The neuromechanics of insect locomotion:

How cockroaches run fast and stably without much thought

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Hal Komsuoglu, Pei-Chun Lin, Richard Altendorfer, Dan Koditschek,
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[5]Intellectual Ventures Lab, Bellevue, WA; [6]ME Dept, Ohio State U; [7]EECS Dept, U Michigan.

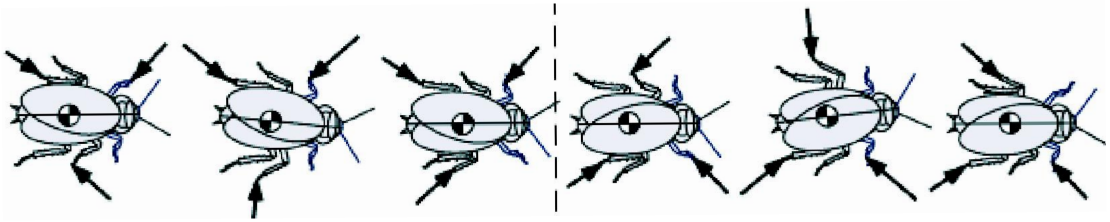
Mathematics Dept., Morgan State U., Sept 27th, 2012.

Thanks to NSF, NIH and Burroughs-Wellcome Foundation, J. Insley Pyne Blair Fund of PU,
and IMA Minnesota, where it all started in 1998.

Terrestrial mechanics

time x 0.2

(courtesy R.J. Full)



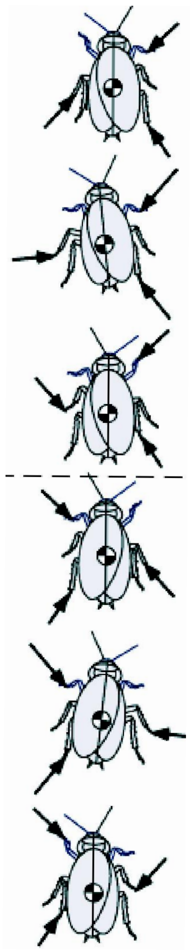
double tripod gait

The importance of stability: what can be done with no or little neural feedback.

The cockroach is a dynamical system (like you & me)

Introduction and background

Neuromechanics of locomotion:



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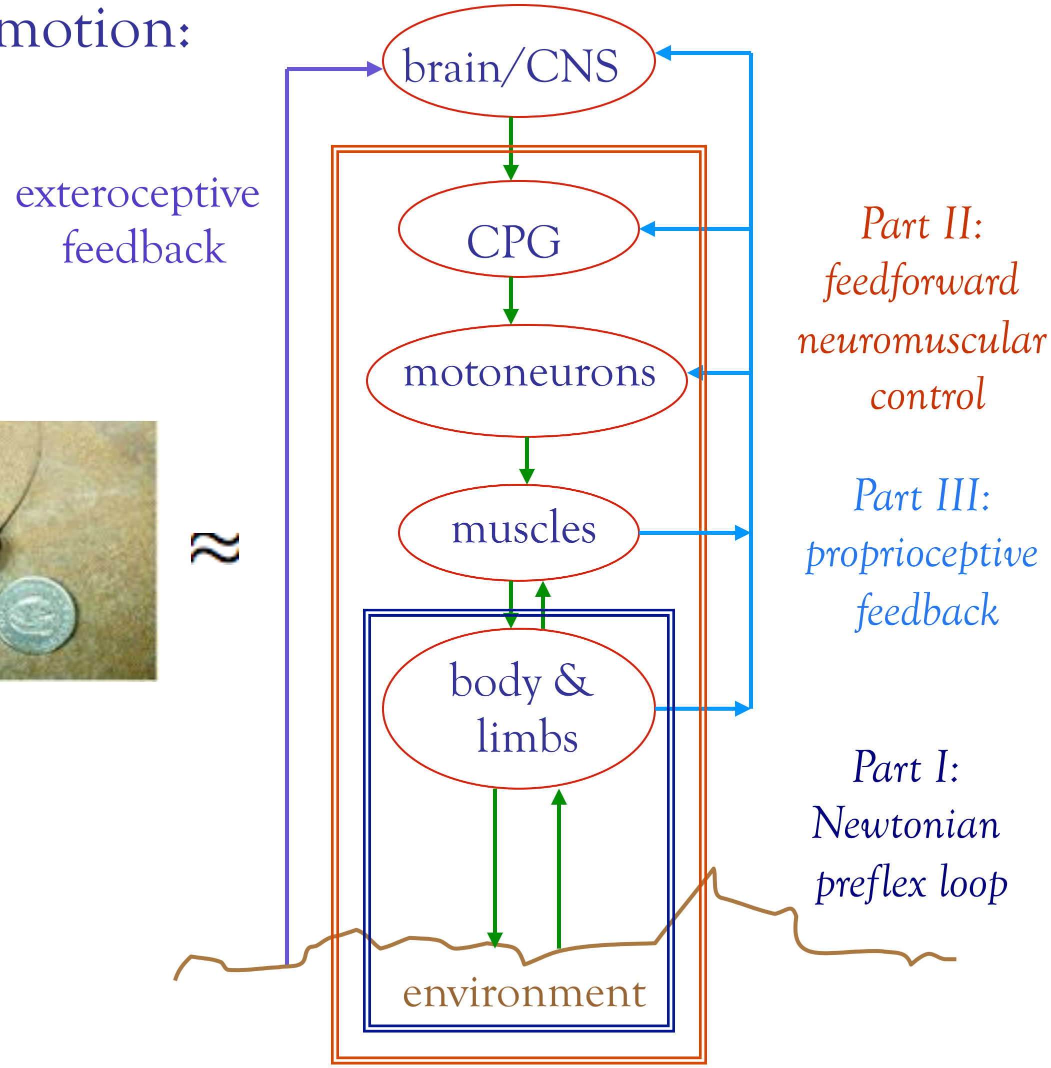


Learn how they run before how they walk!

Introduction: Fast cockroaches: inertia dominates dynamics, simplifying potential neural control strategies. Feedforward **preflexes** dominate **reflexes**.

Part I: Mechanistic theory; passive and active models (1998-2007).
Simple models: Effective bipeds? Passive springs and hybrid, conservative dynamical systems. Proof of preflexive stability.

Parts II: Complicate! Neuromechanical integration (2004-2011).
A hexapedal model with a central pattern generator and muscle actuation.

Part III: Re-simplify! Phase reduction and neural feedback (2004-2012).
Proprioceptive neural reflexes can modulate responses (work in progress).

Summary: Mathematical, biological and neuro-mechanical challenges. Integrative modeling. How much detail is needed? How much is desirable?

Moral: In building models, walk before you run; get the pieces right.

Part I: A passive mechanical model of horizontal plane dynamics

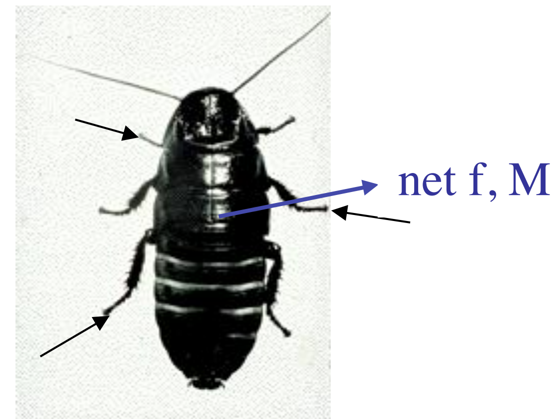
(1998-2007)

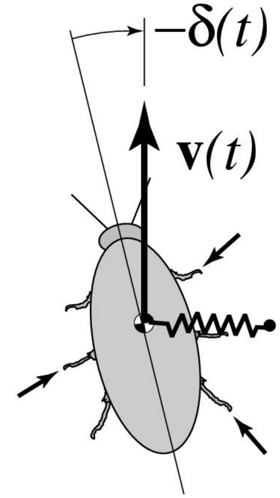
Simple models - LLS

The bipedal Lateral Leg Spring model

The insect: 40+ dof,

100s of parameters.





The LLS model: 3 dof,

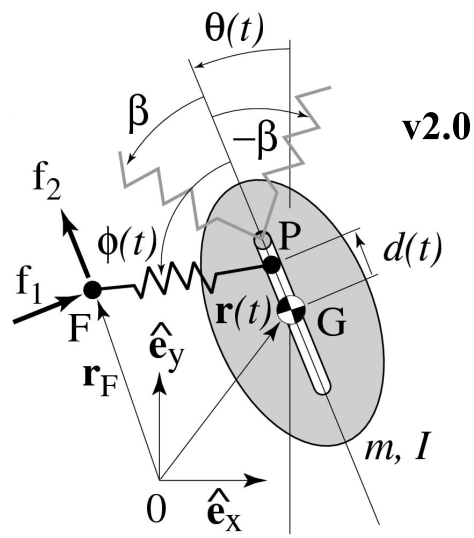
6 parameters:

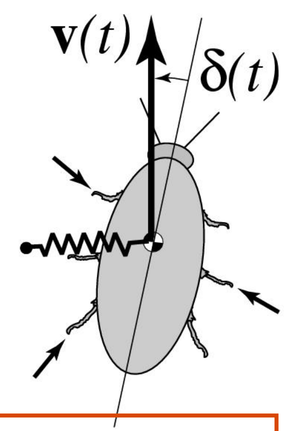
$m,\ I,\ k,\ l,\ d,\ \beta.$

(4 nondimensional:

$\tilde{I} = \frac{I}{ml^2}, \tilde{k} = \frac{kl^2}{mv^2}, \tilde{d} = \frac{d}{l}, \beta).$

+ translation invariance





4 states: $(v, \delta, \theta, \dot{\theta} = \omega)$

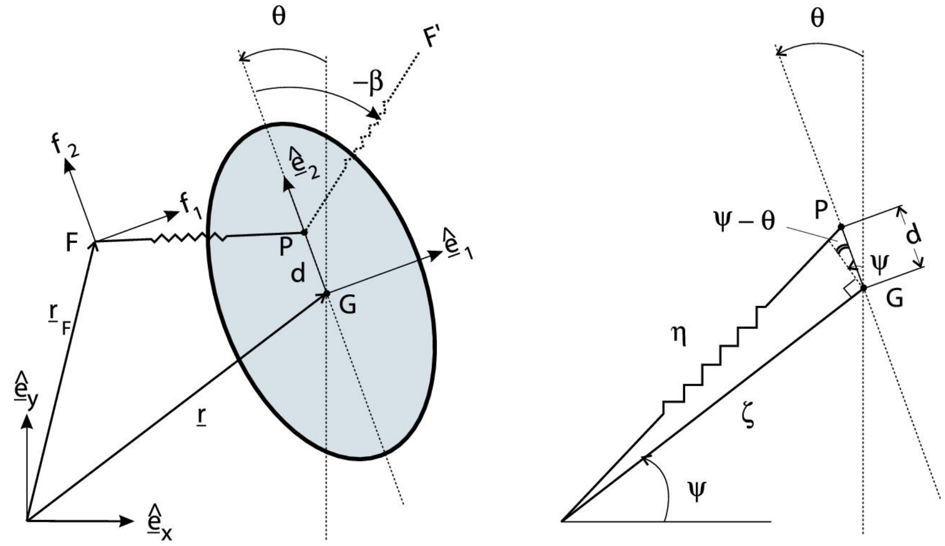
Less is more! Simplify!

J. Schmitt & H, *Biol. Cyb. 83, 86, 89, 2000-2003.*

Newton and Lagrange: a hybrid 3 d.o.f. dynamical system

Simple models - LLS

LLS: equations of motion



(a) (b)

Coupled translation-rotation dynamics: $m\ddot{\mathbf{r}} = \mathbf{R}(\theta)\,\mathbf{f}\,,\ I\ddot{\theta} = (\mathbf{r_F}(t_n) - \mathbf{r}) \times \mathbf{R}(\theta)\,\mathbf{f}\,.$

$\mathbf{f}$ = foot/leg force; $\mathbf{R}(\theta)$ = rotation matrix; $\mathbf{r_F}(t_n)$ = foot position in stance.

During stance, use polar coords about foot:

$$L = \frac{m}{2}(\dot{\zeta}^2 + \zeta^2\dot{\psi}^2) + \frac{I}{2}\dot{\theta}^2 - V(\eta) \ : \ \text{Lagrangian}\,;$$

$$\eta = \sqrt{\zeta^2 + d^2 + 2\zeta d \sin(\psi - (-1)^n\theta))} \ : \ \text{leg length} \begin{cases} n \text{ even L} \\ n \text{ odd R} \end{cases}$$

$$d \equiv d_0\,, \ \text{fixed COP}; \ d = (\psi - (-1)^n\theta))d_1\,, \ \text{moving COP}\,.$$

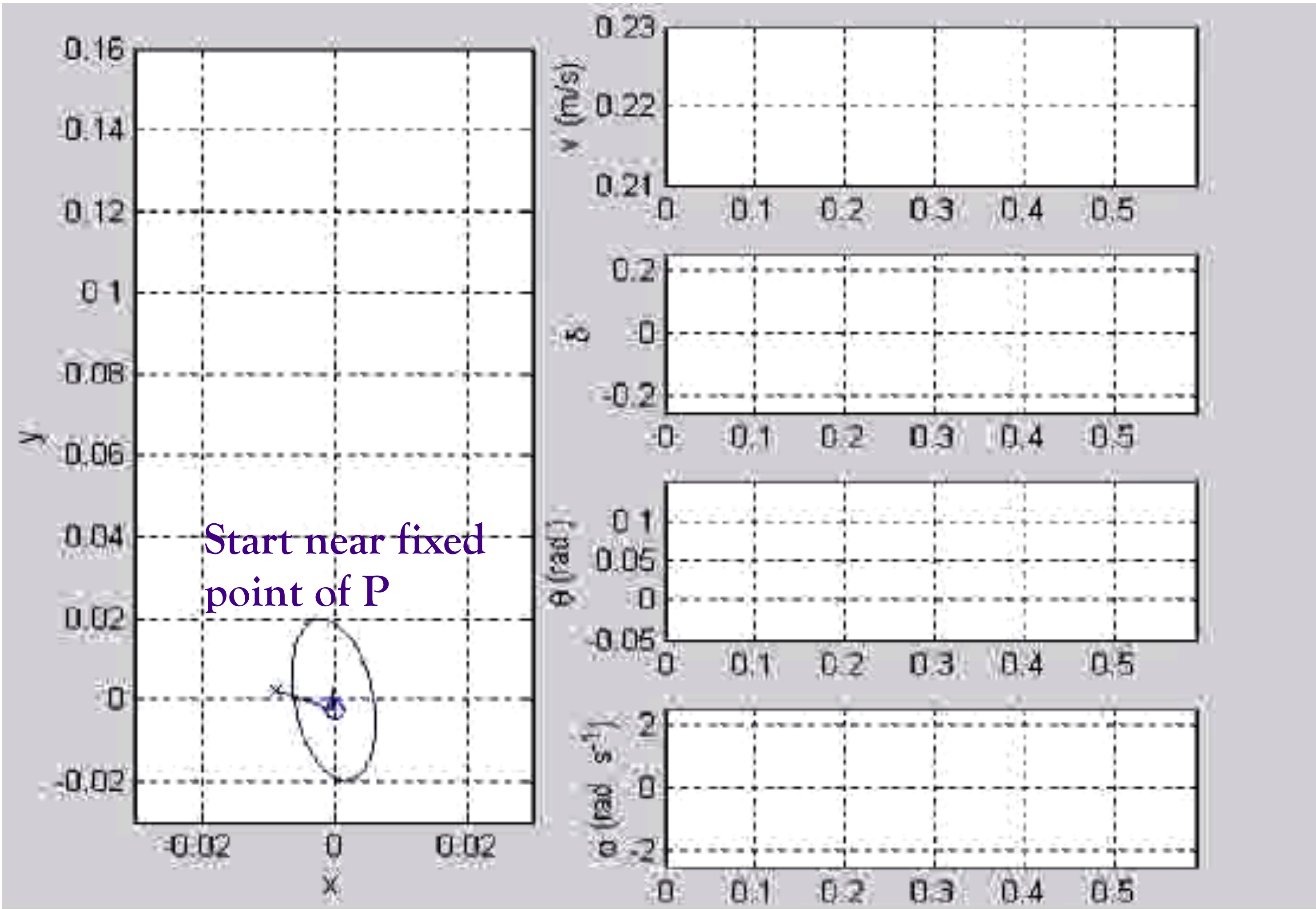
$L_F = m\zeta^2\dot{\psi} \pm I\dot{\theta}$ = AM about stance foot conserved ⇒ **reduces to two dof.**

… it's still non-integrable, but d = 0 yields an integrable hybrid system.

