

AFOSR Final Report – FA9550-07-1-0149

**HIERARCHICAL CONTROL OF MANEUVERABILITY IN WALKING AND
FLYING INSECTS- A NEUROBIOLOGICAL AND HARDWARE MODEL APPROACH**

05/14/2010

The primary goal of our project was to document common control schemes that allow animals to move seamlessly through very diverse and complex terrain. A common strategy among most animals relies upon interactions between circuitry in the brain that processes information from the numerous sensory systems on the animal's head and more local control circuitry that resides in the thoracic ganglia of arthropods or the spinal cords of vertebrates and that responds directly to sensory structures located upon specific appendages (Orlovsky et al., 1999; Ritzmann, 2010; Ritzmann and Büschges, 2007). The head sensors provide a large variety of information which is then processed in the brain to ultimately form descending commands. When these commands reach local control regions, they can re-direct the movements of legs or wings. The question posed by our original proposal was: **How do these descending commands exert their influence on local control systems?** Since the local reflexes act in locomotory patterns, while the head sensors are typically unpatterned, the manner in which interactions occur is not always obvious. In our proposal, we suggested that a common control scheme could exist in various animals by which descending commands influenced movement, not by micromanaging changes, but rather by altering a few critical reflexes then allowing the resulting changes in movement to generate a cascade of additional reflex changes. Ultimately these processes could lead to a new stable set of joint movements associated with a completely different movement such as turning or climbing. Under this strategy, the higher centers work with local systems to influence re-directed movements through critical but subtle changes rather than dictating radically new actions. To examine this hypothesis, we proposed to look directly at the changes that occur in cockroaches when they transition between walking and turning and to generate a hardware model of the cockroach leg that would allow us to test our interpretation of neurobiological data under realistic physical conditions. Because the proposed leg is controlled by realistic reflex circuits, it would also allow us to formulate new hypotheses that could be further tested with biological experiments. Finally, in order to examine how general these control schemes are, we proposed to perform parallel studies on a flight system, focusing upon proprioceptive influences that act on moth flight.

Overview of Results:

Global Analysis of Three-dimensional Joint Kinematics

In the initial years, we described the changes in leg movements associated with turning on an oiled plate tether. This tether allowed us to hold the cockroach's body relatively still while normal walking leg movements are evoked. As a result, we could examine the leg movements in great detail and showed that tactile stimulation of a single antenna evoked turning movements (Mu and Ritzmann, 2005). The middle and front legs on the outside of the turn rotated laterally, but continued to extend during stance. However, the legs on the inside of the turn now extended during swing, then set down and pulled medially during stance. On a normal substrate these inside legs would have pulled the animal laterally executing a turn. These changes clearly were initiated by descending commands, since they started with antennal stimulation.

In the last year, we examined the 3D joint kinematics of turning and walking movements in more detail. This study relied on the development of a custom 3D motion analysis system that was developed by Dr. John Bender (a postdoctoral researcher supported on this grant). This study demonstrated that in both straight walking and turning movements, the pattern of joint movements is not consistent among the various legs. For example, swing movements in the middle and hind legs are initiated by activation of the trochanter-femur (TrF) joint. This small joint is often ignored and in stick insects it is actually fused to the

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14. ABSTRACT We described turning movements in the cockroach middle legs and examined how they change after removal of descending cues. We also used our 3D joint analysis system to document individual joint movements of all leg joints during insect walking at various speeds and turning, demonstrating the unique nature of movement for each leg pair. We then completed a project examining brain activity in a tethered cockroach during walking. Remarkably, brain neurons were recorded that altered their firing rate in tandem with and in some cases in anticipation of changes in step rate. Stimulating in the same region led to changes in step rate. Our hardware cockroach leg model showed for the first time that descending commands can initiate a cascade of reflexes, which change forward stepping to turning movements in the leg. The cockroach leg model was re-designed based upon our kinematic studies, making the joint movements more accurate and updating the underlying control system. A behavioral study of the role of peripheral feedback on moth flight showed that removal of input from all four tegulae were required to degrade flight capabilities. Studies of tethered moth					
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femur. However, in cockroaches, where the legs attach under the thorax rather than on the lateral surface, the TrF joint is critical for rotating the leg upward. In contrast, the front leg initiates swing by rotating the joint between the thorax and the coxa (first leg segment). The coxa-thorax joint swings dramatically in the front leg, but hardly moves at all in the middle and hind legs. As a result of these observations, we now know that we have to be careful to analyze each pair of legs separately as we examine alterations resulting from descending commands.

