Biologcally Inspired Design : Blurring the Boundary Between Sensors and Actuators

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ABSTRACT

All moving systems must acquire information from their surroundings and subsequently process, store, or transmit that information to effect control. That information processing orchestrates motor commands that activate a complex suite of muscles that, in turn, control the movement of actuators and skeletal elements. Animal motion, therefore, represents a highly coupled system with sensors, actuators and mechanical transmission systems interacting with external environmental forces to determine behavior and kinematics of movement. This is particularly evident in the control and dynamics of insect flight, the focus of this paper. We review three case studies of inertial sensing mechanisms in insect flight and suggest biologically inspired design concepts for new methods of inertial information encoding.

INTRODUCTION

In natural moving systems, and flying insects in particular, there is an abundance of sensory information flow, often exceeding our accounting skills. There is, for example, a rich literature showing that visual information flow is crucial for coordinating movement and computing flight paths (Collet and Land, 1975). There have recently been applications of insect visual guidance systems in the development of autonomous flight vehicles (Srinivasan, 2006).

However, visual information processing times can be quite large relative to the time-scales of movement control, particularly under low light conditions (Warzecha and Egelhaaf, 2000). As such, animals rely on multimodal information processing to coordinate movement over a broad range of time scales, using mechanosensory reflexes for responses to rapid perturbations and vision for slower processes. In flies, for example, the haltere is special organ derived from wings that serves a critical role in reflexive responses to body rotations (see Daniel et al., 2009 for a review).

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The wings flies, are the antecedents of halteres and all insect wings are imbued with a rich set of sensory structures (campaniform sensilla) that can detect wing strain and strain rate (Dickinson, 19xx) with high temporal and spatial resolution. As many as 500 strain sensors lie in the wings of flying insects and, despite some basic neural information about these structures, we know remarkably little about how such information could be used, if

at all, in flight control. Indeed, we are not aware of commercial applications that deploy strain sensors in the wings of flying systems.

Importantly, in all of these Multimodal information processing drives multiple actuators in flying insects. For example, both visual and mechanical sensory input controls the dynamics of a wide variety of steering muscles in flies (Sherman and Dickinson, xxx). In locusts and moths, vision and mechanical sensory input control wings and abdominal movements, both of which are involved in the control of flight paths. Thus insects are very much MIMO (multiple input, multiple output) systems.

This paper reviews design principles for flight control with an emphasis on how sensors and actuators are integrated in flying insects. We draw on biological design rules to suggest new ways to monitor and control very small rotational forces. We also suggest that the traditional separation of sensing from actuation may not be seen in biological systems – there are many examples of structures serving the dual rule sensing and actuation.

CASE STUDY 1: HALTERES ARE INERTIAL MEASUREMENT UNITS (IMUs)

Vibrating structure gyroscopes (VSGs) are commercially available inertial measurement sensors whose inspiration may have followed from our understanding of special sensory structures in flying insects. The principles underlying these sensors are similar those for rotating gyroscopes: a proof mass moving in an arc subject to rotation in an orthogonal plane experiences an acceleration that is proportional to the cross product of the two rotational velocities: **a -- 2u c Ca**. The torque associated with that acceleration is proportional to the mass and that acceleration and, for vibrating systems, have components at the driving frequency and twice that frequency.

The biological structure that operates as a VSG is the haltere, found in fruit flies, house flies, and their relatives, mosquitoes and crane flies. These are hind-wings that are reduced to club-shaped structures called (see below) that are oscillated in a plane perpendicular to the body axis. Body rotations in axes orthogonal to their stroke plane induce Coriolis forces that yield strains at the driving frequency and double that frequency. Each haltere contains at its base fields of sensory structures which have been shown to be directly connected via a single neural high-speed neural synapse to the muscles controlling flight (Fayyazuddin and Dickinson,1996). Recent theoretical work (Thompson et al., 2009) has shown that haltere movement could be encoded to produce an effective flight control system. They suggest that if the neural system measured mid-stroke motions with great precision, then one could construct a biologically inspired inertial rate sensor.

