Centralization of Muscular Control in *Blaberus discoidalis* as a Variable of Terrain Roughness

A Thesis

Presented To

The Academic Faculty

by

Philip Aden

In Partial Fulfillment

Of the Requirements for the Degree in

Biomedical Engineering in the

College of Engineering, Georgia Institute of Technology

Georgia Institute of Technology

February 2019

Centralization of Muscular Control in *Blaberus discoidalis* as a Variable of Terrain Roughness

Approved by:

Dr. Simon Sponberg, Advisor
College of Sciences
Georgia Institute of Technology

Dr. Daniel Goldman
College of Sciences
Georgia Institute of Technology

Date Approved: 22 February 2019

Acknowledgements

I wish to thank Prof. Simon Sponberg for his sponsorship and guidance in conducting this project, as well as Dr. Izaak Neveln for his support and technical expertise in assisting with it. This work would not have been possible without their dedication and time.

Table of Contents

List of Figures

Summary

The purpose of this study was to illustrate how the neuromuscular architecture of *Blaberus discoidalis* cockroaches changes in response to variations in their environment. The species *Blaberus discoidalis* shares the single motor neuron physiology of *Periplaneta americana,* widely used in past research in the field, and thus the extensions of its leg muscles were easy to record via electromyography (EMG). By tracking the behavior of the insect's legs, inferences can be made about how the animal's body and brain compensate for perturbations to its running gait. Understanding this control architecture could lead to more robust locomotion systems in robotic design. In this experiment, the insects ran over terrain of varying roughness, quantified by the standard deviation (cm) of a gaussian distribution of pillars. While they ran, EMG electrodes recorded muscle activation in the rear and mid left legs, and a high-speed camera recorded a video in the top-down plane. Using mutual information as a metric, a K nearest neighbor algorithm derived centralization based on the number and timing of the action potentials in each stride. It was hypothesized that the level of centralization exhibited by the insects will increase as the roughness of the terrain they run over increases. The results showed a near linear increase in centralization as terrain roughness increased, supporting the hypothesis. This suggests that greater perturbations in gait causes muscle control architecture to become more centrally mediated. Future research should be conducted to confirm these results and explore how this response interacts with other stabilizing behaviors.

Introduction

Cockroaches are a widely used model for the study of insect running mechanics. This is primarily due to their extremely robust alternating tripod gait and simple motor control architecture (3). The insects are able to maintain balance and compensate for perturbations to their legs even over extremely rough terrain and at high speed (6, 8). This dynamic stability is of great interest to roboticists, who have sought to understand these insects' muscle control architecture and apply it to the creation of more robust walking robots. This research could also lead to the development of mathematical behavioral models that could be applied to other biological running systems.

Work with cockroach models has primarily involved the species *Periplaneta americana* and *Blaberus disoidalis*. These insects are commonly used because their muscular activity and innervation is easy captured via electromyography (6). Such straightforward command structures allow scientists to selectively activate the cockroach's extensor muscles and induce an alternating tripod gate without any contact with the ground or feedback from the proprioceptors on the insect's legs (5). This has led to the general view that the coordination of the organism's limbs depends only minimally on sensory feedback about its environment or their relative position, and instead operates almost entirely on immutable, top down commands from the roach's central nervous system. Researchers thus infer that the robustness of the insects' running stemmed primarily from mechanical interaction between its legs (6).

However, further study about the behavior and relation of the insect's joints suggests that neuronal communication between different limbs may still play a role in their relative positioning and response to extreme perturbations (4, 5, 7). During pharmacologically induced

walking, patterns have been observed between the muscle behavior and joint position of multiple legs and the activation of inter-neurons in the roach's body (4). This suggests interplay between central nervous system (CNS) processing and the kinematic behavior of the insect's body. Multiple studies have been conducted to ascertain the degree to which perturbed running conditions influence muscle activation (1 ,2, 4, 5, 10). These experiments look at the control signals output by the roach's central nervous system, and how it changed as the cockroaches were subjected to different environmental stimulus.

All of these studies deal with the muscular control architecture of the insects. This architecture represents how the animal processes sensory information taken from its environment and uses it to produce motor responses. These responses are mediated though neurological coupling both between individual limbs through the peripheral nervous system, and between the limbs and the central nervous system. The way in which these motor control signals are processed is theorized to increase the robustness of the cockroach's running gait (12, 13, 14). The architecture itself can be illustrated by measuring the information present in the signals being sent by the insect's motor neurons, and whether the central nervous system or the peripheral nervous system is responsible for maintaining balance through the run (12, 13). By better understanding the distribution of this control information, scientists can better understand how these insects are able to retain such a high degree of stability even over rough terrain.

Despite several papers exploring information distribution, its relationship to changes in the outside environment remains significantly underdefined. While there have been some studies that point to a change in muscle behavior over very extreme perturbations (10), the concept is still very much up for debate. This project seeks to better delineate how centralization can be used as a measurement to model running behavior over rough terrain. Building off the

experimental model developed by *Sponberg et al, 2008*, pillars of random heights chosen from a normal distribution were chosen to represent changing terrain roughness. The standard deviation was varied to create a different degree of roughness between each distribution of pillars. An escape response was induced in the insects causing them to run over the terrain at relatively high speed, making it probable that they would run continuously over the entire terrain base. The motor neuron action potentials and kinematics of the insects' legs are recorded as they run over the terrain bases via high speed camera and electromyography (EMG). Through comparison of the mutual information values calculated with regards to the action potentials in the motor input signal, information distribution can be mapped as a function of perturbation intensity (12). Based on any emergent patterns, inferences about how these insects mesh their mechanical stability with top down motor control can be made.

Methods and Materials

In this experiment, the roughness of the terrain the cockroaches run over was modified to assess how their motor control changed as their environment changed. Perturbations were induced through variation in the terrain roughness as opposed to forced lateral movement of the roach's legs (7). This procedure allowed for more perturbed strides to be recorded per run, a more efficient method than the lateral motion utilized in *Revzen et al. 2013*. The terrain pieces were created in SolidWorks using a Gaussian distribution of heights across a grid pattern, mimicking the terrain used in *Sponberg et al. 2008*. The distribution was constructed of PVA plastic as opposed to wood to reduce manufacturing time and increase durability. These heights will have a set standard deviation that will be varied between terrain pieces to elicit varying degrees of roughness. Once a 3D model has been created, it will be materialized using a U-Print 3D printer. The piece will then be secured on the bottom of a tank that confines the insects.