We are currently extending these observations to obtain more complete 3D joint kinematics of all legs during turning movements. We are also examining the motor control of front legs. As suggested by the swing movement analysis described above, the joint actions of each pair of legs are distinct from the other two. (Ritzmann et al., 2004). Thus, a complete understanding of each leg joint on all legs is necessary to completely understand motor transition.

Alteration of Leg Movements by Descending Commands

Ultimately, we would like to understand how descending commands affect changes in walking behavior. In the initial years of this grant, we demonstrated that local reflexes could shift sign as a result of descending activity. For example, relaxing a leg stretch receptor that monitors femur-tibia joint angle normally inhibits activity in the principle extensor motor neuron of the coxa-trochanter joint. However, after eliminating all descending activity by cutting both neck connectives, relaxing this same sensor now excites that motor neuron (Mu and Ritzmann, 2008). Similar studies on stick insect in the Büschges laboratory demonstrated that local reflexes also switch sign when that insect walks backward (Akay et al., 2007).

In order to further identify which brain regions generate descending commands that alter leg movement, we completed two studies last year examining the role of the central complex (CC) of the cockroach brain in altering stepping movements. The CC is a prominent group of midline neuropils found in virtually all insects. It has been suggested that it may play a role in supervising locomotion (Strausfeld, 1999). Large lesions in this region have serious consequences on the cockroach's ability to negotiate a U-shaped track (Ridgel et al., 2007). Lesioned insects tend to bump into the walls or turn in the wrong direction. Moreover, genetic lesions in *Drosophila* also impact walking behaviors (Strauss, 2002). Neurons within the various CC neuropils respond to a range of natural stimuli including polarized light (Heinze et al., 2009; Heinze and Homberg, 2007), mechanical antennal stimulation and ambient light levels (Ritzmann et al., 2008) all of which influence movement.

We extended our examination of brain lesions, looking at effects of more discrete electrolytic lesions on a range of behaviors including turning, tunneling and climbing. This project was begun under our AFOSR grant and completed under a more recent NSF grant. The student who conducted these studies (Cynthia Harley) completed her thesis this year and submitted a paper on this study that is currently in press at the *Journal of Experimental Biology* (Harley and Ritzmann, 2010). The data has also been presented at various conferences. Her study showed that the effect of lesions in different regions of the CC or even in different regions of individual CC neuropils varied from place to place as well as from behavior to behavior. For example, lesions in the lateral region of the fan-shaped body (FB) had profound effects on turning, but FB lesions near the midline had little effect on turning, even though they altered climbing behaviors.

We also completed another project in which we recorded from the CC neuropils with multi-channel recording tetrodes as the tethered cockroach walked on a lightly oiled plate. Two laboratory personnel were involved in this project. The recordings were performed by Alan Pollack, who was funded under our NSF grant, while the analysis of the data was led by Dr. John Bender, who was funded by our AFOSR grant. This division accurately reflects the symbiotic relationship between our NSF grant that seeks to understand how CC units respond to complex sensory stimuli and our AFOSR grant that seeks to understand how these brain circuits influence local leg circuits and motor activity.

