# Cockroaches centralize control as speed and terrain uncertainty increase

Ellen Liu[1], Leo Wood[2], Izaak Neveln[3], Simon Sponberg[4]
[1]School of Physics, Georgia Institute of Technology, USA - *eliu82@gatech.edu*
[2]School of Physics, Georgia Institute of Technology, USA - *leo.w@gatech.edu*
[3]School of Physics, Georgia Institute of Technology, USA - *ineveln2@gmail.com*
[4]School of Physics, School of Biology, Georgia Institute of Technology, USA - *sponberg@gatech.edu*

## 1 Introduction

Centralization in animal and robotic locomotors is an important parameter in the architecture of control, but is difficult to assess empirically [1]. Here, we consider centralization as the coupling between neuromechanical modules (e.g. limbs) that mediate responses to perturbations and disturbances (Fig. 1A) [2, 3]. Centralized systems have strong coupling which may be neural or mechanical. Decentralized systems have weaker couplings and rely more on local feedback. To overcome the challenge of comparing different systems without assuming a specific model, Neveln et al. (2019) proposed an empirical, model-free measure of centralization based on information theory [2]. This measure, based on information decomposition, considers whether variation in the control signals mediating perturbation responses are more informative of local limb states or global body states. It has been validated on animal, robotic, and coupled oscillator simulations and provides a way for comparing the centralization of a system across conditions [2]. While this allows findings from biological organisms to be applied generally to robotic systems, the performance advantages for centralized or decentralized architectures have not been widely explored, especially under changing conditions such as rough terrain.

Locomotor speed and environmental variability are two critical variables that shape the performance of organisms and design of motile robots. Here we challenged agile, running cockroaches (*Blaberus discoidalis*) with large perturbations to the environment and at high speeds to test a larger range of dynamics centralized or decentralized control. Previous work found no significant change in centralization, but only considered slight perturbations in the environment and small increases in speed [2, 4]. For highly variable rough terrains, a centralized architecture might be advantageous to coordinate controlled responses to perturbations across many limbs due to the higher inertia and forces experienced. Alternatively, a decentralized architecture could be better because faster reaction speeds are possible which may prove useful when time to react to perturbations at fast speeds is limited [5]. In addition to centralization, we also analyzed a second information measure, coinformation, to assess the net redundancy of the animal's response [2].

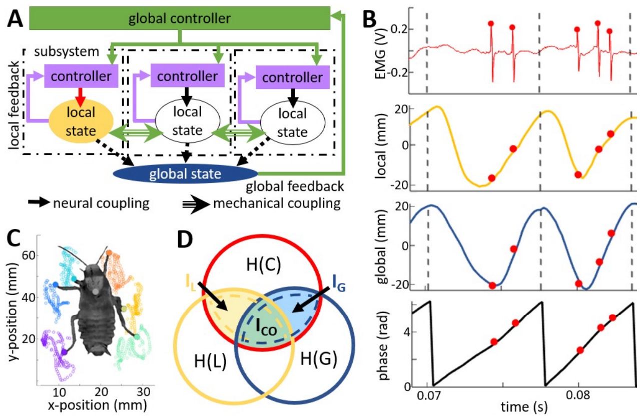


**Figure 1:** A) Simplified control architecture block diagram where green components are stronger than purple for centralized architectures and weaker for decentralized. B) Control, local and global signals recorded from the cockroach. C) Tracking of tarsi. D) Graphical representation of mutual information estimation calculation using entropy (H)

## 2 Methods and Quantifying Centralization

Centralization compares the mutual information between a control signal and each of a local and global state representation. Following [2], we define the local limb states as the fore-aft position of the leg tip (tarsus) in body-centered coordinates (Fig. 1B-C). The global state is defined as the sum of all of the local states (tarsi within the same tripod were added to each other then subtracted from the remaining tripod). The strides were split up by finding the instantaneous phase of the global state variable defining the beginning of the stride as the zero phase crossing approximately when stance is ending (Fig. 1B). The control signal was the number and timing of muscle action potentials (or "spikes") that occurred in the ventral femoral extensor of the middle leg (see [2]), an important control muscle [6]. To ensure a more stable, unbiased information estimate by reducing input dimensionality, the first 4 principal components were taken per stride when estimating the mutual information between each state and the control signals.

The degree of centralization and redundancy is calculated from the mutual information between the control signal and local state ($I_L$), control signal and global state ($I_G$) as well as the control signal and the joint of the local and global state which is the total amount of mutual information ($I_{TOT}$). We estimated mutual information values using k-nearest neighbors distance methods [2, 7]. All estimates were stable to various values of k and subsampling. Centralization, $I_{CENT}$ and coinformation, $I_{CO}$ are calculated as differences in these partial informations (Eqs. (1) to (2), Fig. 1D). Positive values indicate centralization and redundancy, respectively [2].