Despite overwhelming evidence that suggests halteres respond to these small Coriolis forces, there was until quite recently no strong evidence indicating haltere strain sensors (campaniform sensilla) could provide the appropriate temporal resolution and motion phase locking. We (Fox and Daniel, 2008) asked if indeed the single neurons associated with these strain sensors could provide that information to the neural system and the flight control centers. Using an extraordinarily large Dipteran species, the cranefly *Holorusia* (Figure 1), we were able to mechanically stimulate the haltere and record from the neurons receiving strain information.



Figure 1. The crane fly *Holurusia* sp. (left) and the base of its haltere (right). The halteres are the small knobbed structures behind the wings extending from the thorax. Each tiny dome at the haltere base (right image) is a single strain sensor (campaniform sensillum).

Neurophysiological data from intracellular recordings of halteres sensory neurons showed that they are able to provide the appropriate temporal and spatial strain resolution to serve a gyroscopic sensory function (Fox and Daniel, 2008; Daniel et al., 2009). They respond with very low latencies, having values hovering around 4 ms – far faster than the latencies associated with visual information processing (typically those are at least 50 ms). Additionally, when subject to a frequency sweep, haltere sensory neurons are able to encode oscillatory motions at frequencies well above those critical for Coriolis force measurement (typically around 40 Hz, Figure 2).



Figure 2. A sinusoidal motion stimulus sweep from 1 to 150 Hz was delivered to a haltere (upper blue trace) while we recorded the intracellular potential changes from a sensory neuron at the haltere base (middle trace). The firing rate of the neuron (lower trace) shows a linear response to the motion stimulus (lower trace).

Moreover, these sensors phase-lock with a level of precision rarely seen for any biological sensory structure. Phase locking, as measured by vector strength (Fox and Daniel, 2008), varies from 0 (no phase locking) to 1 (perfect phase locking). Barn owl auditory neurons, for example, are associated with exquisite sound localization and show a vector strength between 0.9 and 0.95 (Koppl, 1997). Haltere neurons, on the other hand, have a vector strength of about 0.98 – the highest recorded thus far. If phase-locked strain sensing is crucial for gyroscopic force measurement, then halteres are well equipped to provide that sensory function.

Finally, there remain several tantalizing issues associated with biological VSGs. First, they are able to respond to remarkably small motions. A few degrees of tilt is sufficient to cause depolarization of the sensory neuron. Additionally, the structures that contain the dendrites of these neurons are themselves highly asymmetric, suggesting that they are filtering motion in a single plane. Thus, while the haltere may experience complex three dimensional patterns of strain, it is possible that the campaniform sensilla to which the neuronal dendrites attach could provide a directional filter for information encoding.

CASE STUDY 2: INSECT ANTENNAE ARE IMUS

Like flies, moths and butterflies use both visual and mechanosensory inputs in flight control. While visual systems are crucial for flight control, until quite recently the role of mechanosensory input remained poorly explored. Frye (2001), for example, showed that a single neuron comprising the stretch receptor in the hind-wing of the hawkmoth *Manduca sexta* is crucial for flight control. It encodes at critical frequencies and its ablation compromises the visually-mediated flight response. However, it has not been shown that this cell is critical for balance control.

Sane *et al.* (2007) recently suggested that antennae of moths serve a gyroscopic function. Indeed, they satisfy all of the critical criteria we established above for sensory gyroscopes. Together, the evidence supporting this role is quite strong. For example, antennal removal significantly compromises flight; subsequent reattachment of antennae restores flight. Additionally, the base of the antenna is imbued with a rich set of mechanoreceptors that send neural projections to the motor control centers of the central nervous system .



Figure 3. The antennal apparatus of the moth from Sane et al., (2007)

Like the halteres of flies, the strain sensors at the base of antennae respond with very low latencies (about 2 ms to the motor control center of the brain: Sane et al., 2007). Also like halteres, they can encoded at the critical frequencies associated with Coriolis forces. In flying moths, for example, their wingbeat frequency is approximately 25 Hz suggesting that strain signals will occur at that frequency and at 50 Hz. Unlike haltere which show broad tuning (and linear encoding) over a very braod frequency range, the neural response of antennal mechanosensors suggest that they are tuned to the 50 Hz, the frequency most uniquely associated with Coriolis forces (Sane et al., 2007).