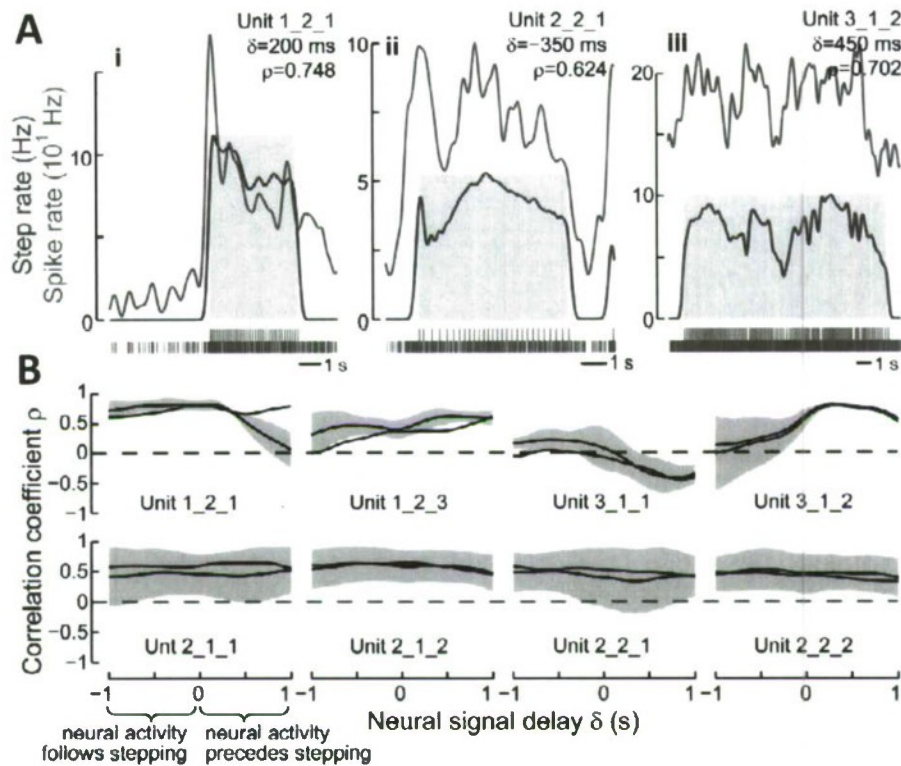


Figure 1. Instantaneous stepping rate and neural firing rate were correlated in some units. (A) The spike and step rasters were convolved with a Gaussian kernel (S.D.=150 ms) to calculate instantaneous frequencies. The firing rate (blue) was shifted to the right by δ and cross-correlated with the step rate (red), leading to the listed maximum value of ρ for each walking bout (gray boxes). Some walking bouts were elicited by a tap to the animal's antenna, which evoked an additional response in some units (i,ii). Panel iii shows steps from an entire 16-s video in which the cockroach was walking before the recording started and continued after the camera's memory was filled (same bout as in Movie S2). (B) The black area shows the mean and S.D. envelope for ρ at each value of δ . These 8 units were the only ones with a peak average $|\rho|$ of at least 0.4. The top row shows units with a peak $|\rho|$ at $\delta > 0$, meaning that changes in spike rate usually preceded changes in step rate. The units in the bottom row had flat curves with peaks at $\delta < 0$. The red lines show the mean calculated after removing the first 1 s of each walking bout to eliminate possible artifacts of antennal stimulation.

The analysis that Dr. Bender applied to these data revealed some remarkable properties of brain activity as recorded in the CC. Because the recordings were made in tethered animals, we were able to monitor stepping movements with high-speed video cameras. Thus, he was able to generate graphs that represented stepping frequency and compare those to inter-spike interval (ISI) curves for individual CC units (Fig. 1A). Even a visual examination of these curves reveals remarkable parallels. As the cockroach changes stepping frequency, the CC units change ISI frequency in tandem. The correlation coefficients for these two functions range from 0.6 to 0.8, remarkably high for such a comparison. However, for four of the units that we recorded, the correlation improved if the ISI curve was advanced relative to the stepping frequency (Fig. 1B). This finding suggests that at least some CC neurons are actually *predicting* changes in stepping frequency; a finding that is consistent with the CC being the source of descending commands that alter stepping movements. Moreover, stimulation through the same electrodes actually caused the animal to increase stepping frequency with a delay that was similar to the delay in the stepping and spike frequency correlation. A paper on this study has been published online in *Current Biology* and the hardcopy publication will occur later this month (Bender et al., 2010). Moreover, we were invited to prepare a video abstract of this paper and it is currently featured at Currently Biology's home web site

<http://www.cell.com/current-biology/home> . This work represents an area that we will continue to examine in future studies under our new AFOSR grant.

