Neuromechanical models of legged locomotion:

How cockroaches run fast and stably without thinking about it.

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Stability and Instability in Mechanical Systems, Barcelona, Dec 2008.

Thanks to NSF, NIH and Burroughs-Wellcome Foundation, and IMA Minnesota, where it all started.
Thanks also to Tere and Angel and the organising committee!

Terrestrial mechanics: La cucaracha

(courtesy R.J. Full)

The importance of stability: what can be done without (much) neural feedback. **Dynamical tools in biology.**

‘Let’s learn how they run before how they walk!’

Introduction: Fast cockroaches: inertia dominates dynamics, simplifying potential control strategies. Feedforward ‘preflexes’ dominate.

Part I: Mechanistic theory; passive models.
Simple models: Effective bipeds? Passive springs and hybrid, conservative dynamical systems. Preflexive stability.

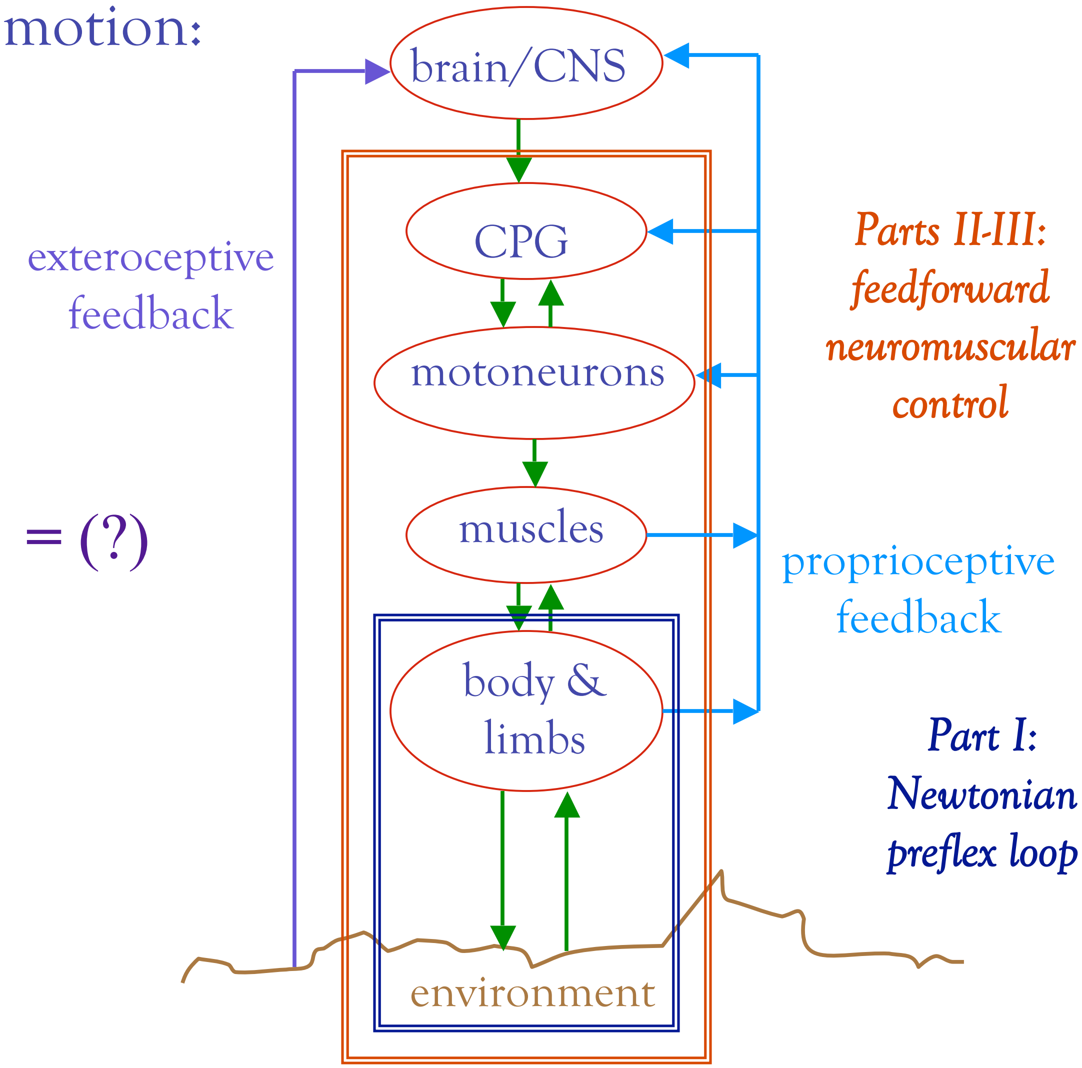
Parts II & III: Towards a synthesis: active models.
Improved models: bursting neurons, a central pattern generator, and muscles actuation in hexapods (work in progress).