Figure 1. The three terrain bases after printing and assembly utilized in this experiment. From left to right, the standard deviations of their gaussian distributions are 0.5cm, 0.2cm, and 0.1cm respectively.

Data was collected by inserting two pairs of EMG electrodes into the coxa of the roach's mid and hind left legs (10, 12, 13). These wires mapped the voltage difference across the

10

muscles as the roach runs along the test chamber floor. These legs were selected because they allowed for one signal to be recorded form each of tripod of legs. The front two legs were not implanted with electrodes due to their small size, though kinematics were still collected from them. Adhesive glue was used to attach the 0.005in wires to the roach's exoskeleton, and then to the ventral midline of the roach's abdomen, so that they protruded directly behind the animal (10, 12). An escape response was elicited from the insects by applying pressure to their dorsal abdomen, causing them to run forward over the terrain base. As the roach ran, a Photron high speed camera positioned directly above the tank recorded video at 800fps for the two-dimensional plane.
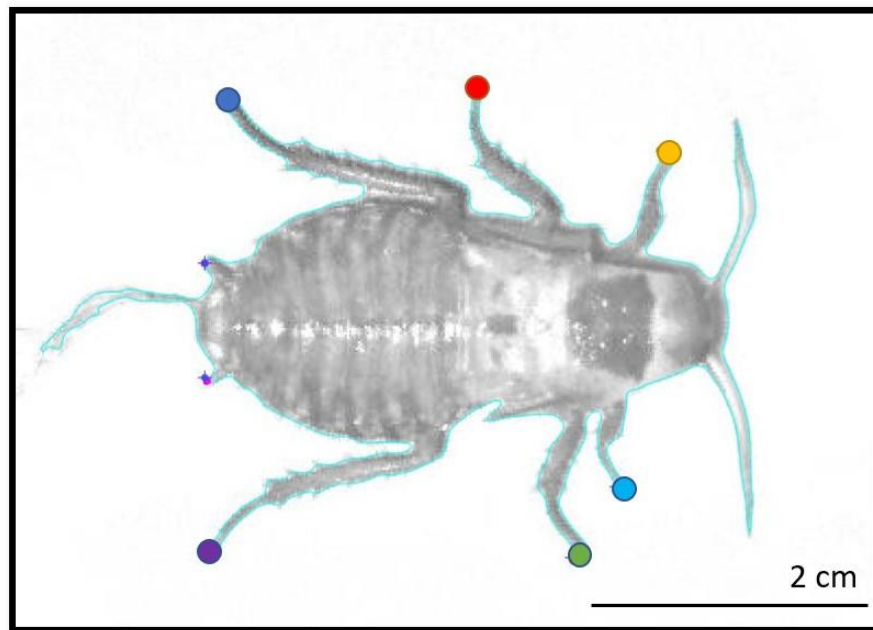

Figure 2. An example frame from the high speed recording of a cockroach running over flat terrain. Using a MATALB program, the background is extracted, and the cockroach is centered in each frame, allowing the end points of each leg to be tracked throughout the run. The legs are marked with positional dots as shown, and their extension is measured relative to the center of the insect.

These videos were processed using a series of MATLAB functions to isolate the roach and track the relative position of each individual leg (12). As shown in figure 2, the body of the roach was centered and isolated in each frame, and the positions of the ends of all six legs were mapped. This process was repeated for each successive frame of the video to measure the

extension of the legs relative to the center of the roach, as well as the timing of each stride the

roach performed. The global phase of the roach was then determined by analyzing the positions

of all six legs throughout their run. Every time all six legs completed one full step, beginning and

returning to the same relative place, one global phase was delineated. Within this global phase,

each individual leg is subject to its own local phase, or stride. A stride was defined as one leg

beginning in one position, going through a complete step, and returning to its original relative

position. Each roach was recorded running over multiple terrain pieces, ensuring in each run that

the insect did not contact the walls of the tank or stop running at any point during the recording.

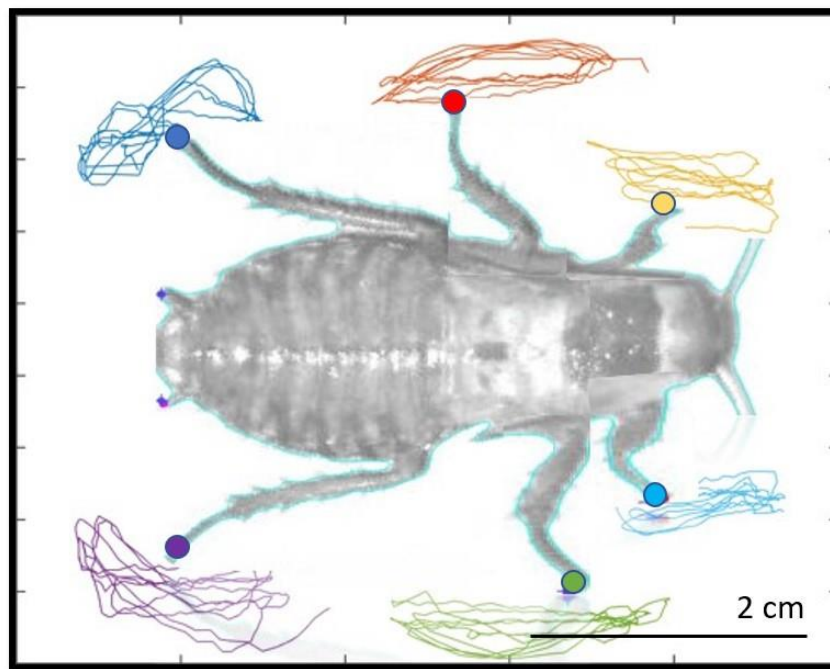Every global phase and every local phase for each leg was calculated using the video data.

Figure 3. The tracked positions of all legs through one run over flat terrain. The colored lines mark the positions of the tip of each associated leg in each frame of the recorded video.