Development of SCASM Hardware Models of Insect Leg Control

Neurobiological and behavioral data indicate that control of insect leg movements relies upon central pattern generators for each leg joint coupled through a series of inter-joint sensory reflexes (Büschges and Gruhn, 2008; Büschges et al., 2008; Ritzmann and Büschges, 2007). The pattern of this control system was captured in a circuit and demonstrated in a software simulation of a stick insect leg (Ekeberg et al., 2004). One of the goals of our AFOSR project was to implement this circuit in control of a hardware model that copies the behaviors of an insect leg moving on an oiled plate tether. Such a robotic leg would then allow us to examine all of the sensory and motor activity in the reflex based controller as we command it to move through various behaviors while it is constrained by realistic physical properties. Such complete analysis of sensors and control would never be possible in an animal.

Our first model leg, in the first year of this project, was based upon the stick insect, because the initial simulation was based upon that insect. The controller for this leg is reflex based and is consistent with the stick insect dynamic simulation of Ekeberg, Blümel and Büschges (Ekeberg et al., 2004). We refer to this control system as “Sensory-Coupled Action Switching Modules” (SCASM). In the second year, we developed a model of a cockroach middle leg (Fig. 3) and adapted SCASM for its control. The differences in leg anatomy between these two insects required some modifications of the control system, because the roles of the body/coxa and coxa/trochanter joints are reversed.

In the last year modeling work the local control methods of the stick insect described by Ekeberg et al. (2004) were further standardized in the SCASM framework, and tools for the use of this concept were developed and demonstrated. The generality of SCASM as a computationally simple control concept was also addressed. For example, an odor tracking SCASM controller was developed, tested and found to be effective (Taylor et al. 2009).

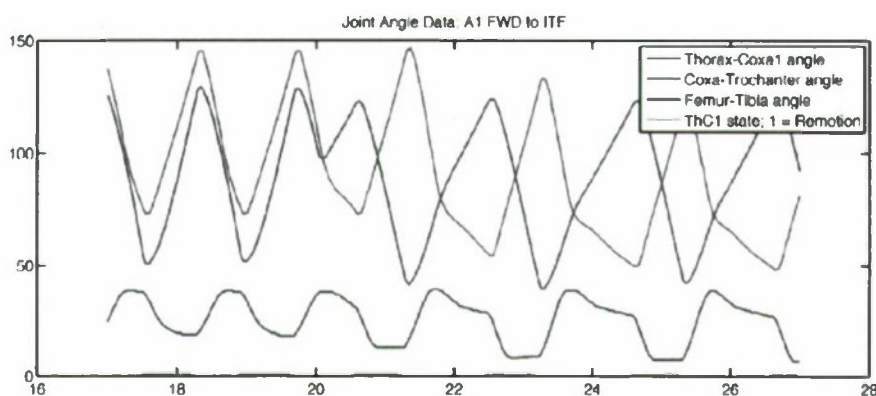


Figure 2. Joint angle (degrees) vs. time (seconds) for a commanded transition at 20 seconds from forward stepping to inside turning. Note the expected change in phase between the femur-tibia and coxa-trochanter angles. There is transient behavior at the switching point, but the appropriate steady state behavior is observed within half of a cycle.

Last year we also discovered pathways in the SCASM network that are consistent with animal studies (Mu and Ritzmann, 2005) that change normal walking movements to turning movements and tested them with the model cockroach leg (Rutter et al., 2008). The major change is that during walking, leg load encourages a change from femur-tibia (FTi) flexion to extension while leg unloading stimulates FTi flexion. In contrast, during inside leg turning, this pattern reverses with unloading generating extension and load stimulating flexion. In addition to these sign changes in the pathways, some

connection weights must also be modified and in this year's work, those weights were optimized for walking and turning. Thus, a descending command can modify the sign of two pathways and change some connection weights and then, through a cascade of reflexes, change the network from walking to turning. The question remained; can the model leg smoothly and stably transition between the two behaviors?