Partial asymptotic stability: she runs straight!

Simple models -- LLS

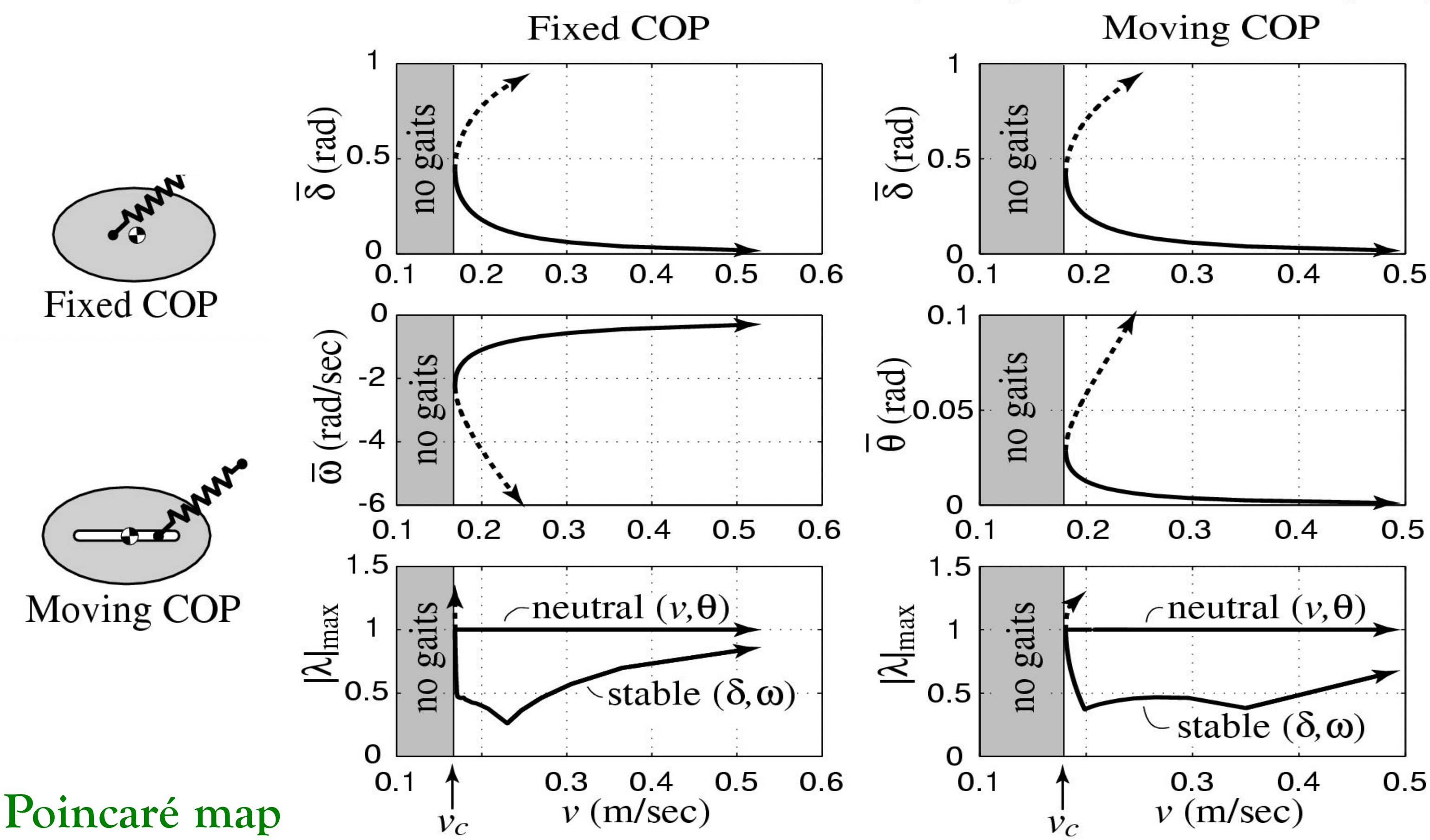
Partial asymptotic **stability** via geometry & piecewise holonomy.



Preflexes: partial asymptotic stability

Simple models - LLS

Branches of stable periodic gaits exist for fixed ($d < 0$) and moving COP ($d \searrow$).



Poincaré map

Eigenvalues of $F_1 \circ F_0$: $\lambda_1 = \lambda_2 = 1$ (v, θ) and $|\lambda_3|, |\lambda_4| < 1$ (δ, ω): **partial asymptotic stability**.

J. Schmitt & H, *Biol. Cyb.* 83, 86, 89, 2000-2003.

Preflexes: partial asymptotic stability

Simple models - LLS

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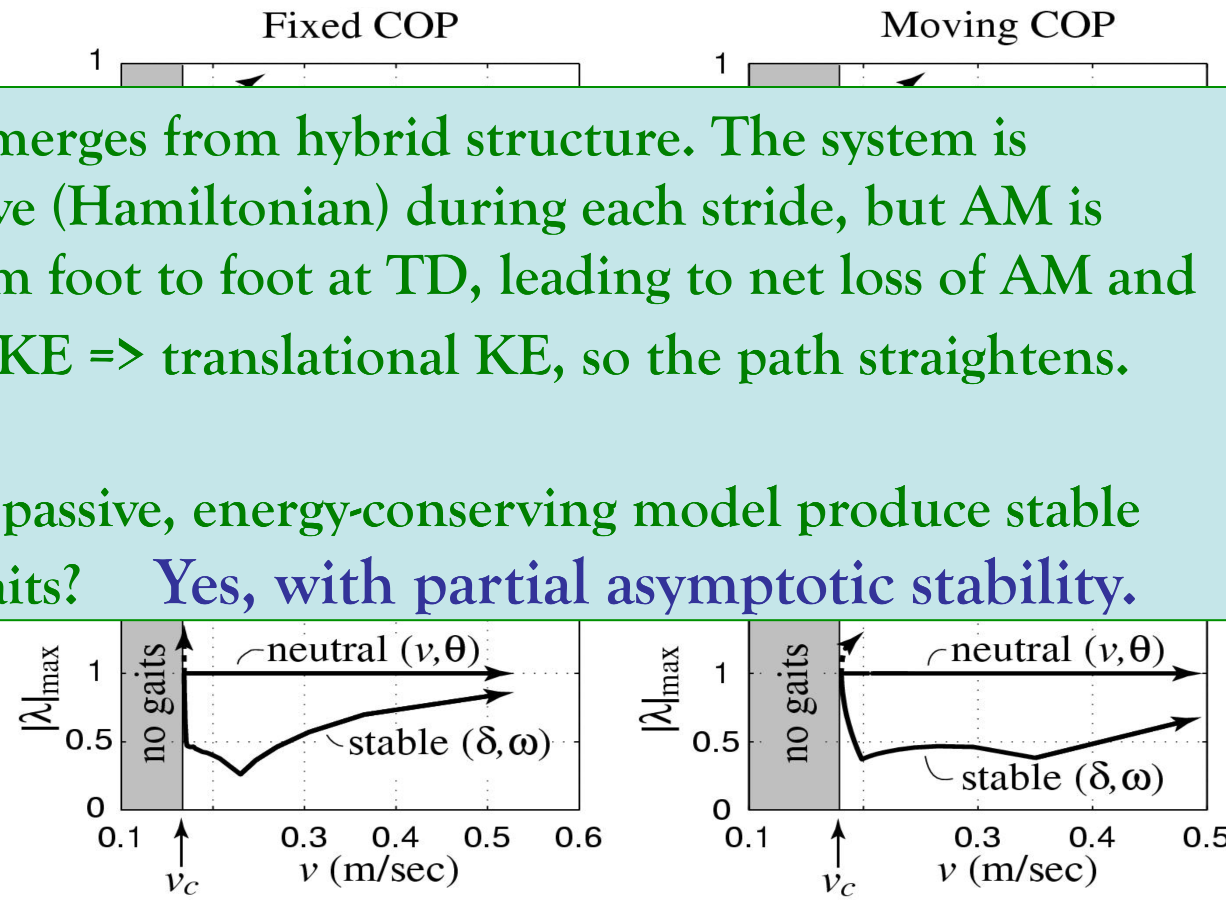


Stability emerges from hybrid structure. The system is conservative (Hamiltonian) during each stride, but AM is traded from foot to foot at TD, leading to net loss of AM and rotational KE => translational KE, so the path straightens.

Q1. Can a passive, energy-conserving model produce stable periodic gaits? **Yes, with partial asymptotic stability.**

Moving COP

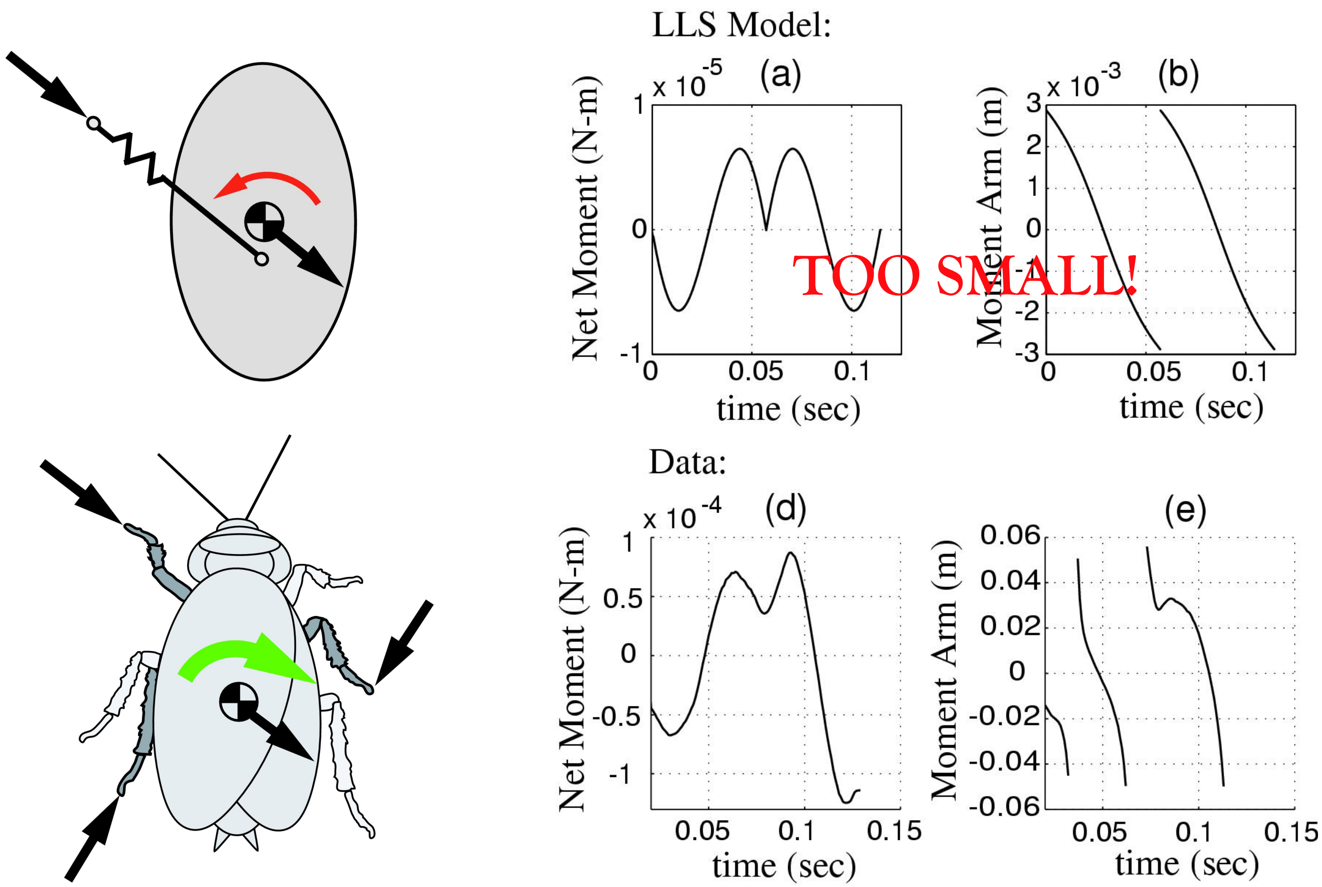
Poincaré map

Eigenvalues of $F_1 \circ F_0$: $\lambda_1 = \lambda_2 = 1$ (v, θ) and $|\lambda_3|, |\lambda_4| < 1$ (δ, ω): **partial asymptotic stability**.

J. Schmitt & H, *Biol. Cyb.* 83, 86, 89, 2000-2003.

Simple models - LLS

COM moments much too small: two legs are not enough!



In stance, insect's support tripod conspires to produce large moments for small net forces.