The kinematic leg tracking and EMG returns were then analyzed to determine the

information distribution of the roach. The action potentials experienced by the recorded muscle

groups, visible as spikes on the EMG returns, were identified, isolated, and compared to the

global phase of the stride, shown in figure 4.a (10). The local kinematics of all six legs with

12

respect to time, displayed in figure 4.b, were averaged together using the phaser algorithm

employed in *Revzen et al. 2008* to determine the global phase (12). The global phase, shown in

figure 4.c, is a representation of the position and behavior all the legs of the roach throughout the

run (12). Each of the saw tooth waveforms represents one complete stride performed by all six of

the roach's legs. These individual strides were partitioned out and compared against the control

signal, represented as the EMG returns, to determine how indicative the behavior of the motor

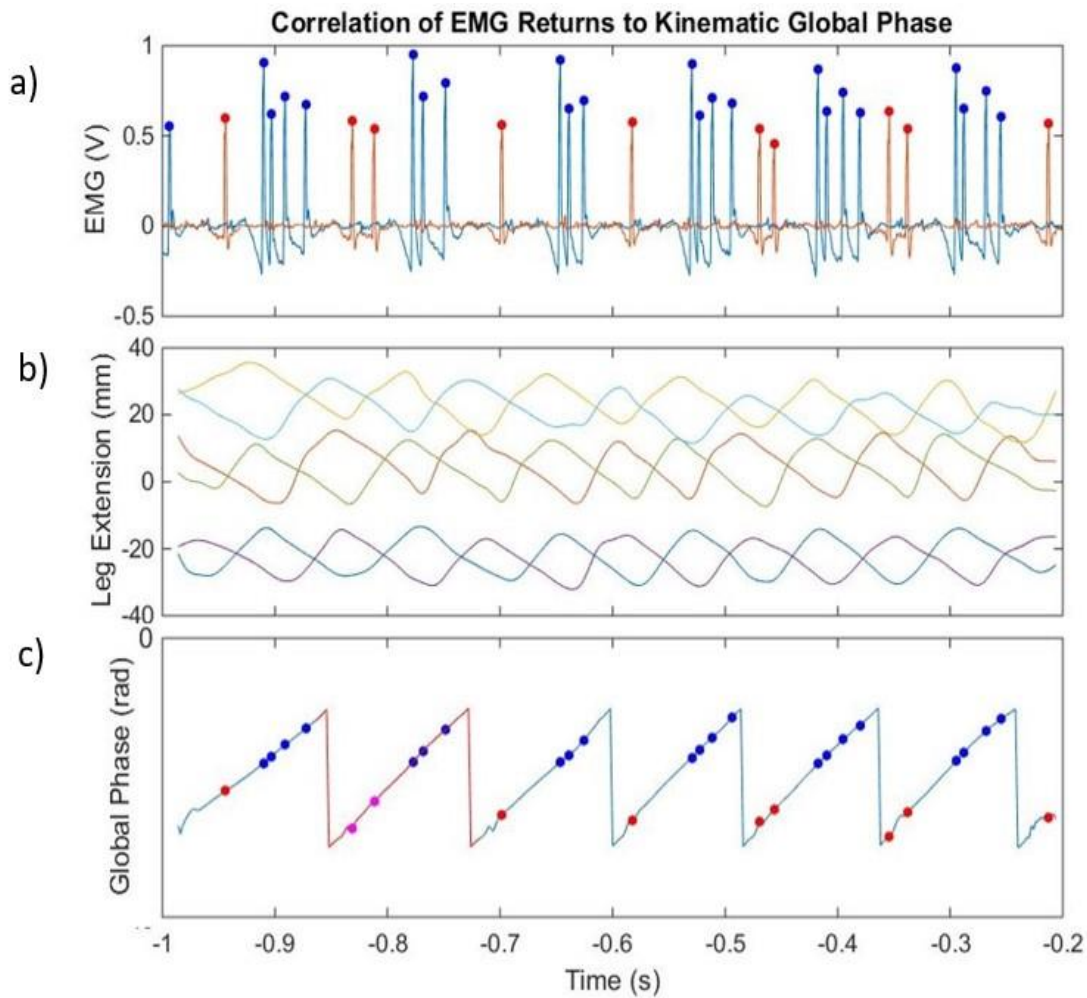neurons is of the local and global behavior (12).

Figure 4. The recoded EMG signal from the cockroach's leg muscles during the run. The timing of the action potential spikes have been located and recorded using a MATLAB function. b) The kinematics of all six legs, as shown in figure 2, plotted with respect to time. The zero position on the Y axis represents the center point on the insect's body. c) The global phase of the cockroach, created by averaging the positions of all six legs at every point in time. Each waveform represents one stride. The timings of the recoded action potentials shown in figure 3 a) are superimposed as red and blue dots

Using a K nearest neighbor algorithm, both local and global mutual information with respect to different elements of the control signal can be calculated (12, 13). The algorithm uses mutual information as a metric to correlate patterns in the EMG spikes to leg behavior, mimicking the arithmetic procedures outlined in *Kraskov et al, 2004*. The patterns chosen for analysis were the number of spikes per stride observed in the middle left leg, shown in red in figure 4, and the percent phase of the stride in which the spikes were observed. The more highly correlated each of these patterns were to the behavior of the leg they were recorded from, the greater the local mutual information (12). The more highly correlated they were to the behavior of all legs, the greater the global mutual information (12). Centralization was defined as the difference in information, measured in bits per stride, between the calculated global and local mutual information (12). This analysis was performed on all strides collected over each terrain base, with 718, 840, 505, and 114 individual partitioned strides analyzed for the 0, 0.1, 0.2, and 0.5cm standard deviation terrain respectively. A total of 8 individual cockroaches were recorded running over the 0cm terrain, 9 over the 0.1cm, 6 over the 0.2cm, and 3 over the 0.5cm.
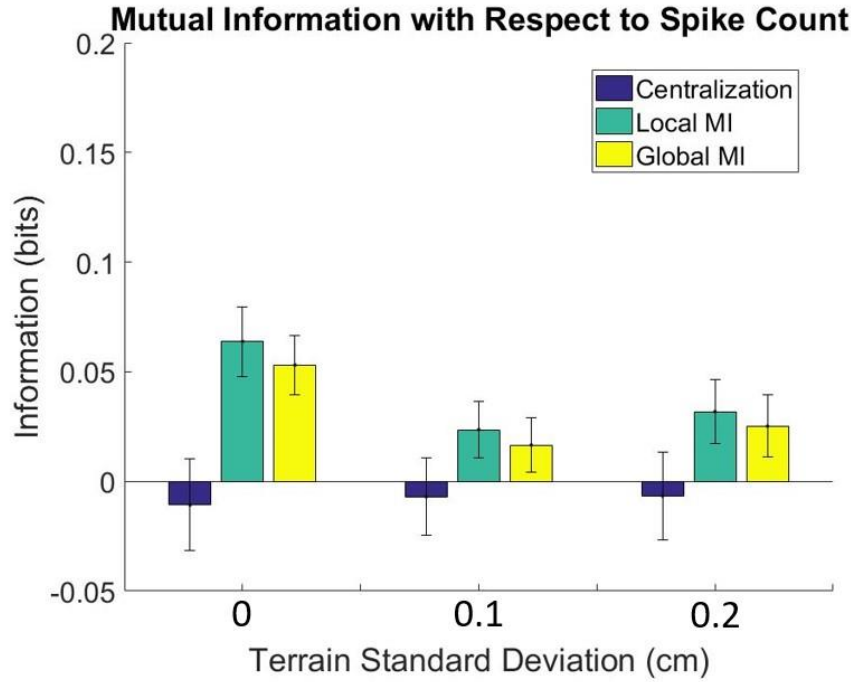
Results