This year's modeling work began to investigate how the interaction of descending commands with local sensorimotor control networks result in the smooth behavioral changes seen in agile legged locomotion. The first demonstration of descending control modifying local behavior was the modification of leg stepping speed. This was achieved by modifying tonic muscle activation signals, effectively gated by the joint action switching modules. Preliminary work was also done to cause the middle leg model to successfully transition between forward walking and "inside turning", wherein the leg performs movements appropriate for the animal to turn toward that leg's side of the body. When the SCASM network parameters were suddenly switched from those appropriate for forward walking to those for inside turning, the leg smoothly transitioned from one behavior to the other as seen in Figure 2 (Rutter et al., 2009). This transition also is successful and repeatable in reverse. This work was completed by Brandon Rutter (Ph.D. May 2010) for his dissertation research in Mechanical Engineering.

In keeping with the goals of this project, we are also developing a more accurate model of a cockroach leg to provide a better tool for testing neurobiological hypotheses regarding mechanisms underlying locomotion in the cockroach. The robotic leg is a 5 degrees of freedom (DOF) model of the left mesothoracic (middle) leg, including a 2 DOF Thorax-Coxa joint, and single DOF Coxa-Trochanter, Trochanter-Femur and Femur-Tibia joints (Fig. 3). This leg includes three major improvements. It has smaller inertia and greater range of motion and the trochanter-femur joint (a joint that has been previously, and incorrectly, assumed to be fixed during walking) has been added. This will allow the leg to more accurately model patterns of joint movement observed during forward walking. The leg was developed by students in our Biorobotics Team Research course. A SCASM network is being developed for this more complex and more life-like model (Fig. 3) by Nicole Doorly, an M.S. student in Mechanical Engineering. With the model operating with the mechanical addition of the Trochanter-Femur joint and the modified SCASM control, future work will focus on (1) analytical comparison with the earlier model and with the cockroach itself to determine whether the improvements provide for a better neuromechanical model, and (2) experimentation with parameters of the SCASM control to test biological hypotheses.

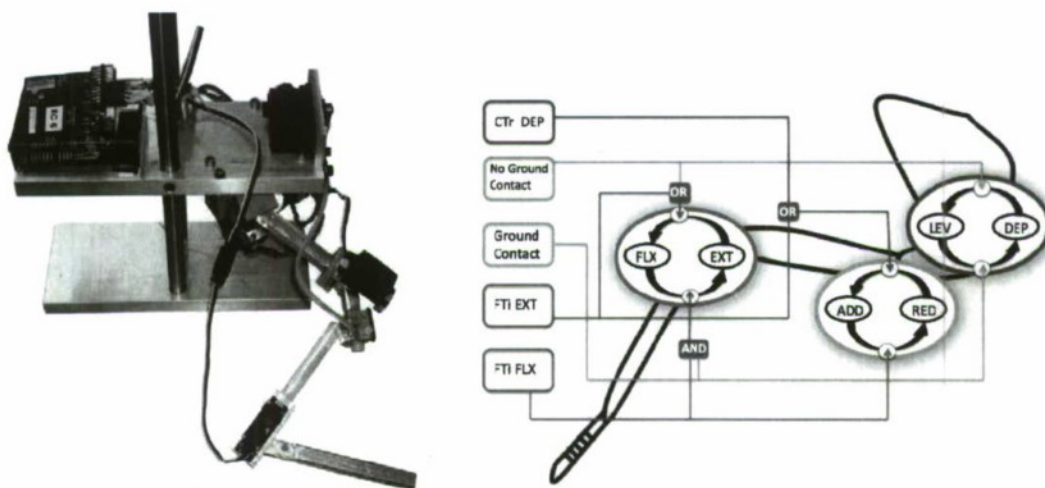


Figure 3. Refined model of cockroach leg with coxa-trochanter joint, which has been found to be normally used in walking (left). A SCASM network for control of the three outboard joints in the leg, which are in used during normal walking (right).