It remains unclear whether antennal mechanosensory systems measure inertial forces associated with rotation, forces associated with aerodynamic drag (Niehaus, 1981) or even gravitational forces for posture control (Kamikouchi et al., 2009). Indeed, it is entirely possible that they serve all three roles! Thus one biological inspiration for design of flight control sensors would be to develop ones that provide these three sensory functions simultaneously.

To explore this possibility, we have developed finite element models of antennal systems with the idea of exploring the three dimensional spatial and temporal patters of strain at the antennal base where the key sensory structures are located. By their very nature, any sensory inputs that reach a mechanosensory system will be influenced by the mechanical properties (stiffness, damping properties, and etc.) of the relevant sensory organ. Accordingly, the physical properties of mechanosensors can significantly influence their function. For example, finite element models of spider slit sensillae have demonstrated that slight differences in geometry can result in

profound differences in bending responses to mechanical stimuli, and thus profound differences in neural encoding are possible in these different sensory organs (Hößl et al., 2006). Additionally, the encoding properties of a population of sensors can be influenced by the spatial distribution of the sensors. For example, flies have campaniform sensillae located in patches at the bases of their halteres, and the trichobothria of ctenid spiders are arranged such that their lengths correspond to the size of the boundary layer (Barth 1993, 2004). Analogously, hawkmoths are equipped to detect strain patterns with fields of sensory hairs at the base of each antenna called Bohm's bristles, as well as a circumferential bundle of stretch receptors called Johnston's organ.

In our analysis, we used a combination of experimental and computational methods to model hawkmoth antennae. We experimentally measured the flexural stiffness and the damping properties of the antennae, both of which influence antennal kinematics and thus antennal mechanosensory function. Using these measurements, we constructed a finite element model (FEM) of the antenna and examined the three-dimensional patterns of strain at its base. In doing so, we have constructed the first computational model of a flexible biological gyroscope with material properties derived from experiments. This model has allowed us to examine the complex mechanical stimuli experienced by hawkmoth antennae (Figure 4).



Figure 4. Results of a finite element model of a vibrating antenna in which the node number refers to the circumferential position around the base. Strain is color coded with hotter colors represents tensile strains and cooler (blue) colors representing compressive strains. The middle panel corresponds to the predicted strain patters for a normal antenna. The left and right panels represent, respectively, those patterns for antennae 0.1 and 10 times as stiff as the normal antenna.

We used the finite element code MARC (MARC Analysis Research Corporation) to simulate static bending, free vibration, and turning experiments on a model of a male hawkmoth (*Manduca sexta*) antenna. The shape of the model was created by rotating a quartic polynomial about the long axis of the model, and the surface of the model was divided into 966 quadrilateral elements, creating a mesh. We used element types with bending resistance and nonzero thickness ("shell elements"). The model antenna was split evenly into 25 sections with varying Young's moduli in order to approximate the flexural stiffness (*EI*) values that we calculated from the static bending experiments. We then adjusted the *EI*, frequency, and damping properties (effective mass and matrix mass multiplier) of each section of the model antenna so that they were similar to the values we calculated from our experiments.

Preliminary results of our finite element model shows that there is a rotating pattern of strain at the base of the antennal with a strong dependence on the mechanical properties of that structure (Figure 4). Plotting one component of the strain tensor $\begin{pmatrix} & 22 \end{pmatrix}$ as a function of both position and time shows that even a single vibrating structure gyroscope could encode both Coriolis information and static forces (gravity or wind).

The pattern of rotation around the base could be used to develop biologically inspired coincidence detector that is modeled velocity sensitive visual neurons sensors. Here we suggest that a correlator model similar to that associated with visual motion sensitive neurons could be deployed in antennal sensors. A summing neuron with delay between two spatially separated patches of strain sensitive neurons the antennal base could provide gyroscopic information and have the static load removed by a common mode rejection method. To our knowledge this has not been applied to VSGs (Figure 5).