Figure 5. The calculated mutual information and centralization through analysis of spike count in the control signal across terrain with standard deviations of 0, 0.1, and 0.2 cm. Centralization was taken as the numeric difference between the global and local mutual information, with standard deviation equal to the upper and lower bounds of the combined standard deviations of the respective mutual information statistics.

Figure 5 shows the global and local mutual information and the resulting centralization values for each terrain standard deviation. The global and local information was calculated using a K nearest neighbor algorithm correlating the number of action potential EMG spikes recorded during each leg extension with leg behavior (16). Centralization was calculated by subtracting the local mutual information from the global mutual information for each terrain piece. The resulting means of centralization were -0.011, -0.007, and -0.007 bits/stride, with standard deviations of 0.027, 0.022, and 0.028 for terrain standard deviations of 0, 0.1, and 0.2 cm respectively. Trials over 0.5 cm standard deviation terrain were excluded from this analysis due to insufficient quantity of data. A two-tailed t test comparing the centralization values yielded no significant difference between the means of the 0 cm and 0.1 cm terrain, no difference between

the 0.1 cm and 0.2 cm terrain, and no difference between the 0 cm and 0.2 cm terrain. An alpha
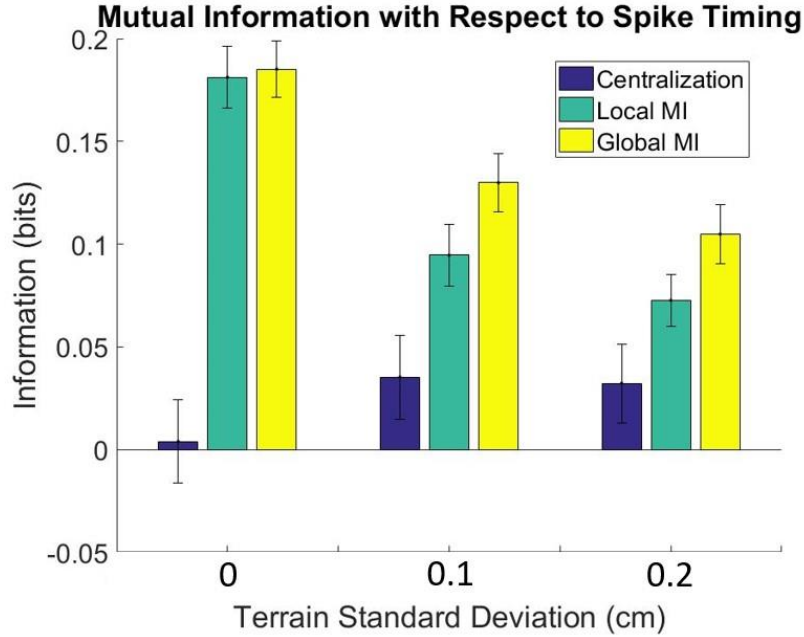
value of 0.05 was used for all cases.

Figure 6. The calculated mutual information and centralization through analysis of spike timing in the control signal across terrain with standard deviations of 0, 0.1, and 0.2 cm. Centralization was taken as the numeric difference between the global and local mutual information, with standard deviation equal to the upper and lower bounds of the combined standard deviations of the respective mutual information statistics.

Figure 6 shows the global and local mutual information and the resulting centralization

values calculated for each terrain standard deviation. The local and global information was

calculated using a K nearest neighbor algorithm correlating the time within each stride the action

potentials were observed to the local and global behavior of the legs (16). Centralization was

calculated by subtracting the local information from the global information. The resulting

degrees of mutual information were 0.004, 0.035, 0.032 bits/stride with standard deviations of

0.020, 0.021, and 0.019 for terrain standard deviations of 0, 0.1, and 0.2 cm respectively. Trials

over 0.5 cm standard deviation terrain were excluded from this analysis due to insufficient

quantity of data. A two-tailed t test comparing the centralization values yielded a significant

difference between the means of the 0 cm and 0.1 cm terrain and between the 0 cm and 0.2 cm

terrain, but no difference between the 0.1 cm and 0.2 cm terrain. An alpha value of 0.05 was
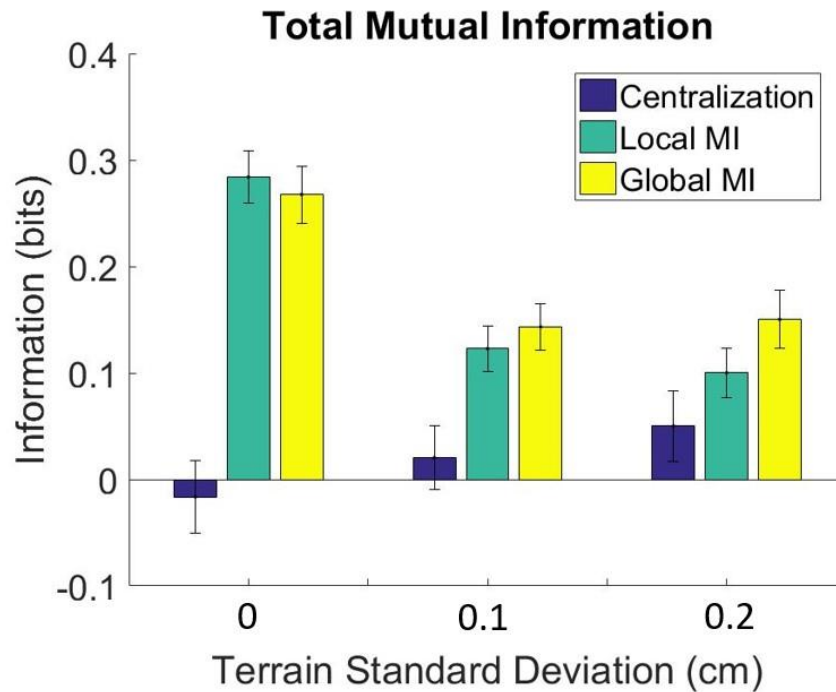
used for all cases.