But the passive LLS model is too simple:

Simple models - LLS

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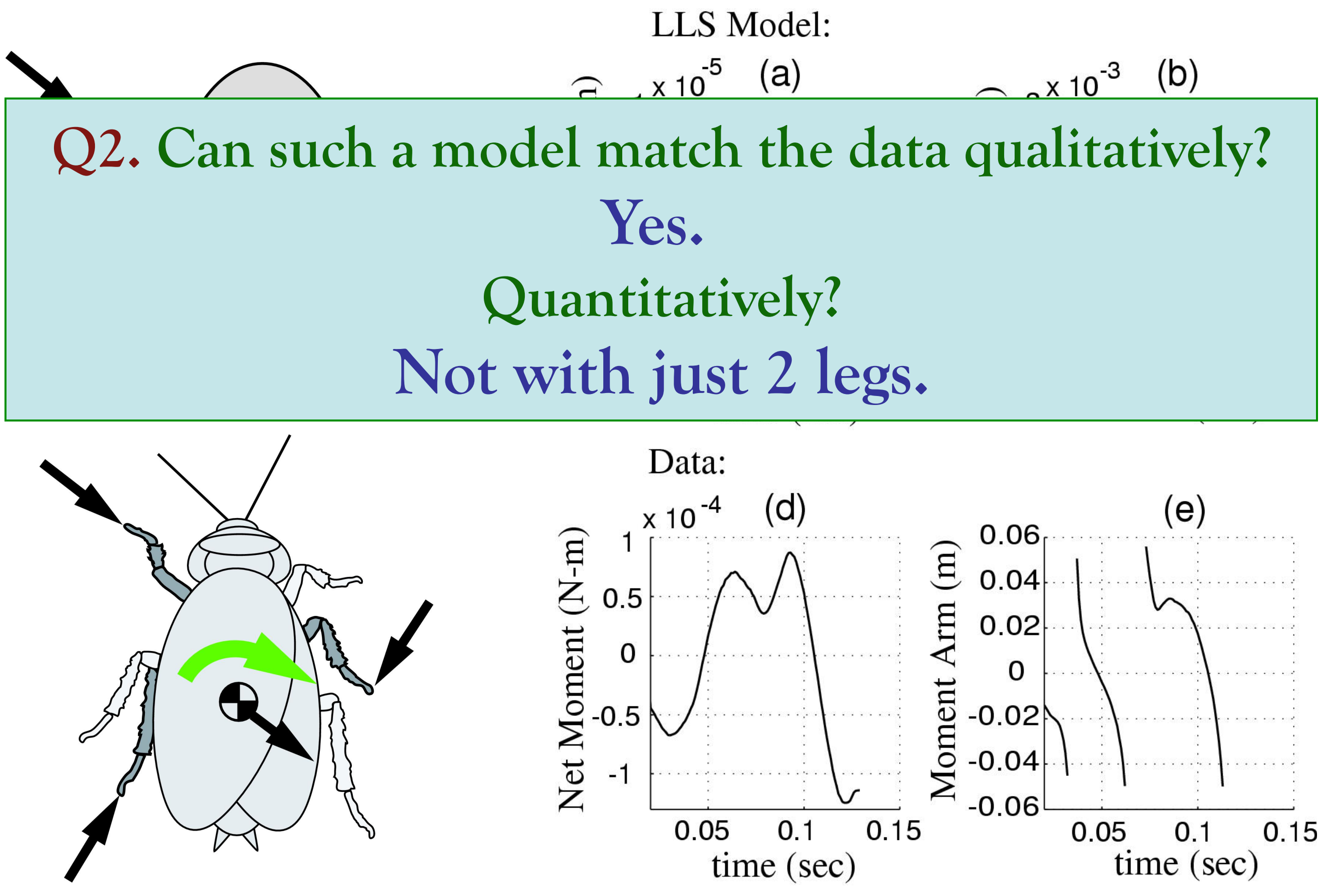


Q2. Can such a model match the data qualitatively?

Yes.

Quantitatively?

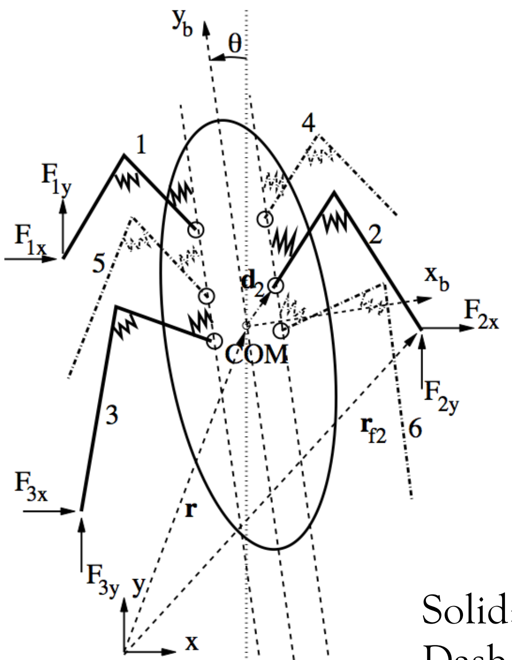
Not with just 2 legs.

In stance, insect's support tripod conspires to produce large moments for small net forces.

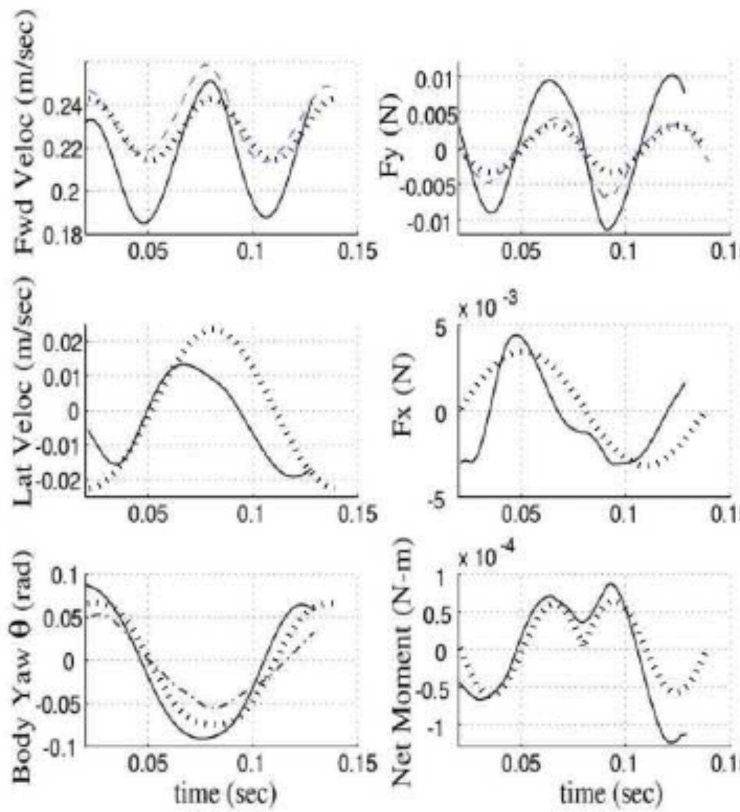
Build a hexapedal mechanical model: get the geometry right

Integrated CPG-muscle-hexapedal models

Given measured foot forces and COM motions, we solve an inverse problem to derive feedforward preferred angles to joints, producing torques and foot forces that match the data. The feedforward model runs like a roach!



Solid: experiment
Dashed: model



R. Kukillaya & H, *Biol. Cybern.* 97, 2007.

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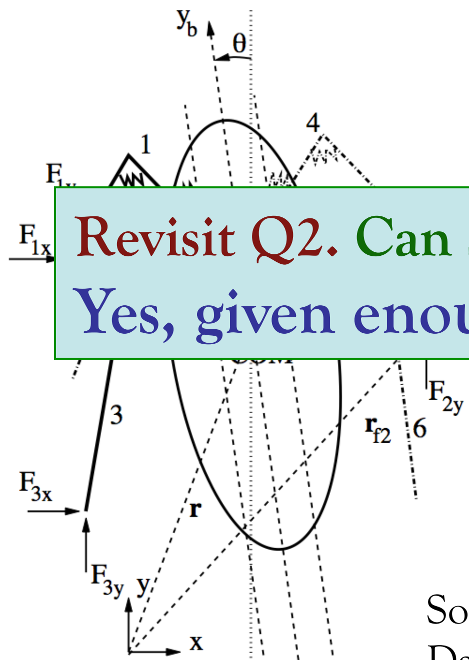
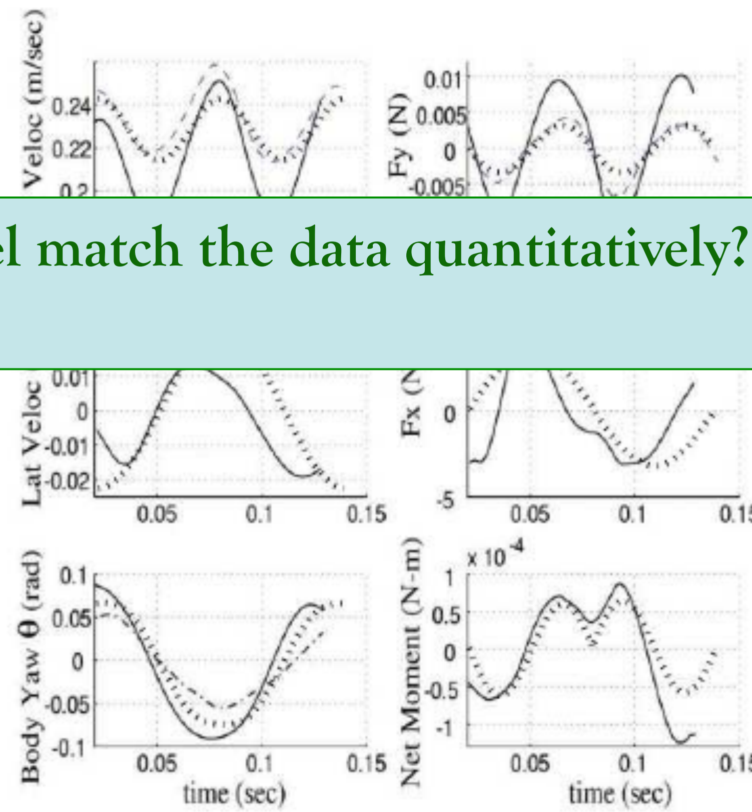




Revisit Q2. Can such a model match the data quantitatively?

Yes, given enough legs,

Solid: experiment
Dashed: model

R. Kukillaya & H, *Biol. Cybern.* 97, 2007.

Part II: An integrated neuromechanical model (2004-2011)

Integrated CPG-muscle-hexapedal models

Central Pattern Generator

CPG is in 3 thoracic hemisegments. When we began, little had been done on cockroaches since the 1970s.

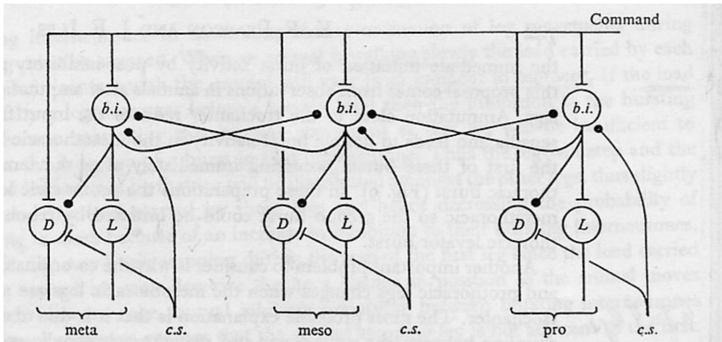
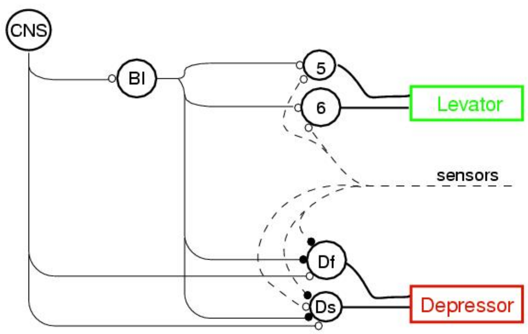
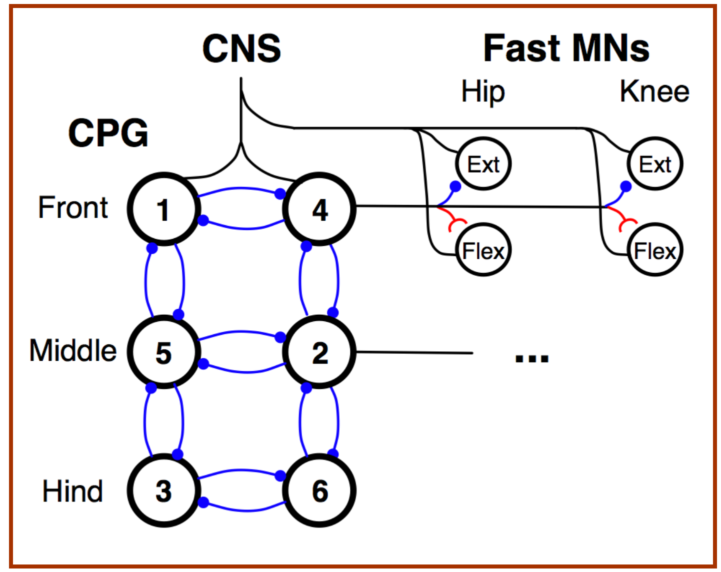


Fig. 11. Hypothetical scheme for describing the patterning of activity in the coxal levator and depressor motoneurones of the homolateral legs during walking. Filled endings, inhibition; bar endings, excitation; *b.i.*, bursting interneurone; *c.s.*, campaniform sensilla; *D*, depressor motoneurones; *L*, levator motoneurones. See text for details.



} ⇒



Each hemisegment

K.G. Pearson et al., 1970-73.

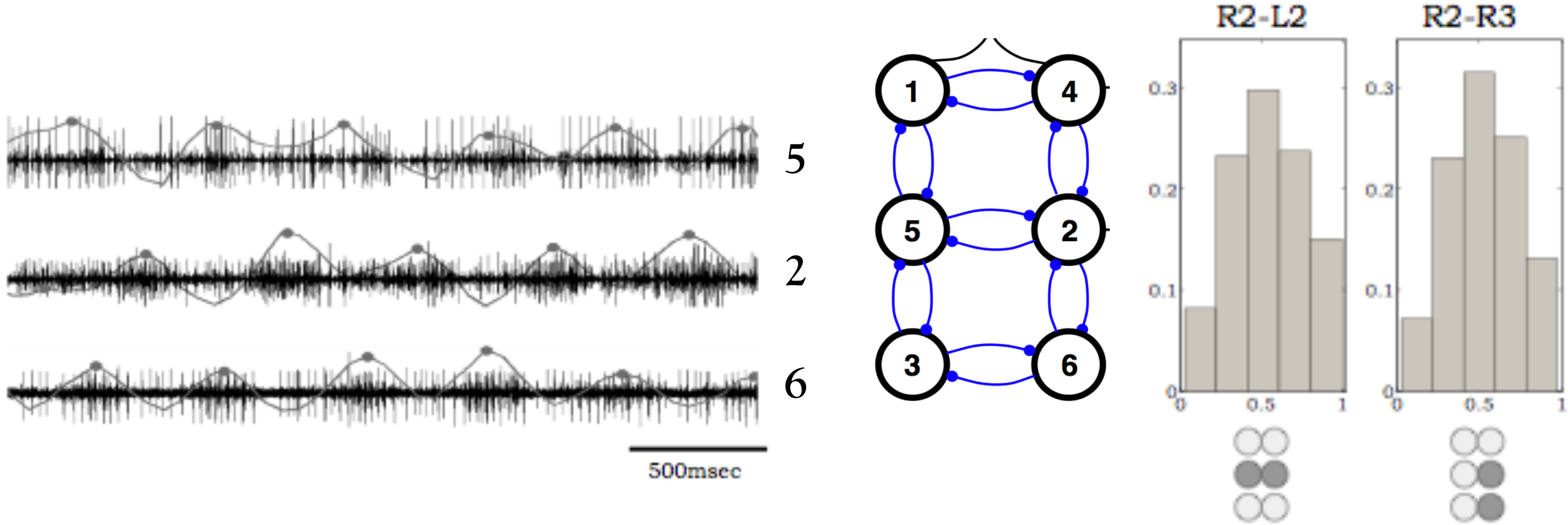
R. Ghigliazza & H, *SIAM J Appl. Dyn. Sys. 3(4), 636 & 671, 2004.*

For mathematical simplicity, and not knowing biology, we chose "symmetric" contra- and ipsi-lateral connection strengths.