$$I_{CENT} = I_G - I_L \tag{1}$$

$$I_{CO} = I_G + I_L - I_{TOT} = I_R - I_{SYN} \tag{2}$$

## 3 Results and Discussion

We ran cockroaches over flat and rough terrain (Fig. 2A) which is known to cause large perturbations in the system and over a large range of speeds (Fig. 2B) [6]. Increasing speed on the flat terrain caused a slight decrease in centralization in absolute terms (Fig. 2C), but overall the control signals were less informative of the kinematics (lower $I_{TOT}$) and the system was slightly more centralized relative to $I_{TOT}$ (Fig. 2D). This is reflected in a reduced redundancy between how the muscle controls the local and global states (lower $I_{CO}$). Centralization relative to total information increased even further on the rough terrain, consistent with an increase in neuromechanical coupling between limbs. In this, when the cockroach changed the activation to an individual limb it was more than twice as informative about the coordinate response of the body than of the kinematics of the individual leg in which the muscle resides ($I_G > I_L$). In both faster and rougher conditions the control of local and global states was much less redundant than at slower speeds.

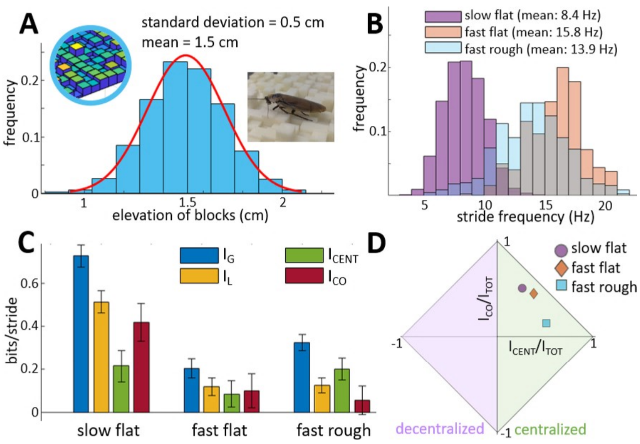


**Figure 2:** A) The rough terrain quantified by the standard deviation of a Gaussian distribution of surface heights. B) Variation in individual stride frequency. C) Absolute mutual information estimates. D) Normalized information estimates by dividing the total information of each respective system, represented in control architecture space.

The data supports the hypothesis that centralized control is beneficial to maintaining dynamic stability in faster and more uncertain conditions. The potential issue of this centralization requiring longer delay times, especially in organisms, may be mitigated if the animal uses more mechanical coupling rather than neural coupling. Mechanical coupling does not necessarily suffer from the same time delays as neural coupling. It is important to note that this measure for centralization only quantifies the strength of the couplings and does not identify the degree to which the coupling is neural or mechanical. Regardless, the system may compensate somewhat for potential drawbacks of centralization by decreasing the degree of coinformation thus inducing a less redundant control architecture where separate information is conveyed by the individual limb and coordinated response of the body. Such a threshold appears to arise only at large perturbations, as for the rough terrain while the coinformation is reduced significantly, centralization increases substantially. This strategy could be used when applying varying architectures found in biological organisms to robotic systems to improve their performance. Introduction of mechanical coupling to maintain centralization could help to minimize computational requirements and simplify the control system [2].

Our results support that cockroaches have the ability to vary their control architecture either through neural feedback or through interactions with their environment. We observed the control architecture to change with the empirical centralization metric gaining more insight to how cockroaches are able to navigate complex environments effectively. A centralized architecture may be beneficial on complex terrain to maintain dynamics stability. For sudden perturbations due to the limited time available for the feedback to be properly accounted for by a central global controller, the system becomes less redundant and could be exploiting the reaction speeds of global mechanical coupling [5].

### References

[1] P. Holmes, R. J. Full, D. Koditschek, and Guckenheimer, J. ”The Dynamics of Legged Locomotion: Models, Analyses, and Challenges,” *Siam Review*, Vol. 48, pp.207-304, 2006

[2] I. Neveln, A. Tirumalai, and S. Sponberg, ”Information-based centralization of locomotion in animals and robots,” *NATURE COMMUNICATIONS*, Vol. 10, 13 Aug, 2019

[3] E. Couzin-Fuchs, T. Kiemel, O. Gal, A. Ayali , and P. Holmes, ”Intersegmental coupling and recovery from perturbations in freely running cockroaches” — *The Journal of Experimental Biology*, Vol 218, pp. 285-297, 2015

[4] I. Neveln, C. Dallmann, and S. Sponberg, ”Using Mutual Information to Analyze Adaptations to Loading Speed and Terrain,” *9 International Symposium on Adaptive Motion of Animals and Machines (AMAM 2019)*, Switzerland, 2019

[5] H. Cruse, V. Durr, ans J. Schmitz, ”Insect walking is based on a decentralized architecture revealing a simple and robust controller,” *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, Vol. 365, Issue 1850, pp. 221–250, 2007

[6] S. Sponberg and R. J. Full, ”Neuromechanical response of musculo-skeletal structures in cockroaches during rapid running on rough terrain,” *Journal of Experimental Biology*, Vol 211. Issue 3, p 433, 2008

[7] C. M. Holmes, and I. Nemenman, ”Estimation of mutual information for real-valued data with error bars and controlled bias,” *Physical Review E*, Vol. 100. Issue 2, 6 Aug, 2019