Figure 7. The summation of the mutual information and centralization shown in figures 4 and 5, representing the overall information distribution in the insects across terrain with standard deviations of 0, 0.1, and 0.2 cm. The standard deviations are equal to the upper and lower bounds of the combined standard deviations of the respective mutual information and centralization statistics.

Figure 7 shows the summation of the data presented in figures 5 and 6. This illustrates the

overall change in information distribution across all terrain types. The resulting amounts of

centralization information were -0.016, 0.020, 0.050 bits/stride with standard deviations of 0.034,

0.030, and 0.034 for terrain standard deviations of 0, 0.1, and 0.2 cm respectively. Trials over 0.5

cm standard deviation terrain were excluded from this analysis due to insufficient quantity of

data. A two-tailed t test comparing the centralization values yielded a significant difference

between the means of the 0 cm and 0.1 cm terrain and the 0 cm and 0.2 cm terrain, but no

difference between the 0.1 cm and 0.2 cm terrain. An alpha value of 0.05 was used for all cases.
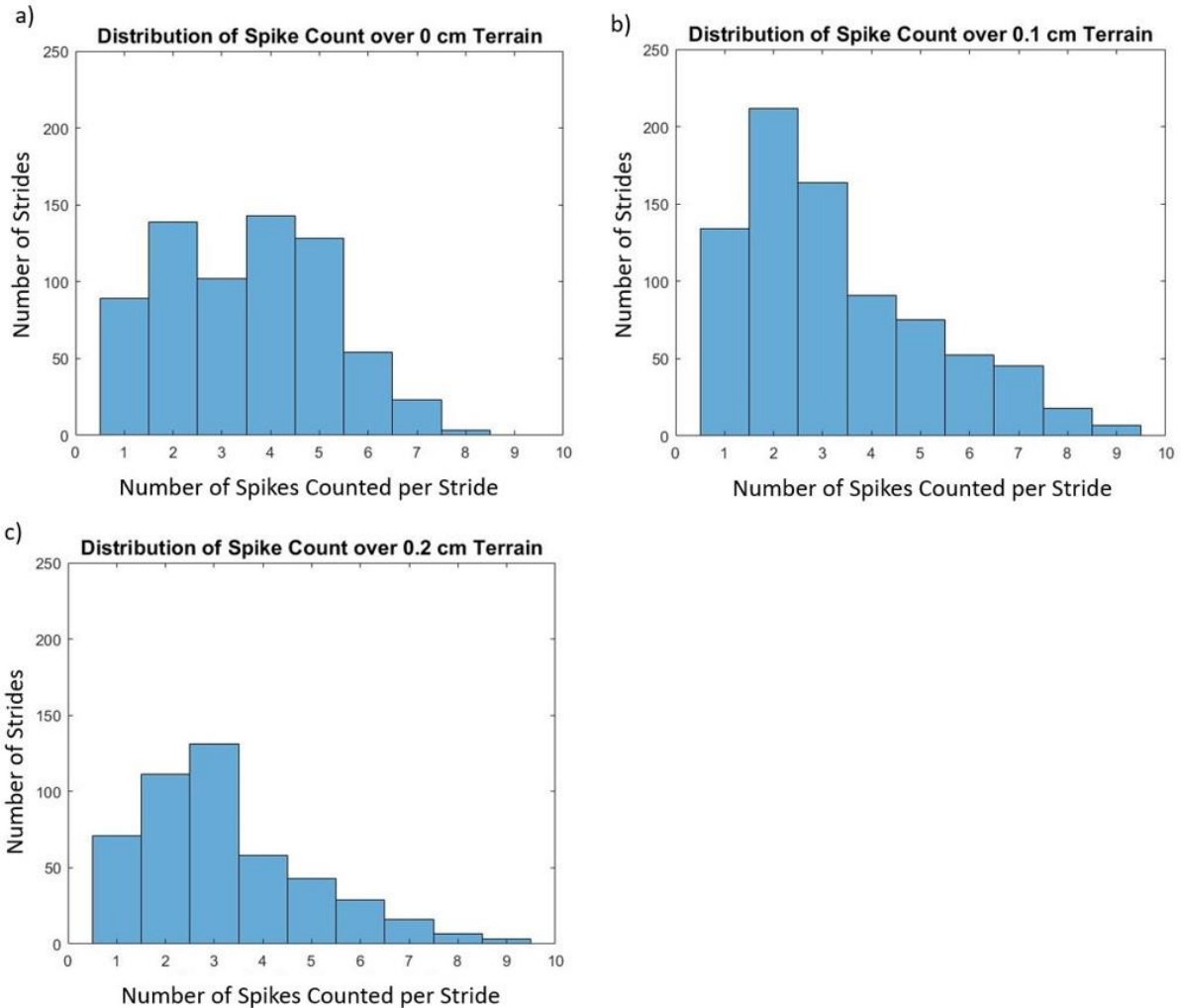

Figure 8. a) The distribution of the number of spikes recorded in each isolated stride of the cockroaches tested over the 0 cm standard deviation terrain. All data is was collected from the mid left leg, illustrated in red in figure 4. b) The distribution of the number of spikes recorded in each isolated stride of the cockroaches tested over the 0.1 cm standard deviation terrain. All data is was collected from the mid left leg, illustrated in red in figure 4. c) The distribution of the number of spikes recorded in each isolated stride of the cockroaches tested over the 0.2 cm standard deviation terrain. All data is was collected from the mid left leg, illustrated in red in figure 4.