Examine Local Control of Moth Flight:

The tegulae are moveable pieces of the insect's body wall positioned where the leading edge of each wing meets the thorax. They each possess an array of touch sensors that provide feedback information on their wing's position and movement to local control circuits in the thorax. This year's progress has revealed that removal of the feedback information provided by the tegulae significantly affects the flight capabilities of our moths, but only upon complete removal of all four tegulae. However, this loss of function appears to be context-dependent. Many of the same individuals that showed loss of flight capabilities showed at least partial recovery when challenged to track a plume of female pheromone in flight. Analyses of tethered flight experiments performed in parallel have now shown that loss of tegular feedback causes consistent changes in the activation patterns of the flight muscles. These changes in the motor patterns could underlie the loss of flight performance we observe in freely flying moths.

We have focused our efforts on three tasks:

- 1) To complete the analyses of a large behavioral study to determine the effect of removing tegulae input on freely flying moths.
- 2) Complete necessary additional experiments revealed during preparation of the manuscript describing the behavioral study.
- 3) Completion of preliminary analyses of the effects of tegulae removal on the activation patterns of flight muscles during tethered flight.

Removal of local feedback information from the tegula has a significant effect on flight and flight control in our moth. This year's large scale flight experiments revealed that only moths with all of their tegulae removed showed statistically significant differences in their performance compared to intact controls. In our experiments we compared the performance of our experimental moths in clean still air to their flight response to wind-borne pheromone. In still air, only 5% of the intact controls did not take flight, while 43% of the moths with **all tegulae removed** did not fly. In contrast, when challenged to fly upwind in female sex attractant pheromone all of the intact controls took flight and only 19% of moths with no tegulae did not take flight. Thus, descending commands associated with pheromone-activated flight in wind "rescued" the flight capabilities of 21% of the moths with no tegulae (Fig. 2). Analyses of individual moth flight trajectories in the different experimental conditions is ongoing. In summary, most moths were able to initiate and take flight in the absence of normal feedback from their tegulae, even though the quality of that flight may be significantly affected. It is our working hypothesis that the influence of descending commands from the brain on local control circuits may be critical in enabling functional flight in the absence of tegulae.

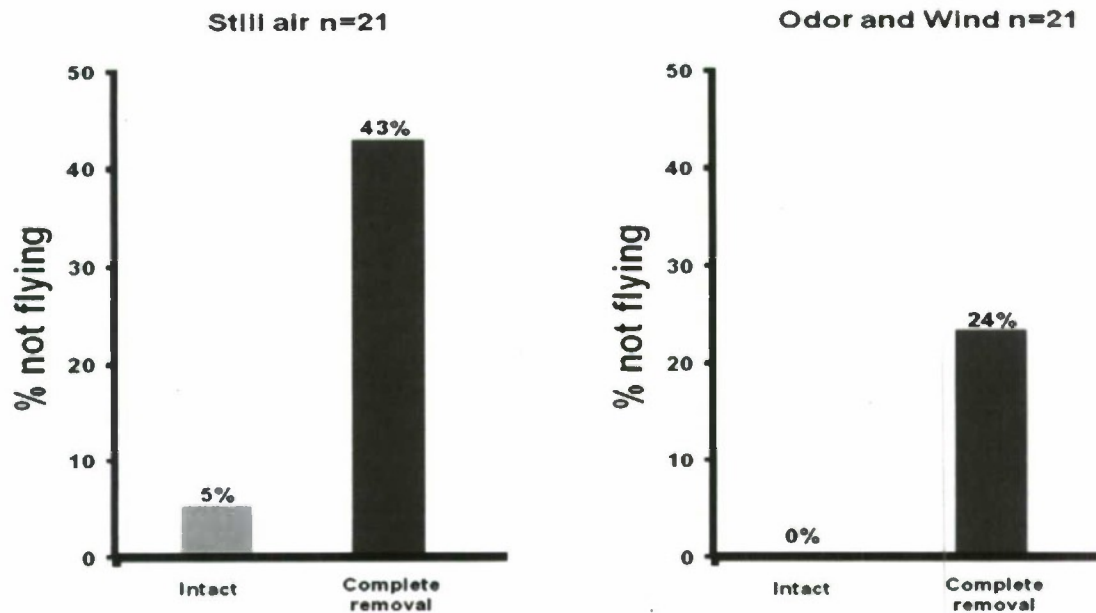


Figure 2. Percent of intact virgin *M. sexta* males, and those with their tegulae removed, taking flight in still air and responding to a pheromone plume in wind.