Current work on CPGs 1

Hexapedal models - CPG and muscles

New data on P. Americana (Einat Fuchs, Amir Ayali's lab, Tel Aviv U)



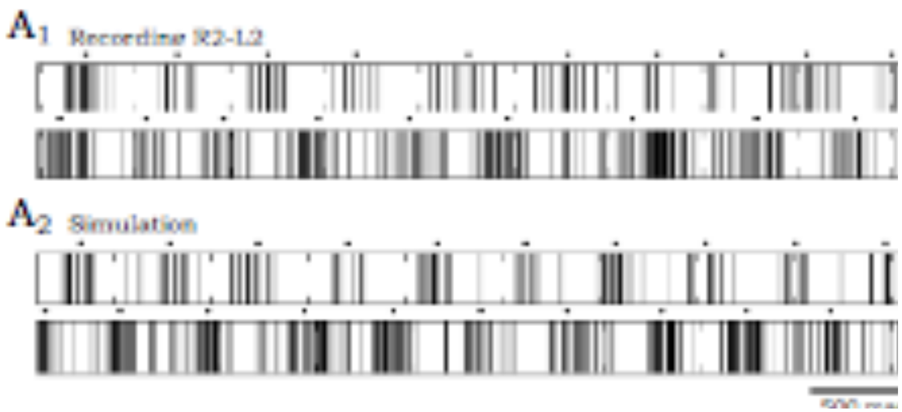
Current work to better characterize cockroach CPG circuit connectivity. Note (variable) double-tripod phasing, evidence of weak inhibitory coupling between neighboring hemiganglia. Method: Deafferent and amputate all legs or leave 1 leg, fix animal above treadmill and stimulate with pilocarpine. Make extracellular recordings from meso- and meta-thoracic ganglia nerves 4 and 5 to legs: depressor (extensor) and levator (flexor) motoneuron axons.

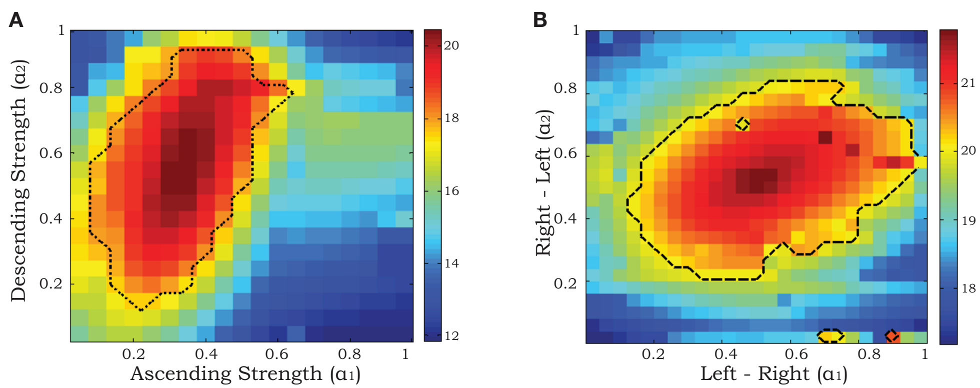
E. Fuchs, H, T. Kiemel & A. Ayali, *Frontiers in Neural Circuits, 2011.*

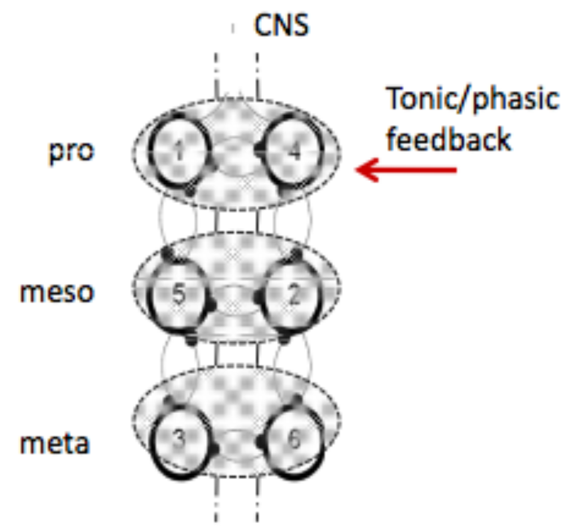
Current work on CPGs 2

Hexapedal models - CPG and muscles

Fit stochastic phase oscillator model to data and estimate coupling strengths







Ipsilateral coupling:
descending > ascending

Contralateral coupling:
equal strengths

E. Fuchs, H, T. Kiemel & A. Ayali *Frontiers in Neural Circuits, 2011.*

Integrated CPG-muscle-hexapedal models

A hexapedal model with a central pattern generator

Main ingredient: **bursting interneurons**, modeled by ion channel (Hodgkin-Huxley type) dynamics, reduced to 3 equations by equilibrating (very) fast gating variables

$$
\begin{aligned}
C\dot{v} &= -[I_{\mathrm{Ca}} + I_{\mathrm{K}} + I_{\mathrm{KCa}} + \bar{g}_{\mathrm{L}}(v - E_{\mathrm{K}})] + I_{\mathrm{syn}} + I_{\mathrm{ext}} \, , \\
\dot{m} &= \frac{\epsilon}{\tau_m(v)} [m_\infty(v) - m] \, , \qquad\qquad \delta \ll \epsilon \ll \frac{1}{C} \, . \\
\dot{c} &= \frac{\delta}{\tau_c(v)} [c_\infty(v) - c] \, ;
\end{aligned}
$$

$$
I_{\mathrm{Ca}} = \bar{g}_{\mathrm{Ca}} n_\infty(v)(v - E_{\mathrm{Ca}}) \, , \quad I_{\mathrm{K}} = \bar{g}_{\mathrm{K}} m \cdot (v - E_{\mathrm{K}}) \, , \quad I_{\mathrm{KCa}} = \bar{g}_{\mathrm{KCa}} c \cdot (v - E_{\mathrm{KCa}}) \, .
$$

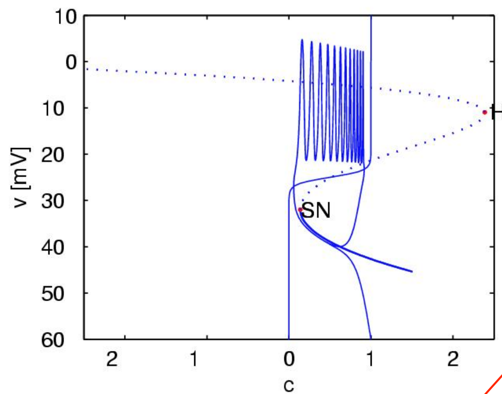
Synaptically coupled

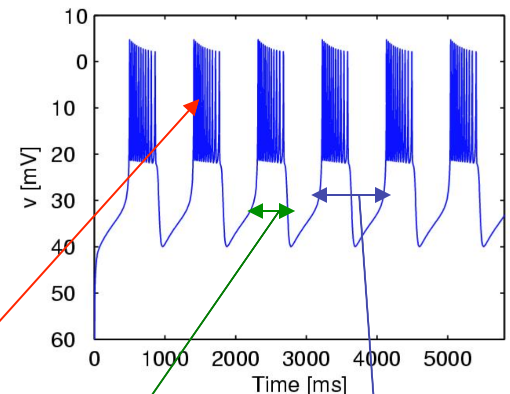
via I_{syn}:

$$\dot{s} = \frac{s_\infty(1-s)-s}{\tau_{\mathrm{syn}}} \, ,$$

$$s_\infty = \frac{1}{1+e^{-k_{\mathrm{syn}}(v-v_{\mathrm{syn}})}} \, ,$$

$$I_{\mathrm{syn}} = \bar{g}_{\mathrm{syn}} s(v - v_{\mathrm{syn}}) \, .$$



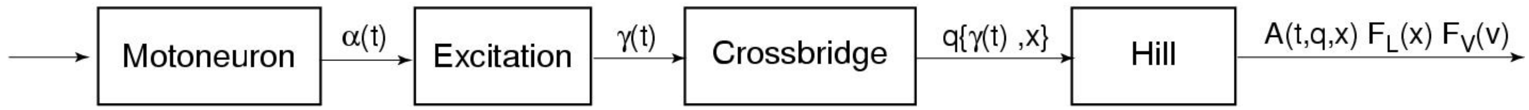


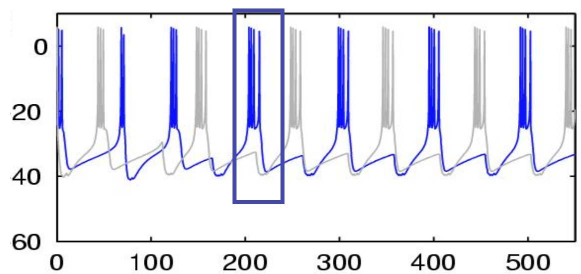
Key output params: Spiking freq. Duty cycle Stepping freq. Need to understand how input currents and conductances tune them.

Muscles

Integrated CPG-muscle-hexapedal models

Calcium release and uptake dynamics: a model for muscles (after A.V. Hill)

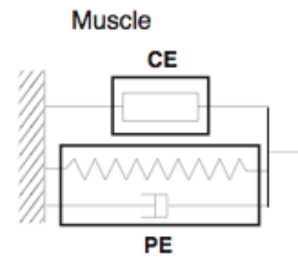




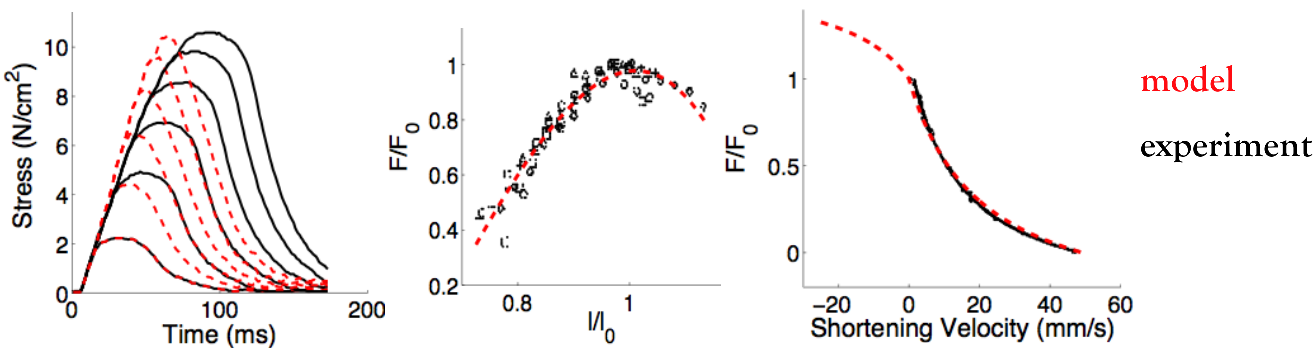
+

$$\ddot{\beta} + c_1\dot{\beta} + c_2\beta = c_3 u(t),$$
$$\ddot{\eta} + c_4\dot{\eta} + c_5\eta = c_6\beta(t),$$

$$A(t) = \frac{a_0 + (\rho\eta)^2}{1 + (\rho\eta)^2}.$$



$$F(t) = F_0 \times A(t) \times F_l(l/l_0) \times F_v(v/v_{\max})$$

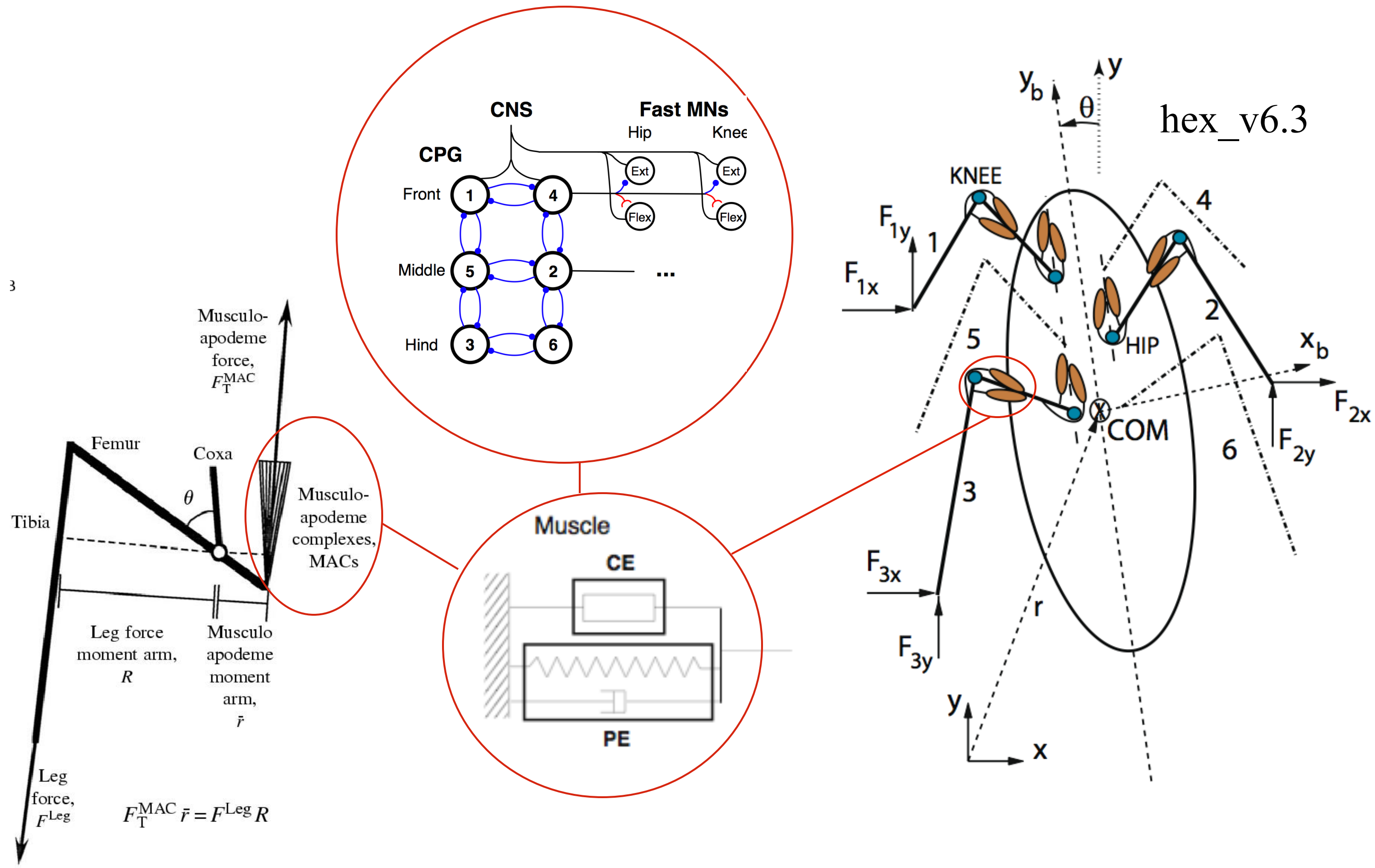


Match isolated EMG, isometric & const. veloc muscle data from Ahn, Meijer & Full, *1998-2006*.

