proportional to the square of wing velocity. Lastly, the asynchronous torque is generated from state-dependent feedback to model the dSA behavior as discussed below. Recent experiments with a dynamically-scaled spring-wing system have highlighted the validity of this model to capture the resonant behavior of the insect wingstroke in the presence of an elastic thorax and wing inertia [2].

## 3 Delayed Stretch-Activation acts as a 2nd-Order Low-Pass Filter on Strain Rate

Delayed stretch-activation has been quantified by fitting the sum of three exponents to stretch-and-hold tests on activated muscle [5] :

$$F(t) = K_2e^{-r_2t} + K_3(1 - e^{-r_3t}) + K_4e^{-r_4t} + c \quad (2)$$

However, it has been observed that the rate parameter  $r_3$  (Units:  $s^{-1}$ ) is of the same magnitude of and linearly related to wingbeat frequency in asynchronous insects [5]. This



**Figure 2:** The robophysical implementation of the simplified dSA model. a) The system approximates the dynamics of a flapping wing in air and the closed-loop feedback acts as the asynchronous forcing. b) Changing  $r_3$  across two orders of magnitude shows no oscillation at low values; high-frequency, low-power oscillations at high values; and an optimum near  $r_3 \approx 10f_n$ . The gray dotted line at  $r_3 = 2\pi f_n$  indicates Pringle’s prediction of maximum power

suggests that it is the critical rate parameter that defines the time-delay necessary for self-excitation, whereas  $r_2$  is typically much higher the wingbeat frequency. Thus, we simplify the function in Eq. (2) by dropping the  $r_2$  and offset  $c$  term and setting  $K_3 = K_4 = 1$ , resulting in a two-parameter function (Fig. 1):

$$g(t) = -e^{-r_3 t} + e^{-r_4 t} \quad (3)$$

This equation describes the response of the muscle to a strain-rate impulse, which means that by taking its Laplace transform, we can derive the transfer function from strain rate to muscle force:

$$\mathcal{L}\{g(t)\}(s) = \frac{r_3 - r_4}{s^2 + (r_3 + r_4)s + r_3 r_4} = G(s) = \frac{F(s)}{\Theta(s)} \quad (4)$$

The transfer function in Eq. 4 has second-order dynamics and may be described as a second-order low-pass filter with cutoff frequency  $\omega_o = \sqrt{r_3 r_4}$ .

#### 4 Experimental Methods

We implemented dSA feedback in a dynamically-scaled robophysical model. The system, shown in Fig. 2a, consists of a custom silicone torsion spring, a BLDC motor (ODrive, D6374 150KV) and driver (ODrive v3.5), and a fixed-pitch

acrylic wing in a 115-gallon tank of water (30”x30”x30”, Chem-Tainer). Air bearings (New Way, #S301201) are used to minimize friction. Self-excitation is achieved via a Simulink Desktop Real-Time (Mathworks) model ( $t_s = 1ms$ ) that monitors wing angle from an encoder (US Digital, 4096 CPR), computes the angular velocity, applies the dSA filter dynamics in two antagonistic ”muscle” subsystems, and sends a signal to update the applied torque.

To investigate the effect of  $r_3$  on flapping power and frequency, we set  $r_4 = 0.9r_3$  and swept across 20 values of  $r_3$  from  $r_3 = f_n$  to  $r_3 \approx 50f_n$ , where  $f_n = \sqrt{k/I} = 2.4Hz$ . The output of dSA dynamics was multiplied by an additional constant gain term to overcome friction in the system.

#### 5 Results & Discussion

The results of the rate parameter sweep are shown in Fig 2b. We see that oscillations do not occur when  $r_3 < 3f_n$ , but that above that, the oscillation frequency increases with  $r_3$ . However, when  $r_3 > 15f_n$ , those oscillations are very low-power and are not useful for flight. Therefore, we see an intermediate regime,  $3f_n < r_3 < 15f_n$  where asynchronous self-excitation is useful for flight.

This basic experiment corroborates two major results from muscle physiology. First, the increase in frequency with  $r_3$  matches the observation of Molloy et al. [5] that wingbeat frequency increases with  $r_3$  across species. Second, we note that peak power occurs at roughly  $r_3 = 10f_n$ , which is quite close to  $r_3 = 2\pi f_n$  (gray dashed line in Fig. 2b), which was predicted by Pringle [6] to be the frequency of maximum power of asynchronous muscle in a flapping system. These results suggest that our simplified model of delayed-stretch activation shares some important features with insect muscle physiology and is therefore a valid model to continue study of asynchronous spring-wing systems. Now, armed with a simple linear feedback model, it is possible to apply the techniques of linear and nonlinear dynamics and controls to questions of efficiency, agility, and robustness in asynchronous insect flight.

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