Figure 5. A biologically inspired coincidence detector for an IMU. Two spatially separated patches of strain sensors, one with a delay, could pass information to a summing unit, providing tuning to the Coriolis frequency.

CASE STUDY 3: WINGS MAY SERVE DUAL ROLES AS ACTUATORS AND IMUS

The two case studies above set the stage for understanding the more complex and enigmatic roles associated with wing strain sensors. All insect wings contain campaniform strain sensors (see Figure 6 below), some have vast arrays of these (moths) whereas others may be equipped with a few distributed along principal wing veins. In general we are unsure about how sensory information is used in these for any flying insect. We have, therefore, a reverse engineering problem: identify what sensory information is used by wings in flight control. Might wings possibly provide information about Coriolis forces? Might strain sensing be critical in the control of aerodynamic forces?

A bit of evolutionary history may inform us about the unique potential for this combined sensor and actuator. As mentioned above, halteres are derived from the hind wings of some ancestral dipteran insect. For natural selection to have favored a gyroscopic function for these structures, there must have been a wing imbued strain sensors that provided at least rudimentary Coriolis force information. Indeed, we can reasonably assert that all

wings experience a Coriolis force when an animal's body rotates in a plane orthogonal to that of the wing stroke plane. The question is whether that force is encoded and processed by the central nervous system in such a way that wings not only actuate flight, but also serve as an inertial measurement unit.

Many large insect wings deform quite dramatically during flight (Combes and Daniel, 2003). That deformation was shown to be dominated less by aerodynamic loading than by inertial and elastic processes for wings having the structural properties similar to insect cuticle (Daniel and Combes, 2002). Hence high wing beat frequencies drive inertial bending of wings which (a) may have an aerodynamic function and (b) may experience Coriolis forces with some complex pattern of strain.

The flexibility of wings has an important aerodynamic function. Using high-speed digital particle image velocimetry for isolated and robotically actuated wings we were able to show that compliant wings (those from recently emerged moths) generate significantly more lift-favorable momentum flux than stiffer wings of the same mass (Mountcastle and Daniel, 2009). The mechanisms that underlie this increased momentum flux are still unclear but likely relate to favorable passive wing pitching motions as well as elastic bending waves that propagate in the spanwise direction.

Taken together, the information we have above suggests that wing bending occurs, it is aerodynamically important and could be sensed and used flight control. The sensory capability of wings is only partially explored. In the hawk moth *Manduca sexta*, there is a rich set of campaniform strain sensors distributed over the surface of the wing (Figure 6). Approximately 250 sensors adorn the front wing with the majority located at its base. About another 150 sensors are distributed over the surface of the hind wing, again with the bulk of them located near the wing base.



Figure 6. Diagrammatic representation of the strain sensor distribution in the wings of Manduca sexta. The right diagram represents a simplified view of a campaniform sensillum

Drawing on our experience with halteres and antennae, we examined the encoding properties of these sensory structures, asking whether they can detect information at appropriately high frequencies and with appropriate precision. We used identical techniques as above (intracellular recording of the sensory axons, mechanical

stimulation of the wings) to characterize their response functions we found that indeed there are low latencies (approximately 1 ms) and tight phase locking of these sensors to stimulation (Figure 7)>



Figure 7. Upper trace represents a frequency sweep for a mechanical stimulus varying from 1 to 100 Hz. The middle trace shows the firing rate (raster plot in red below) for three trials of a campaniform sensory axon. The firing rate of wing campaniform strain sensors varies linearly with mechanical stimulation frequency.

Using band limited white noise stimulation we were also able to show that these cells encode with very high coherence at frequencies well in excess of those associated with the wing beat or Coriolis forces, rolling off near frquencies of 180 Hz (Figure 8). Taken together, these data suggest wings could serve as inertial measurement units as well as detectors of aerodynamic loading.



Figure 8.

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