Build the entire (brainless) beast:

Integrated CPG-muscle-hexapedal models

Inserting extensor-flexor muscle pairs at each joint, motoneurons and the CPG, we assemble an integrated neuromechanical model.

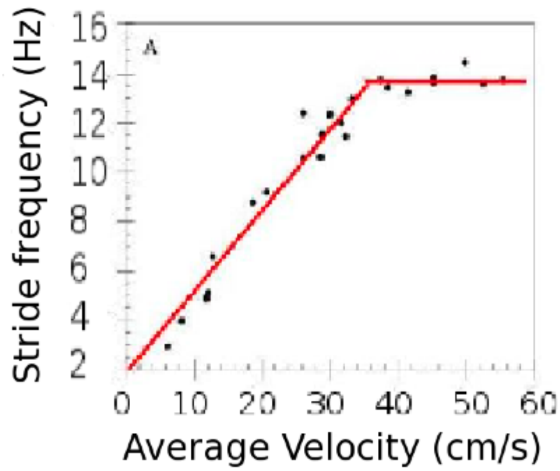


R. Kukillaya & H, *J Theor. Biol., 2009;*
R. Kukillaya, J. Proctor & H, *CHAOS 19, 2009.*

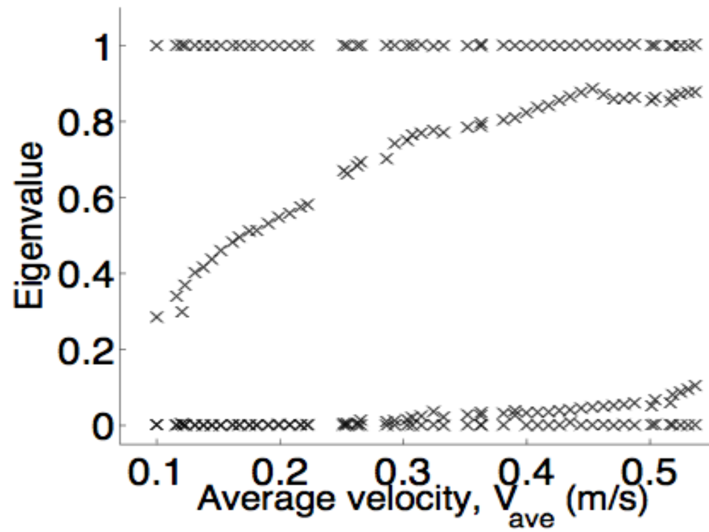
Let her run:

Integrated CPG-muscle-hexapedal models

With appropriate spike inputs, leg cycle frequency and stride length variations, a branch of stable gaits exists over the physiological speed range. Again we use stride-to-stride Poincaré maps. Note 2 strongly stable modes, one weakly stable, one neutral (rotational invariance).



Black: expt.
Red: model.



Eigenvalue dependence on speed;
eigenvectors reveal local dynamical geometry.

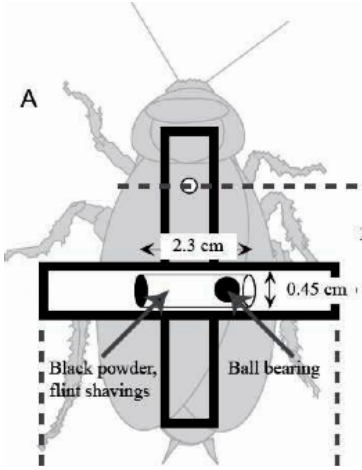
L. H. TING[1], R. BLICKHAN[2] AND R. J. FULL[1],
J. exp. Biol. ***197***, *251–269 (1994)*

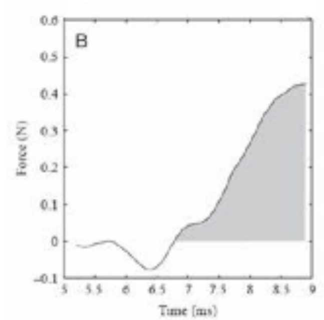
R. Kukillaya & H, *J. Theor. Biol. 261, 2009.*
R. Kukillaya, J. Proctor & H, *Chaos 19, 2009.*

Test the model: A bug with a cannon

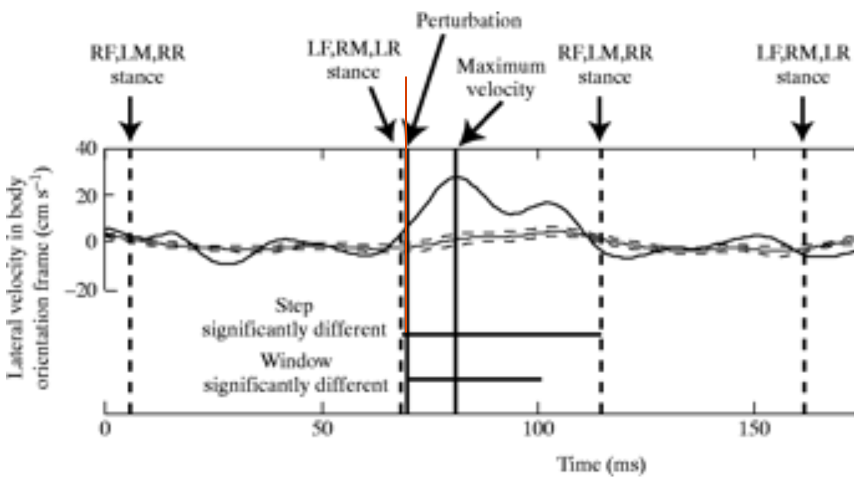
Stability: experimental evidence for preflexes:

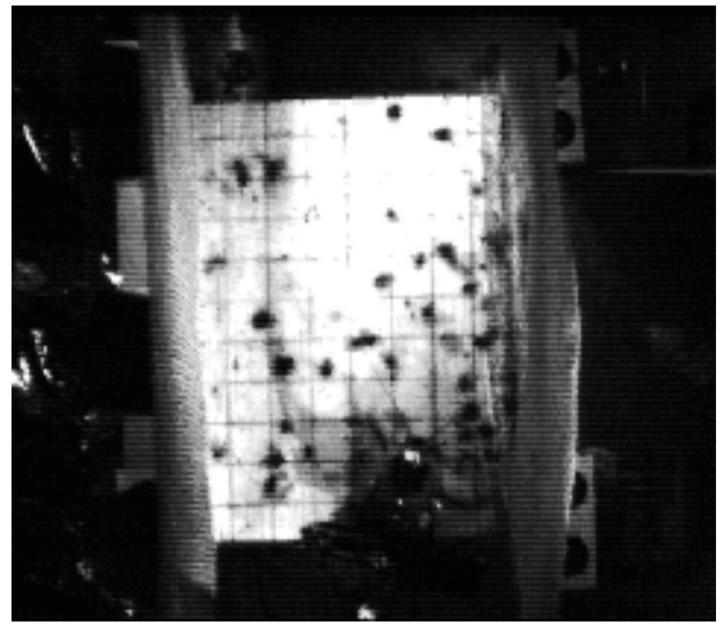
a rapid impulse perturbation (RIP), and its consequences.





Force impulse





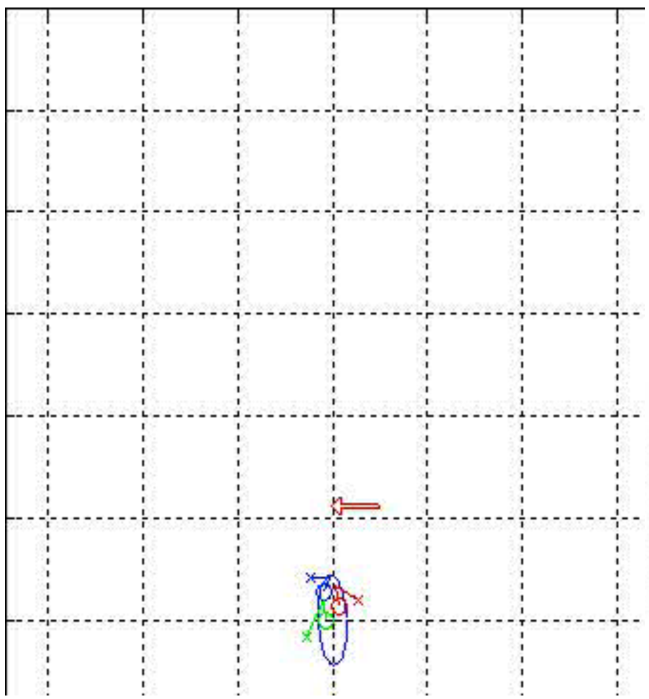
Recovery within 1 stride: 15-35 msec: too fast for neuromuscular corrections via proprioceptive sensory system.

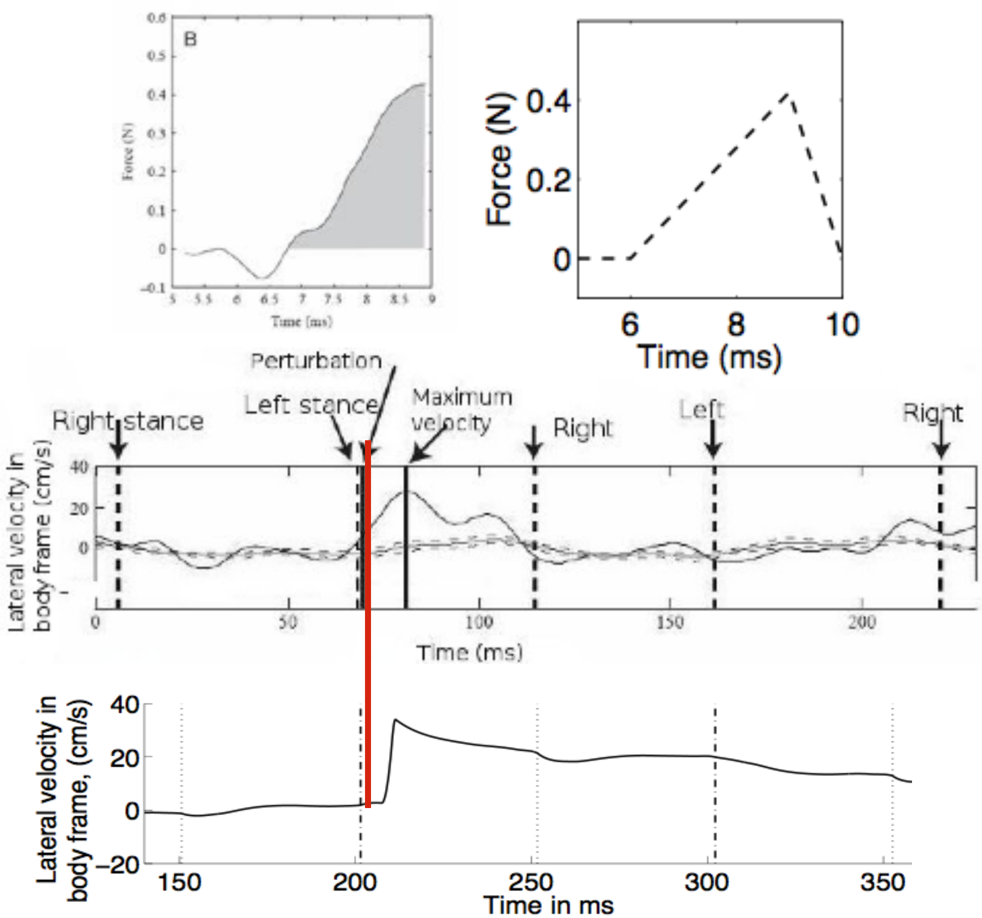
D. Jindrich & Full, *J Exp. Biol. 205, 2002.*

The model recovers similarly

Integrated CPG-muscle-hexapedal models

We apply RIP to the model, without corrective steering, showing that the purely feedforward actuated system is also preflexively stable.





R. Kukillaya, J. Proctor & H, *CHAOS 19, 2009.*

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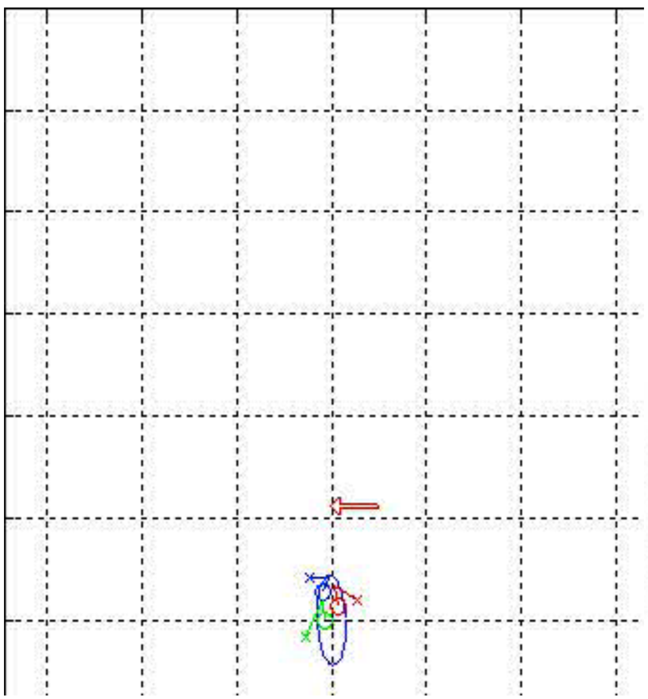
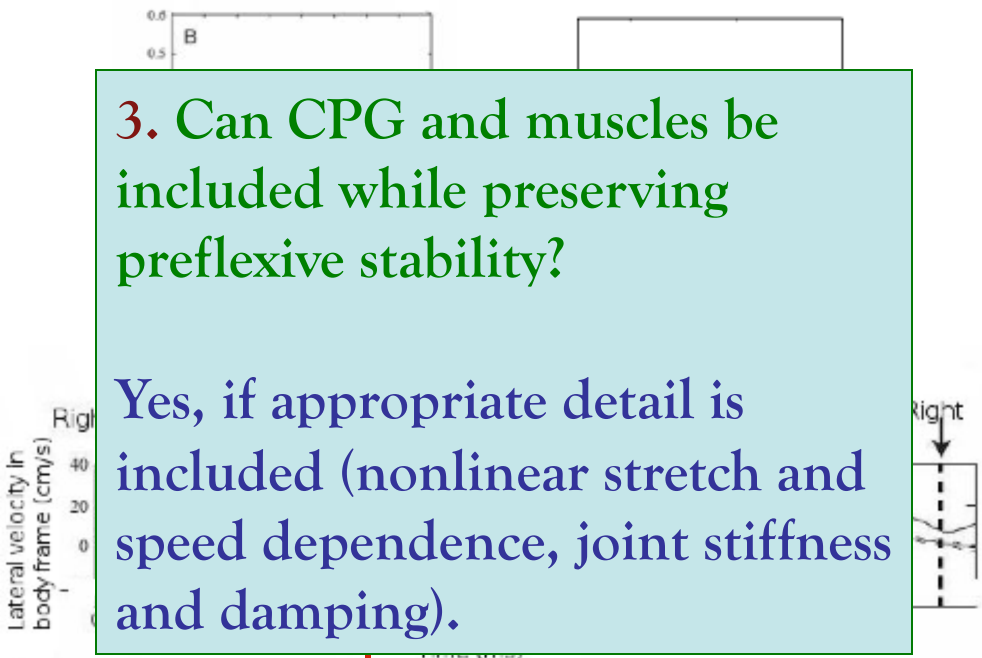
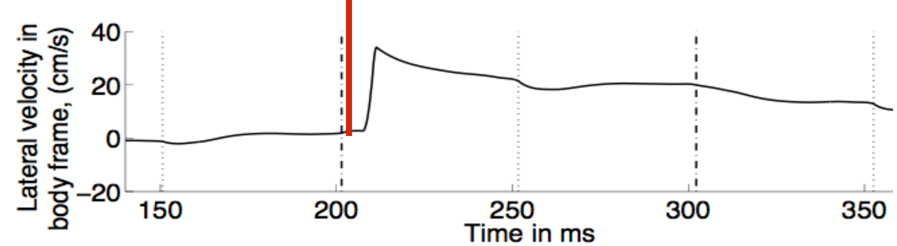




3. Can CPG and muscles be included while preserving preflexive stability?

Yes, if appropriate detail is included (nonlinear stretch and speed dependence, joint stiffness and damping).