Figure 8 illustrates the distributions of spike count across the 0 cm, 0.1 cm, and 0.2 cm

terrains. Spike count is defined as the sum of all spikes detected during the phasic analysis

displayed in figure 4. The number of spikes in each stride was calculated and partitioned into

groups depending on the terrain roughness over which the stride was collected. In total, 718

strides were recorded over flat terrain (figure 8.a), with a mean of 3 spikes per stride, a median

of 3 spikes, and a mode of 4 spikes. 840 strides were collected over the 0.1 cm standard

deviation terrain (figure 8.b), with a mean of 3 spikes per stride, a median of 3 spikes and a

mode of 2 spikes. 505 strides were collected over the 0.2 cm standard deviation terrain (figure

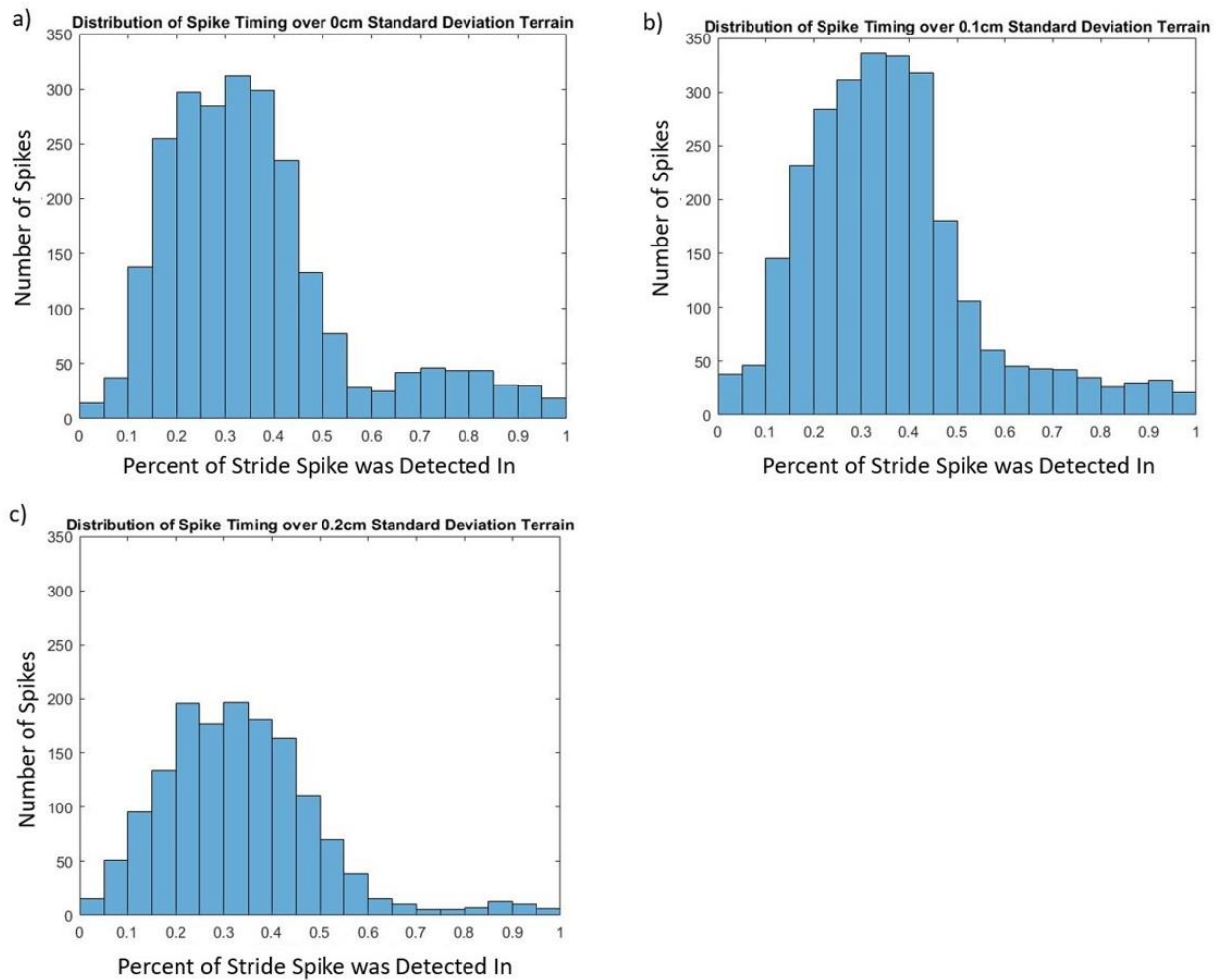8.c), with a mean of 3 spikes, a median of 3 spikes, and a mode of 3 spikes.

Figure 9. a) The distribution of spikes with respect to the percent of the stride they were recorded in over flat, 0 cm standard deviation terrain. All data is was collected from the mid left leg, illustrated in red in figure 3. b) The distribution of spikes with respect to the percent of the stride they were recorded in over the 0.1 cm standard deviation terrain. All data is was collected from the mid left leg, illustrated in red in figure 3. c) The distribution of spikes with respect to the percent of the stride they were recorded in over the 0.2 cm standard deviation terrain. All data is was collected from the mid left leg, illustrated in red in figure 3.

Figure 9 illustrates the distribution of spike timing within each stride across the 0 cm, 0.1 cm, and 0.2 cm terrain. Timing was calculated as the percent of the stride in which the spike was recorded. All spikes that were recorded in each individual stride are included in these distributions. The spike timings were allocated to the terrain data set over which their associated stride was recorded. The 0 cm terrain incorporated a total of 2389 individual spikes, with a mean timing of 0.361, or 36.1% of the stride, and a median of 0.328. The 0.1 cm terrain included 2660 spikes, with a mean of 0.363 and median of 0.342. The 0.2 cm terrain accounted for 1500 spikes and had a mean of 0.333 and a median of 0.319.