We initiated tethered flight studies aimed at determining the changes in flight muscle activation patterns that must underlie the loss of performance observed in freely flying moths with their tegulae removed. These studies have shown that in the intact flight system the left and right wing depressor and elevator muscle pairs are activated at the same time, and the elevators are activated approximately 180° later than the depressors (Fig. 3A). Once the tegulae are surgically removed the left and right elevators no longer fire at the same time, and both have variable activation times with respect to the depressors (Fig. 3A). In addition, loss of tegulae input causes the elevator muscles to dramatically increase the number of wing beat cycles in which they are not activated (Fig. 3A & B). Loss of tegulae input also causes a significant decrease in wing beat frequency and changes in the relative activation between the wing elevator and depressor muscles.

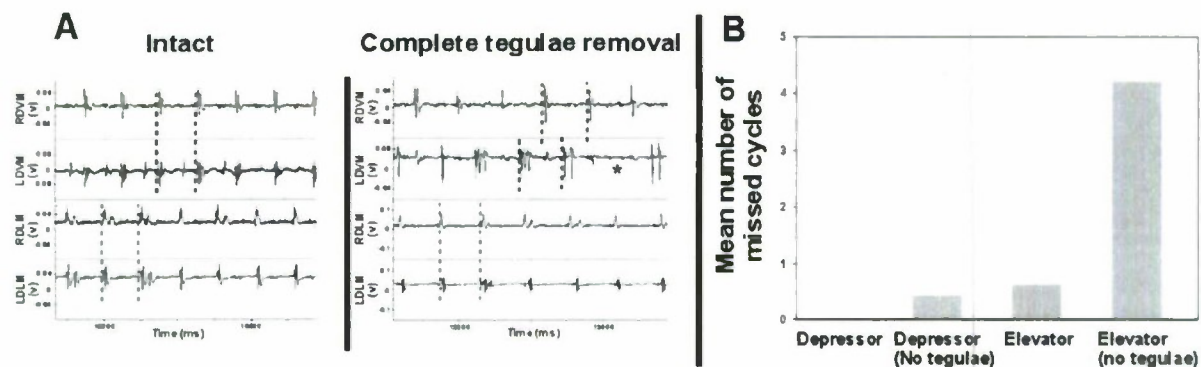


Figure 3. Effects of tegulae removal on flight muscle motor patterns. A, recordings of flight muscle activation patterns from an *M. sexta* male before (Intact) and after (Complete tegulae removal) the surgical removal of all tegulae. Note the general similarity in the wing depressor muscles (DLM) before and after lesion (blue dashed lines), and the asynchronous activity between left and right elevators (DVM) (red dashed lines) and missing spikes in left DVM (red asterisk) after removal of the tegulae; B, mean missed activation cycles of depressor and elevator before and after complete loss of tegulae.

Our completion of analyses of the free flight behavioral study will provide us with a characterization of the effects of removing the tegulae on goal oriented tasks. The fact that most moths with their tegulae removed continue to take flight suggests that inputs to the head sensors enable the higher control centers in the brain to compensate partially for the loss of information on the wing movements from the tegulae.

Our continuing research will be aimed at recording motor patterns from freely flying moths with and without their tegulae to see if we observe motor patterns with disruptions similar to those observed in tethered flying moths. We also plan to test the idea that input from head sensors can help overcome the loss of information the local feedback sensors (i.e., the tegulae).

Summary

We have completed the goals of our proposal and are in an excellent position to continue our examination of interactions between descending and local control of insect leg movements both biologically and in the context of our hardware models. By contrasting these two sets of experiments, we can make unprecedented progress in understanding hierarchical control. With the addition of data on flight, we can eventually extend our analysis to biological and simulated flight control. In this way, we hope to identify generalized principles of control for a range of natural behaviors that can be implemented in artificial motor control networks. We will continue these studies in our new AFOSR grant that started on March 1, 2010.

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