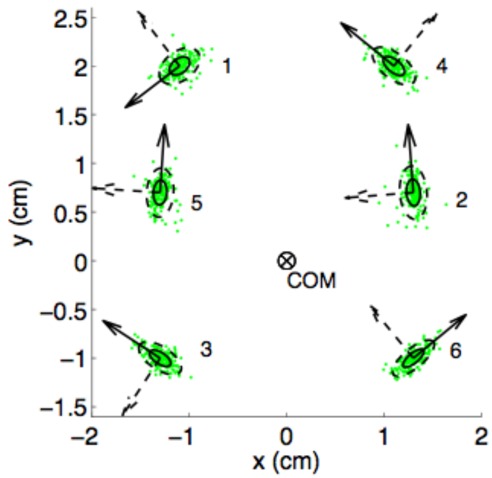
R. Kukillaya, J. Proctor & H, *CHAOS 19, 2009.*

Random perturbations

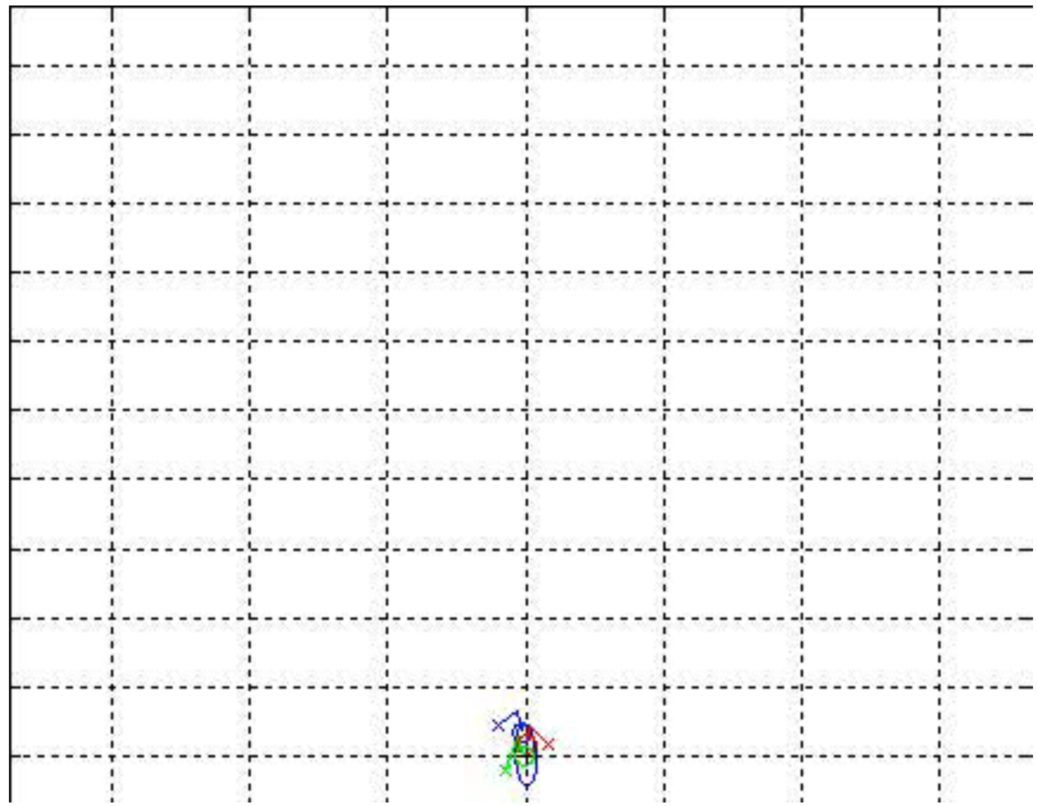
Integrated CPG-muscle-hexapedal models

Stability 2: the model is robust to realistically variable touchdown foot placements (without reflexive feedback)

Data supplied by Shai Revzen, Polypedal Lab, UC Berkeley.



PCA analysis of video from running roaches, fit Gaussian distributions of TD positions in body frame.

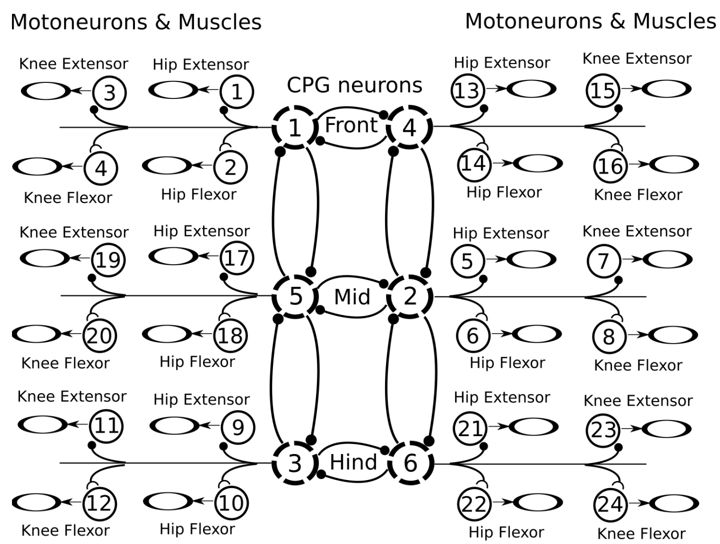


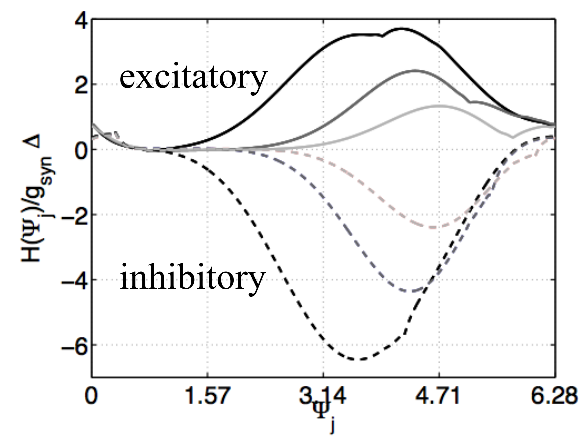
Fast eigenvalues filter out high frequencies, leave slow heading changes, easily corrected by steering. Also robust to variable neural spike timing.

Part III: Phase reduction and proprioceptive feedback (2004-2012)

Phase-reduced CPG-muscle-hexapedal models

The full model has almost 300 ODEs! It's effectively unanalyzable. But since the feedforward CPG-motoneuron subsystem has a "big" periodic orbit, we can use **phase reduction** to eliminate all but the 24 motoneuron phases, to which reflexive feedback is applied. **264 neural ODEs collapse to 24 ODEs.** Great simulation speedup **and improved understanding.**





joint torque feedback.

1 phase eqn for each MN

$$\dot{\psi}_j = G_{1j}(\psi_j - \psi_1) + h^E_{sj}(\psi_j + \omega_0 t, t) + h^I_{sj}(\psi_j + \omega_0 t, t); \; j = 1, \cdots, 24.$$

CPG clock input.

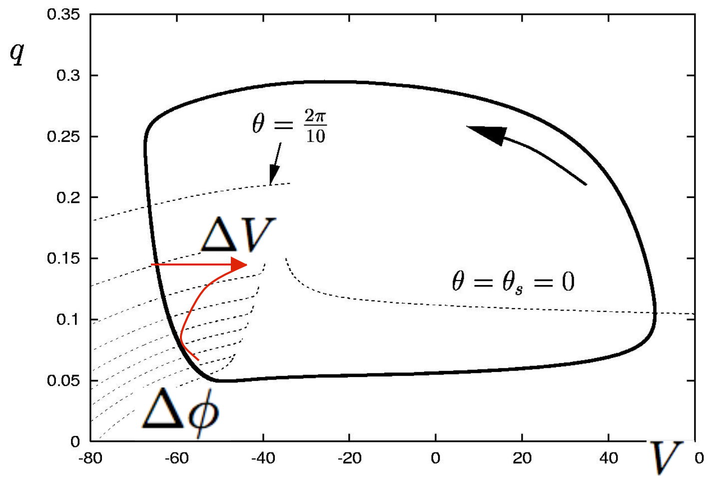
J. Proctor, R. Kukillaya & H, *Phil. Trans Roy. Soc. A, 2010.*

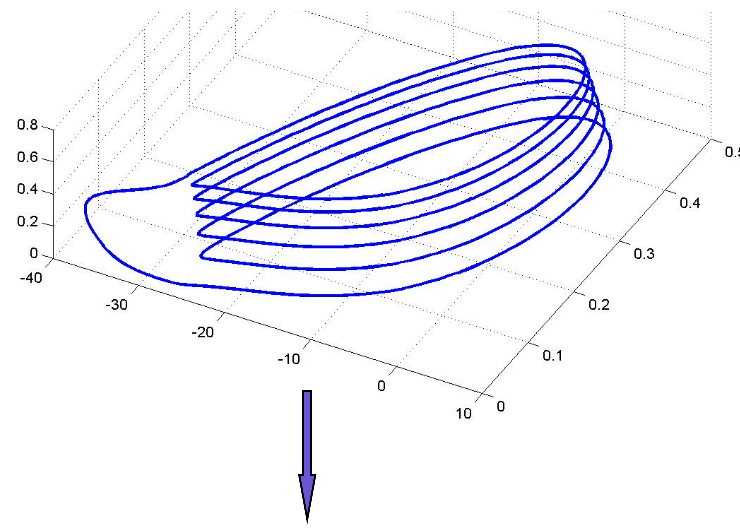
Simplify! Reduce each oscillator state to a single phase angle

Phase-reduced CPG-muscle-hexapedal models

Good coordinates! Phase response curves (PRC) for periodically bursting cells:

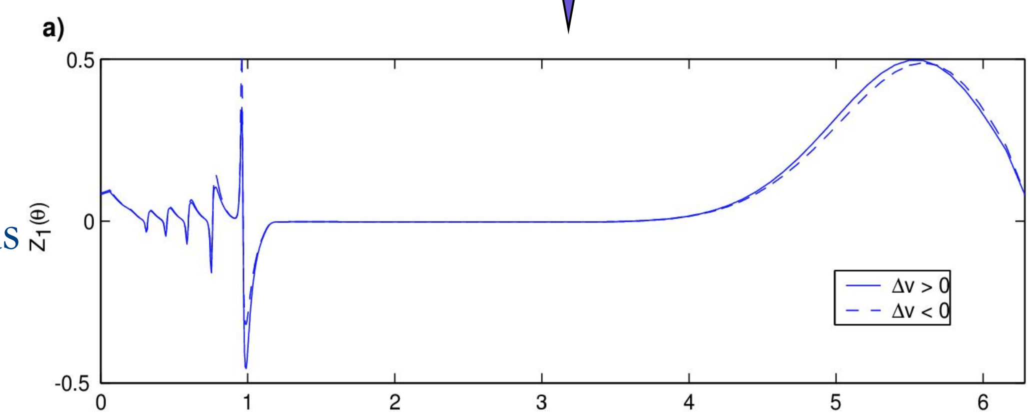
I. Malkin, A. Winfree, J. Guckenheimer, G.B. Ermentrout





$$\text{PRC} = \frac{\Delta\phi}{\Delta V} \overset{\text{def}}{=} Z(\phi);$$

$$\dot{\phi} = \omega + Z(\phi)[\text{inputs}].$$



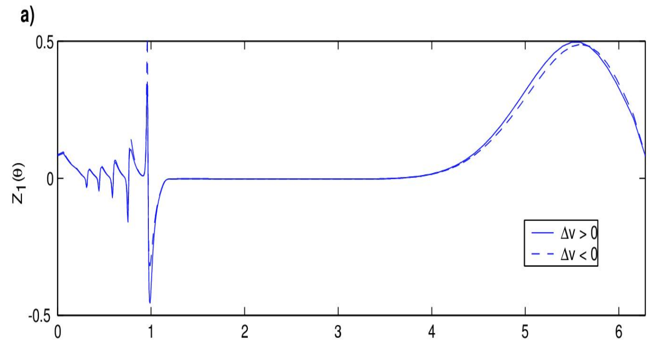
PRC tells how phases shift as a function of input phase, explain coordination.

Simplify further: average over the step period

Phase-reduced CPG-muscle-hexapedal models

Use **phase response curves (PRCs)**. For a pair of identical oscillators, coupled via mutual inhibition (half-center model), 8 ODEs reduce to 1, for phase differences.