Discussion

The changes in centralization observed in figure 7 seem to indicate a tentative positive correlation between terrain roughness and centralization in the insects. The means of each trial increased almost linearly, but the high variances in each group yielded p values that suggested no statistical difference between neighboring groups. There was however, a discrete difference between the centralization observed in the 0 cm trial and the 0.2cm trial. This would suggest a definite positive correlation between terrain roughness and centralization, though the exact behavior of that trend would require more precise analytical methods to fully illustrate. Centralizations values would likely plateau after a certain degree of roughness is reached, as the local mutual information statistic approaches zero. This trend can best be seen in figure 7, where the both the global and local mutual information decrease generally as roughness increases. These decreases appear to occur at different rates, with the local mutual information decreasing faster than the global mutual information, which results in the positive trend in centralization observed. If this trend continued, the local mutual information would approach zero, after which the observed global mutual information would either stop decreasing, resulting in a plateau in centralization, or continue to decrease until it too reached zero, causing centralization to begin decreasing. More trials should be conducted over terrain of 0.5cm standard deviation or greater to better describe this relationship.

The observed changes in centralization suggest alterations in the insects muscular control architecture (12). As the magnitude of the perturbations felt by the insect increase, motor control shift away from passive, mechanically driven stabilization towards more centralized, top down coordination. This is illustrated by the near zero value for centralization over flat terrain (figure 6), suggesting a very decentralized system relying mostly on the mechanical coupling between

the legs to retain gait stability (6). As terrain roughness increased, that passive mechanical stability was no longer sufficient to retain balance, and the muscle control shifted to be more centrally defined. This shift is visible in the proportionately greater value of global mutual information to local information over the 0.2cm standard deviation terrain. The control signal was more indicative of the behavior of all six legs than it was of the individual leg it was collected from, suggesting that the motor input it was receiving was attempting to coordinate all the legs in the system, not just continue the motion of that one leg. This sort of behavior has also been seen in coupled oscillator models for insect running when they are exposed to perturbations, wherein discrete coupling values between neighboring legs produced reproduced experimental behavior (14). The work performed by *Fuchs et al 2015* suggests that its uniform central coupling through neural communication contributes to robustness of gait, and through using centralization as a metric, the results described in this study suggest that the degree of central coupling increases along with perturbation intensity (12, 14).

This increase in centralization may be beneficial for negotiating rough terrain as it allows for more sensory feedback to be incorporated into the kinematics of each of the insect's legs. When the control signal becomes more indicative of global behavior relative to local behavior, it means that the signal has incorporated more information about the environment into its commands. The central nervous system of the cockroach is processing proprioceptive data from all of its legs and sensory organs in order to better respond to the perturbations it is suffering, and not just relying on local mechanical or short-range neural coupling to stabilize each leg. This behavior increases the insect's ability to maintain its gait across rough terrain as all six legs can be coordinated and compensate for much larger variances than if the system remained more decentralized.

The implications of this behavior on muscle control architecture are twofold. Firstly, it suggests that this architecture is dynamic and can be altered as the animal is exposed to different stimulus. Unlike common robotic models, the central nervous system of the insect can actively respond to changes in its environment and have a greater or lesser degree of coordination over all its limbs depending on the intensity of the perturbations it is facing. The fact that centralization remained close to zero over flat terrain, and then increased as terrain roughness increased, suggests that the default pattern for this architecture is to minimize centralized input, relying on passive mechanical stability as much as possible. To confirm this conjecture, centralization could be calculated when the cockroaches were not physically goaded over terrain, and instead allowed to move of their own volition. Theoretically, the flight response induced by the prodding also generates an increased degree of centralization relative to normal movement over equivalent terrain, and if such a relationship could be illustrated, it would serve as evidence towards maximization of passive stabilization being the default for these animals' control architecture.

Secondly, this trend suggests that the control signal observed becomes less indicative of both local and global behavior as terrain roughness increases. Across all terrains, both the local and global mutual information statistics decreased or remained equal relative to the previous data set. This suggests that the motor control architecture in the insects becomes less definite as larger and larger perturbations are felt by the animal. The control signal becomes less and less indicative of the kinematics of both the local and global variables, likely due to the increasing magnitude of the disruptions in the animal's gate. Any robotic models attempting to mimic this control architecture would likely suffer the same problems as their stabilization systems would not be able to fully compensate for all felt perturbations. Such issues may be resolved by improved proprioception and computing power within the robot's control system. If the

computer can detect and compensate for perturbations faster than the central nervous system of the cockroaches, theoretically the local and global mutual information values would decrease less relative to each other.

The relatively small number of strides processed in this study may be a significant source of error. In total, 719 strides over 0cm standard deviation terrain were included in the information analysis, 846 for 0.1cm, and 510 for 0.2cm. Though these numbers are large enough for the K nearest neighbor algorithm to work, a larger number would likely have reduced the high variances seen in figures 4, 5, and 6, and lowered the associated p values between sets. The strides collected from the 0.5cm standard deviation terrain were excluded from the analysis all together because they numbered only 114, which was too low for the analysis to be performed with an acceptable degree of accuracy. The primary reason for the relatively lesser numbers of strides over rougher terrain is that the kinematic processing method was not very effective at those magnitudes of perturbation. The leg tip identification process, shown in figure 2, broke down when the legs would be moved under the roach's abdomen for prolonged periods of time. This would occur when the insect moved against a relatively tall pillar on the terrain base, and cause one or more legs to go untracked for several frames of the video. The result would be an irregularity in the local kinematics, illustrated by figure 4.b, that would distort the calculated global phase for that stride. Because of this distortion, especially if the untracked leg was one of those with the implanted electrodes, that stride could not be successfully analyzed and had to be discarded. This was a phenomenon extremely common over the 0.5cm standard deviation terrain, and almost not at all over the flat or 0.1cm standard deviation terrain and caused proportionately fewer strides to be recorded over the 0.5cm and 0.2 cm terrain.

Other factors that impacted stride processing were noise in the EMG returns that rendered the spike patterns unintelligible and instances of the insects changing speed throughout the run. In some trials, the implanted electrodes would become detached from the targeted muscle groups in one or more locations, leading to a large amount of ambient radiation displaying itself as high frequency noise in the signal returns. This would make it impossible for the MATLAB program used to isolate and time stamp the action potential spikes to work properly and caused a large percentage of strides to be discarded, even if their kinematics were recorded successfully. This behavior was observed to occur more frequently in trials over high roughness terrain, as the electrode wires were more likely to snag on the relatively tall pillar heights, and likely contributed to the paucity of data recoded in those conditions. At random intervals, the animals were observed to change speed during their runs over the terrain, causing some of the recorded spikes to appear outside their associated global phase. This was because the global phase waveform, shown in figure 3.c, was created through averaging the kinematics, with the beginning and end of each stride chosen by preset algorithms in the processing code. This means that bursts of spikes observed in the EMG may have correlated to the beginning of their associated local phase but fall directly on the beginning or end of the global phase. Spikes from such a stride would appear in their neighbors, and force that stride to be discarded as it would falsely inflate the spike count metric. Such instances also appeared to occur more commonly over the rougher terrain, as the very large perturbations experienced in those trials would cause dramatic shifts in the insects' speed.