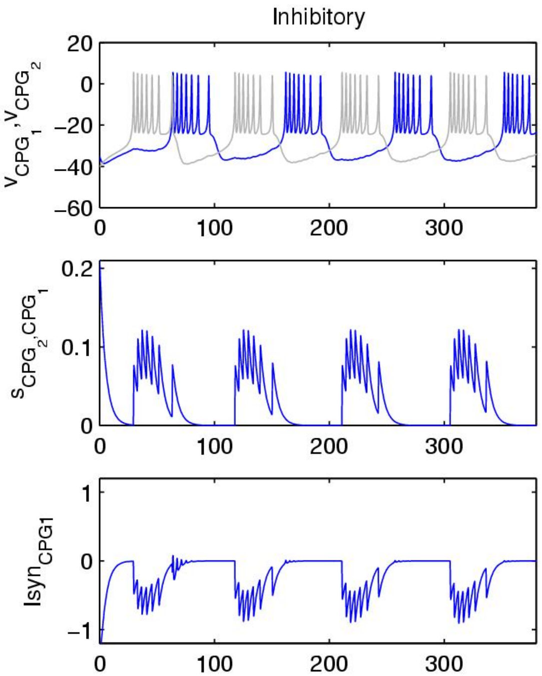
I. Malkin, A. Winfree, G.B. Ermentrout



$$\dot{\phi}_1 = \omega_0 + \alpha_1 Z(\phi_1) f(\phi_1, \phi_2),$$

$$\dot{\phi}_2 = \omega_0 + \alpha_2 Z(\phi_2) f(\phi_2, \phi_1),$$

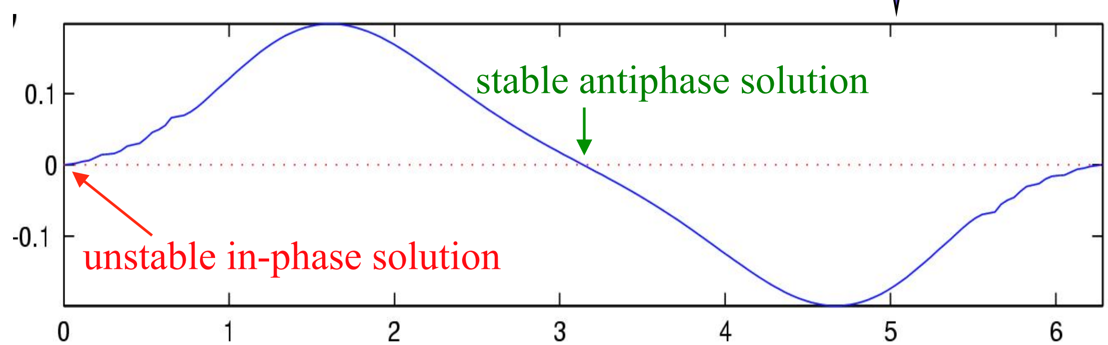
Let $\phi_j = \omega_0 t + \psi_j$ and average over "fast" time:



$$\dot{\psi}_1 = \alpha_1 H(\psi_1 - \psi_2),$$

$$\dot{\psi}_2 = \alpha_2 H(\psi_2 - \psi_1),$$

subtract $\Rightarrow$ $\dot{\psi}_1 - \dot{\psi}_2 = G_\alpha(\psi_1 - \psi_2).$

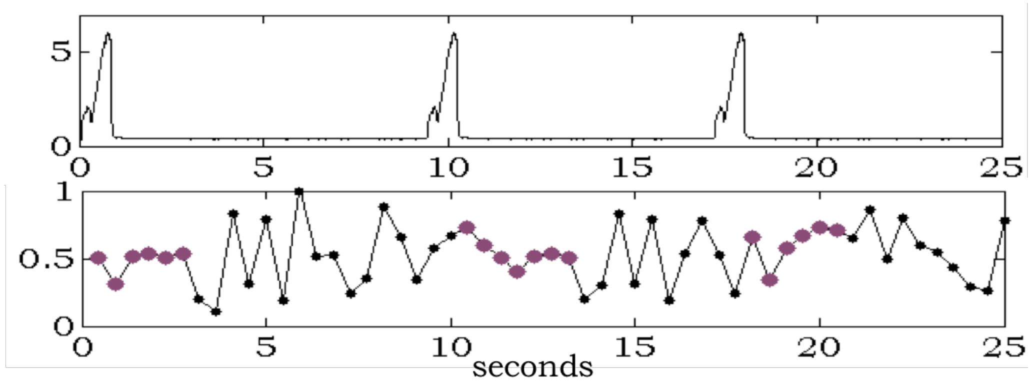


R. Ghigliazza & H, *SIAM J Appl. Dyn. Sys.* 3, 2004.

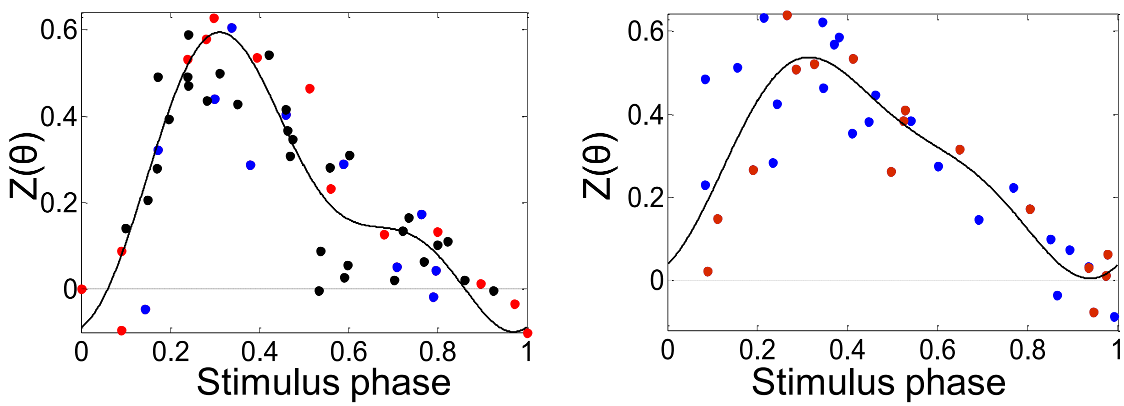
Current work on CPGs 3

Phase-reduced CPG-muscle-hexapedal models

Proprioceptive feedback from stepping leg reduces phase variability:



Can estimate phase response curves (PRCs) from data:

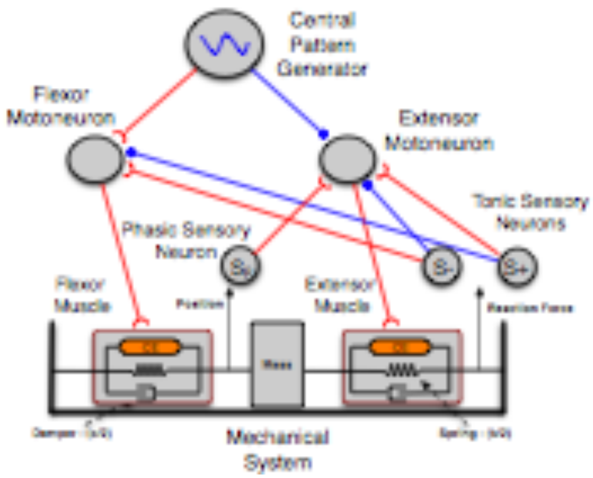


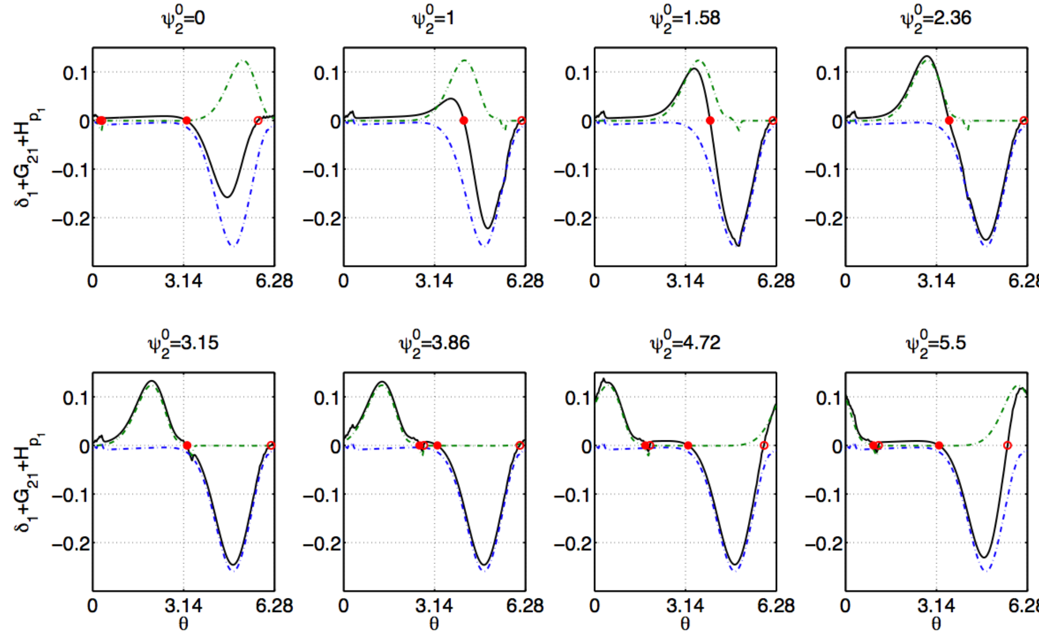
E. Fuchs, H, I.David & A. Ayali *J. Exp. Bio. 215, 2012.*

Add proprioceptive feedback

Phase-reduced CPG-muscle-hexapedal models

Add proprioceptive sensing: tonic feedback of forces (joint torques) and phasic feedback of joint angles and angular velocities are all available to the insect. Start with a simple 1 degree of freedom joint.





$$\dot{\psi}_j = G_{1j}(\psi_j - \psi_1) + h^E_{sj}(\psi_j + \omega_0 t, t)$$

Phasic feedback of joint angle: in phase reduced theory, coupling functions from CPG (blue) and reflexive circuit (green) add linearly, shift phase of MN spikes to modify forces. Phase reduction illuminates feedback mechanisms.

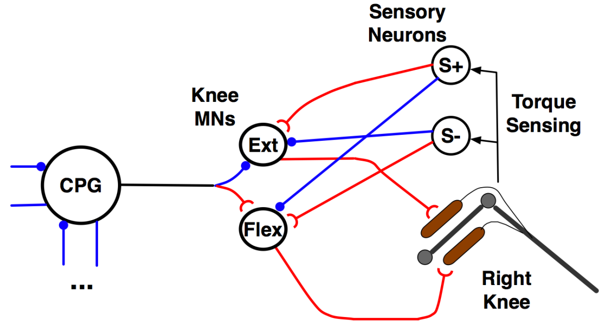
J. Proctor & H, *Biol. Cybern. 2010.*

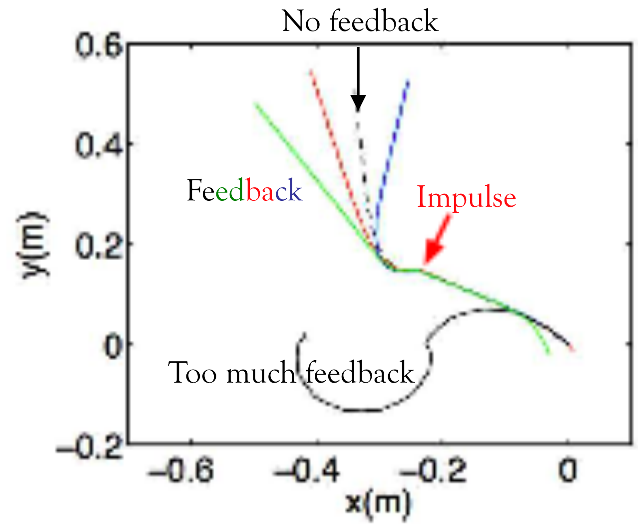
The phase-reduced model with proprioceptive feedback

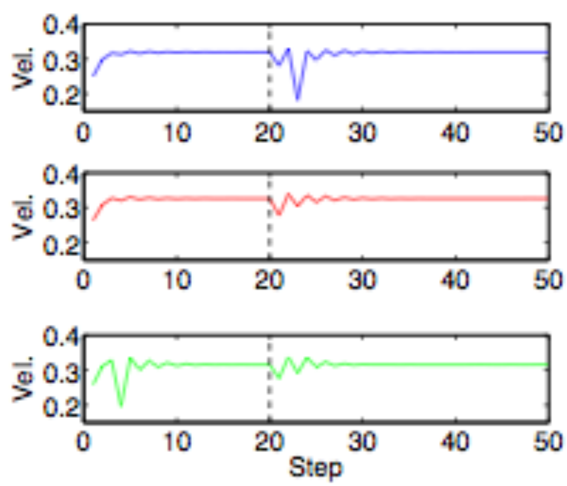
Phase-reduced CPG-muscle-hexapedal models

Tonic (spike rate) feedback of joint torques: model campaniform sensilla that sense forces in exoskeleton, excite and inhibit appropriate motoneurons to compensate for applied loads.

Feedback circuit for each leg







Body paths with, without, and with too much feedback, in response to impulsive perturbation. Needs right balance of excitation and inhibition to minimize effect (net angle turned).

J. Proctor, R. Kukillaya, H, *Phil. Trans. Roy. Soc. A. 2010.*
J. Proctor, PhD thesis, 2011.

The phase-reduced model with proprioceptive feedback

Phase-reduced CPG-muscle-hexapedal models

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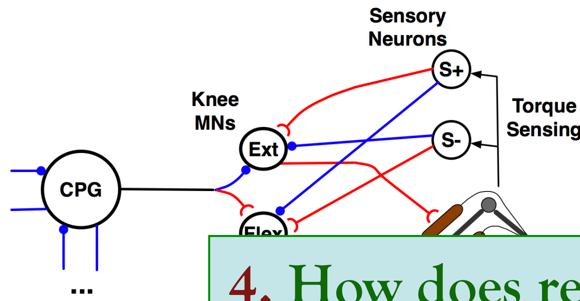
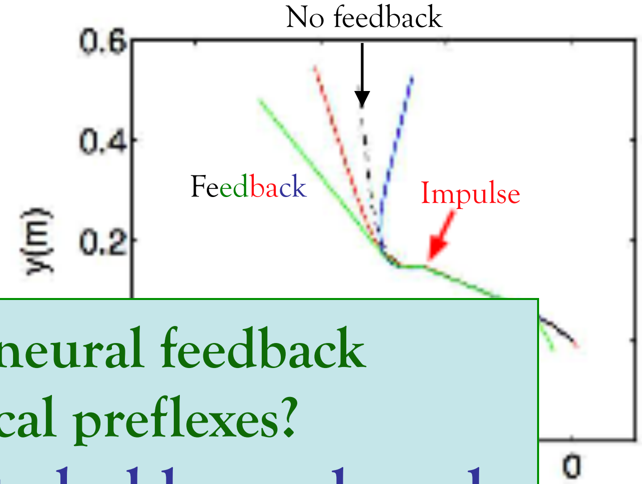
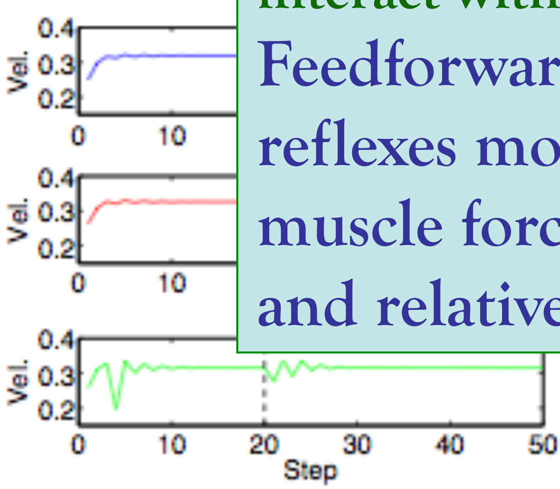






oo much

rturbation.

inhibition

4. How does reflexive neural feedback interact with mechanical preflexes?

Feedforward stability holds good, and reflexes modify spike timing to tune muscle forces. The effects are small, and relatively slow (30+ msec).

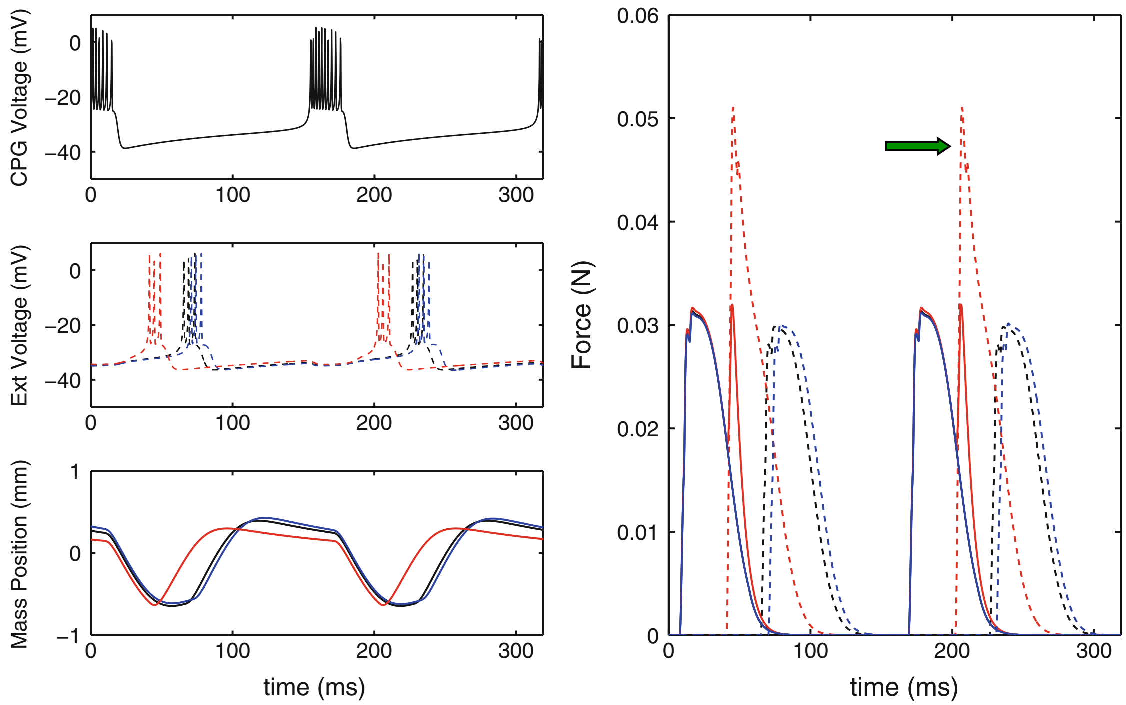
J. Proctor, R. Kukillaya, H, *Phil. Trans. Roy. Soc. A. 2010.*
J. Proctor, PhD thesis, 2011.

Synergies between motoneuron spikes and muscle states

Phase-reduced CPG-muscle-hexapedal models

Recall that muscle forces are greatest when activations arrive during muscle lengthening. E.g., phasic position feedback can prevent leg overswing.

Fig. 9 Effects of phasic feedback on periodic mass motions. *Left*: CPG and extensor motoneuron bursts (*top and middle*) and mass position (*bottom*) without feedback (*black*) and with phasic feedback at $L^0 = -1.25 \times 10^{-4}$ with $\dot{x} < 0$ (*red*) and $L^0 = -5.78 \times 10^{-4}$ with $\dot{x} > 0$ (*blue*). *Right*: corresponding forces in extensor (*dashed*) and flexor (*solid*); color key as at left



Black: no feedback – solid: flexor force, dashed – extensor force.
Red: early excitatory feedback to flexor MN, before max flexion.
Blue: late excitatory feedback to flexor MN, after max flexion.

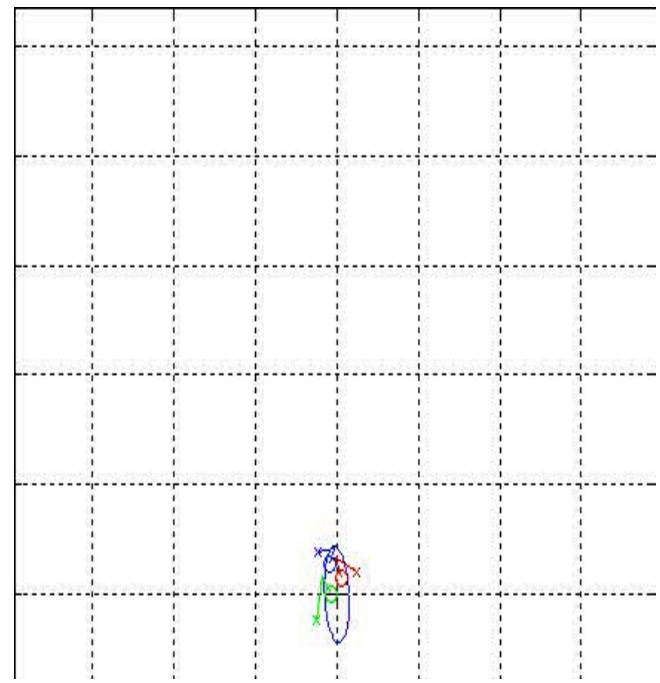
J. Proctor & H, *Biol. Cybern. 2010*; cf. E.D. Tytell, H and A.H. Cohen, *Curr. Op. in Neurobiol. 2011.*

Maneuvers

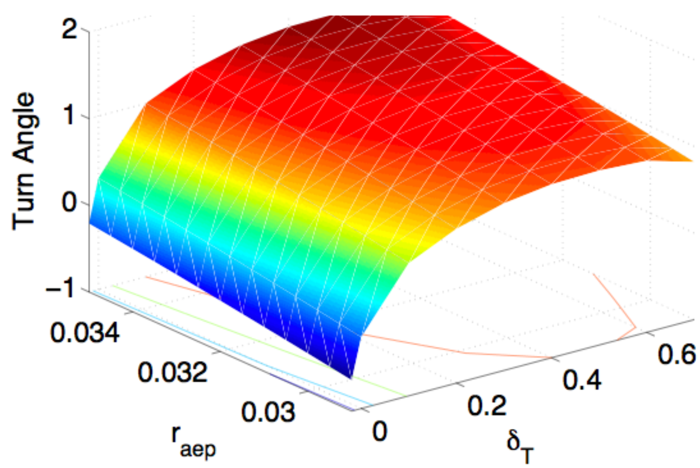
Phase-reduced CPG-muscle-hexapedal models

Steer by adjusting foot positions at TD to make the weakly-stable mode unstable; transient feedforward control. Motivated by experiments.

Hexapod: extend front leg further at TD, advance MN spike to middle leg extensors. Turn shown with random TD perturbations.



3 step turn map



D. Jindrich & R.J. Full, *J. Exp Biol. 202, 1999.*
J. Proctor & H, *Reg & Cha. Dyn., 13(4), 2008.*

Maneuvers

Phase-reduced CPG-muscle-hexapedal models

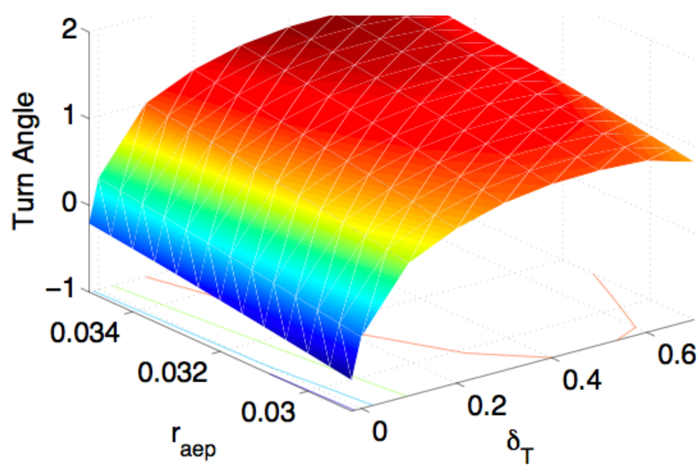
Steer by adjusting foot positions at TD to make the weakly-stable mode unstable; transient feedforward control. Motivated by experiments.

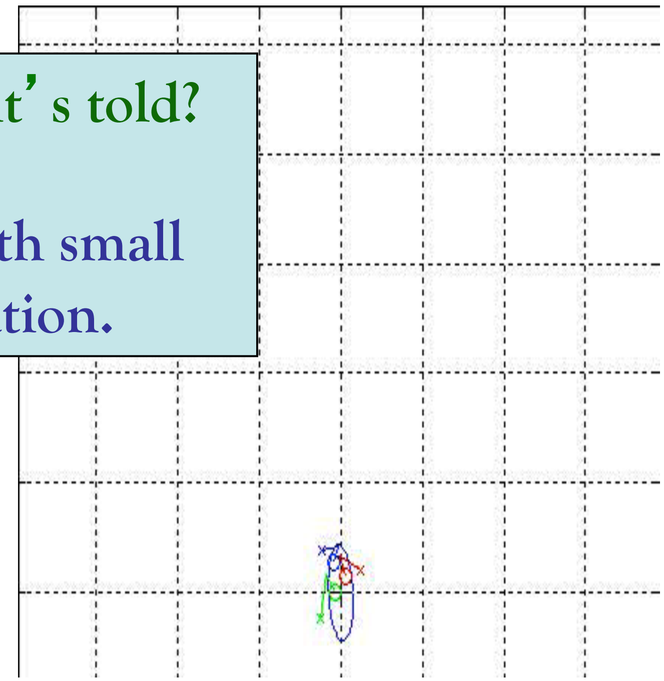
Hexapod: extend front leg

5. Can the model go where it's told?

Yes, steering can be done with small adjustments to muscle actuation.

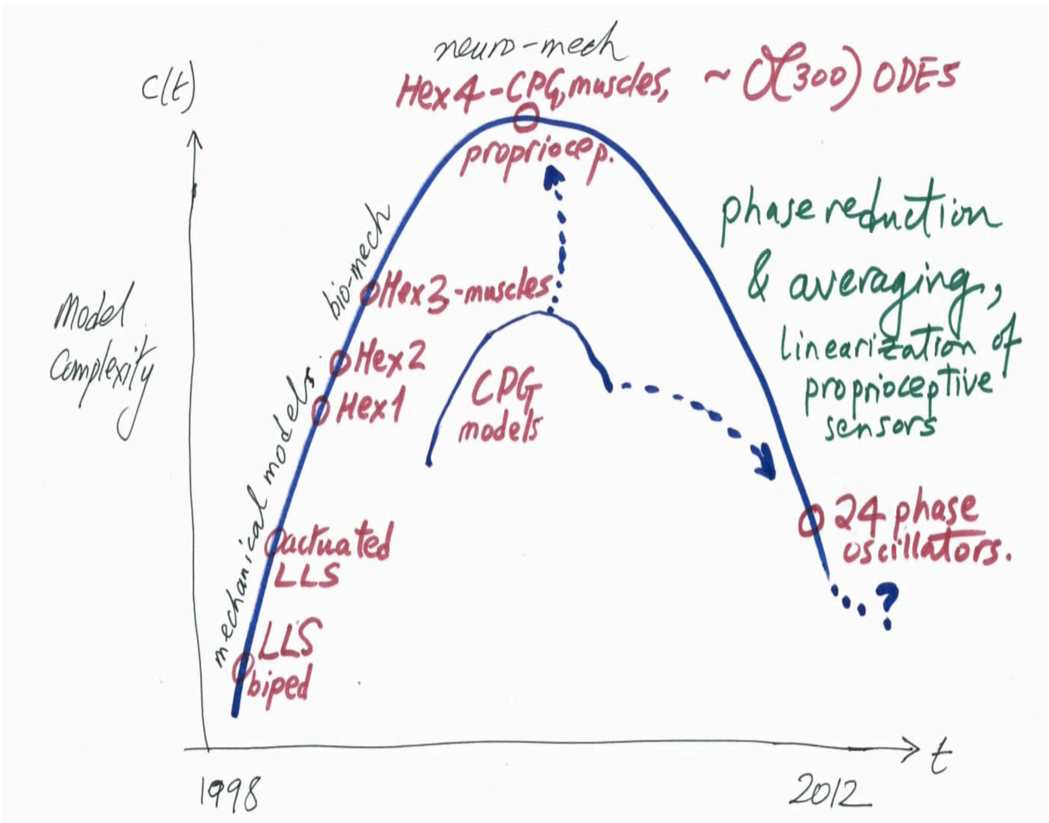
3 step turn map





D. Jindrich & R.J. Full, *J. Exp Biol. 202, 1999.*
J. Proctor & H, *Reg & Cha. Dyn., 13(4), 2008.*

A good modeling strategy for other systems?



Make it real enough, without making it unanalyzable

Isolate a key question and build a simple model to study it.
Model motivates new experiments => more data, adjust model.
If it partially succeeds, make the model more realistic.
Model motivates new experiments => more data, adjust model.
Reduce dimension: simplify model without losing essential biophysics.
Analyze the reduced model; understanding motivates new ... etc. etc.

That's all

1. Passive springy legs + biped geom + intermittent stance phases can stabilize: preflexes beat reflexes on short timescales.

2. Integrate CPG, motoneurons and muscles: get leg forces right, preflexive stability preserved.

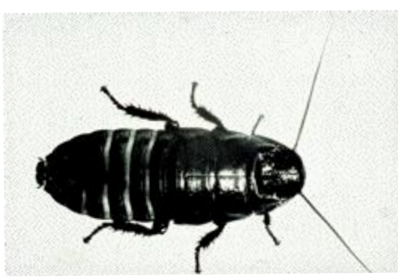
3. Phase reduction and sensory feedback: proprioception supplements preflexes, modulates muscle actuation.

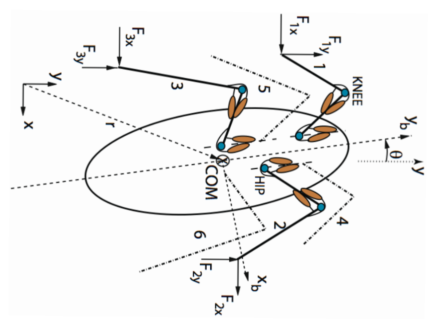
4. Stability/maneuverability tradeoff: steering by transient destabilization.

Math tools: deterministic & stochastic dynamical systems, control theory, classical mechanics, ….

Persistent question: How much detail do we need?

Moral: Integrative (neuro-) biology needs mathematics and mechanics, micro- and macroscale modeling: molecules, cells, kinetics don't explain everything!





Review article: Holmes, Full, Koditshek & Guckenheimer, SIAM Review 48(2), 207-304, 2006.