Further anomalies may stem from the distribution of the number of cockroaches tested over each terrain. In total, 8 insects were tested over the flat terrain, 9 over the 0.1cm, and 6 over the 0.2cm. However, not all these animals contributed the same number of strides to each

terrain's data set. For example, one subject contributed 42 strides to the flat terrain set, 86 to the 0.1cm set, and 74 to the 0.2cm set. Some subjects contributed to only two data sets and had no recoded strides over the third. Because of this, and the relatively small number of individual cockroaches used in the trials, if there were any physiological differences between insects, they could have a more pronounced effect on some data sets than (Kraskov, Stögbauer, & Grassberger, 2004)others. Moreover, if there was one cockroach which behaved irregularly, it could be overrepresented in any or all of the data sets due to the small population size.

Any further research done on this topic should seek to increase the size of the analyzed data sets, especially the 0.2cm and 0.5cm standard deviation terrain sets, in order to decrease the variance observed in the information calculations and thus solidify the study's conclusions. A more robust method of collecting the kinematic data would likely be the best way to accomplish this, as a large number of strides were discarded or unable to be calculated due to the legs being hidden from the camera's view. A new method could also seek to improve the robustness of the control signal collection process. Electromyography was successful in representing muscle activation in the stride, but the electrode implantation was not extremely secure, and trials would often have to be terminated early due to unintentional removal of one electrode by either the insect or the terrain. This made the process of data collection extremely temperamental and inefficient, and contributed significantly to the small size of the data sets over all terrain types. New methods of information analysis could also be implemented, refining the K nearest neighbor algorithm to see if variance in mutual information could be reduced.

Conclusion

In this experiment, the nervous-muscular behavior of _Blaberus discoidalis_ cockroaches was tracked while running across terrain of variable roughness. Using 2D body kinematics and electromyography, mutual information between a control signal and individual legs was calculated using a K nearest neighbor algorithm. As terrain roughness increased, centralization was observed to positively increase as well. This suggests that as they are exposed to more extreme perturbations during their escape response, the insects maintain their gait by increasing cognitive control of their legs, relying less on passive mechanical suspension. Local and global mutual information were also observed to decrease with increasing terrain roughness, suggesting that the control signal observed in the leg muscles became less indicative of leg behavior as perturbation size increased. The high variance seen in the calculated results may be the result of insufficient numbers of processed strides, physiological differences between individual insects coupled with unequal contribution to each data set, or unknown flaws in the data analysis method. Further research should be conducted to supplement the data used in the information and find a more robust method for measuring kinematics over extremely rough terrain.

References

1. Biewener AA, Daley MA. Unsteady locomotion: integrating muscle function with whole body dynamics and neuromuscular control. *Journal of Experimental Biology.* 2007;210(17):2949.

2. Büschges A. Sensory control and organization of neural networks mediating coordination of multisegmental organs for locomotion. *Journal of neurophysiology.* 2005;93(3):1127-1135.

3. Carbonell, C.S. (1947) The Thoracic Muscles of the Cockroach Periplaneta Americana (L.). *Smithson. Misc. Collect.* 107, 1–23

4. Fuchs E, Holmes P, David I, Ayali A. Proprioceptive feedback reinforces centrally generated stepping patterns in the cockroach. *The Journal of Experimental Biology.* 2012;215(11):1884.

5. Fuchs E, Holmes P, Kiemel T, Ayali A. Intersegmental Coordination of Cockroach Locomotion: Adaptive Control of Centrally Coupled Pattern Generator Circuits. *Frontiers in Neural Circuits.* 2011;4(125).

6. Koditschek DE, Full RJ, Buehler M. Mechanical aspects of legged locomotion control. *Arthropod Structure & Development.* 2004;33(3):251-272.

7. Revzen S, Burden SA, Moore TY, Mongeau J-M, Full RJ. Instantaneous kinematic phase reflects neuromechanical response to lateral perturbations of running cockroaches. *Biological Cybernetics.* 2013;107(2):179-200.

8. Schmitt J, Garcia M, Razo RC, Holmes P, Full RJ. Dynamics and stability of legged locomotion in the horizontal plane: a test case using insects. *Biological cybernetics.* 2002;86(5):343-353.

9. Spagna JC, Goldman DI, Lin PC, Koditschek DE, Full RJ. Distributed mechanical feedback in arthropods and robots simplifies control of rapid running on challenging terrain. *Bioinspiration & Biomimetics.* 2007;2(1):9.

10. Sponberg S, Full RJ. Neuromechanical response of musculo-skeletal structures in cockroaches during rapid running on rough terrain. *Journal of Experimental Biology.* 2008;211(3):433.

11. Uluc S, Martin B, Daniel EK. RHex: A Simple and Highly Mobile Hexapod Robot. *The International Journal of Robotics Research.* 2001;20(7):616-631.

12. Neveln I, Triumalai A, Sponbeg S. Just How Centralized is Cockroach Locomotor Control? Comparison of Robotic and Computaional Models. *Integrative and Comparative Biology.* Vol 5. 2018.

13. Srivastava KH, Holmes CM, Sober SJ. Motor Control by Precisely Timed Spike Patterns. *Proceedings of the National Academy of Sciences of the United States of America.* 2017;114(5):1171-1176.

14. Couzin-Fuchs E, Kiemel T, Gal O, Ayali A, Holmes P. Intersegmental coupling and recovery from perturbations in freely running cockroaches. *Journal of Experimental Biology.* 2015

15. Revzen S, Guckenheimer JM (2008) Estimating the phase of synchronized oscillators. *Physical Review* E 78(5):051907

16. Kraskov, A., Stögbauer, H., & Grassberger, P. (2004). Estimating mutual information. *Physical Review E, 69*(6)