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

Introduction and background

Neuromechanics of locomotion:

= (?)



Some questions:

0. Persistent question: How much detail do we need at each stage?
1. Can a passive, energy-conserving model produce stable periodic gaits?
[minimal feedforward TD & LO rules allowed.]
2. Can such a model match the data qualitatively? Quantitatively?
3. Can CPG and muscles be included while preserving preflexive stability?
4. How does reflexive neural feedback interact with mechanical preflexes?

In case you have to leave early ...

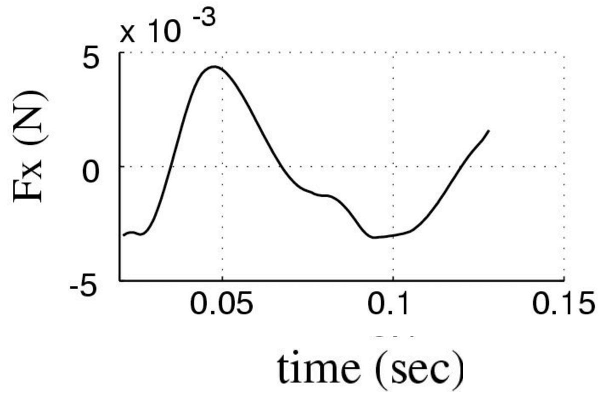
some answers:

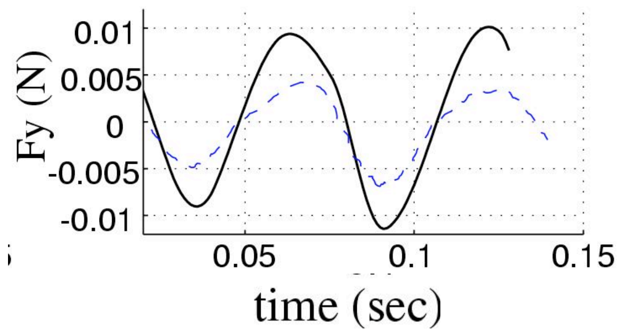
1. **Yes**. **2.** Not with 2 legs; with 6, **Yes**. **3. Yes**. **4.** Be patient!
[**5.** ??, but our experience is growing.]

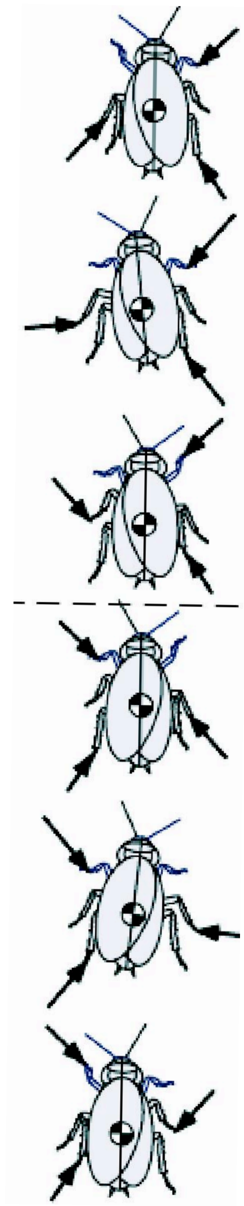
Introduction: how (some) bugs run:

Introduction and background

Net force and moment time histories







Double tripod gait

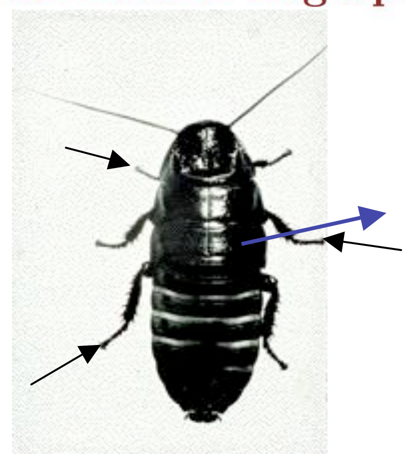
Part I: A passive mechanical model for horizontal plane dynamics:

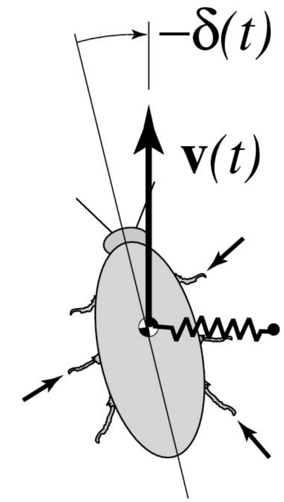
Simple models - LLS

The bipedal Lateral Leg Spring model

The insect: 40+ dof,

100s of parameters.





The LLS model: 3 dof,

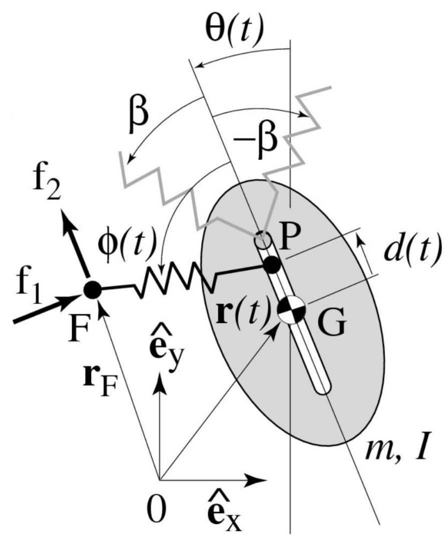
6 parameters:

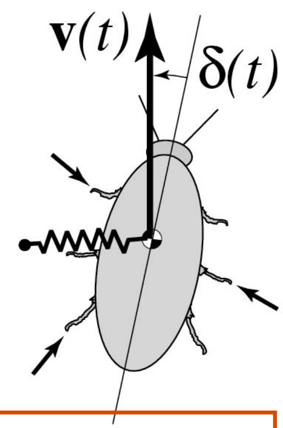
m, I, k, l, d, β.

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

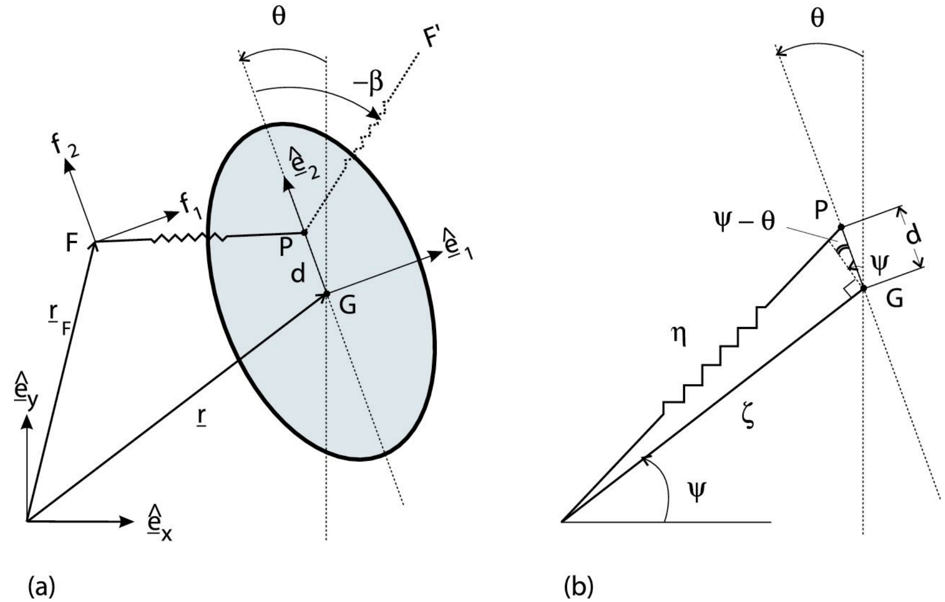
Less is more! Simplify!

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

Newton rules, in piecewise-smooth, hybrid form:

Simple models - LLS

LLS: equations of motion



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

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

During stance, use polar coords about foot:

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

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

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

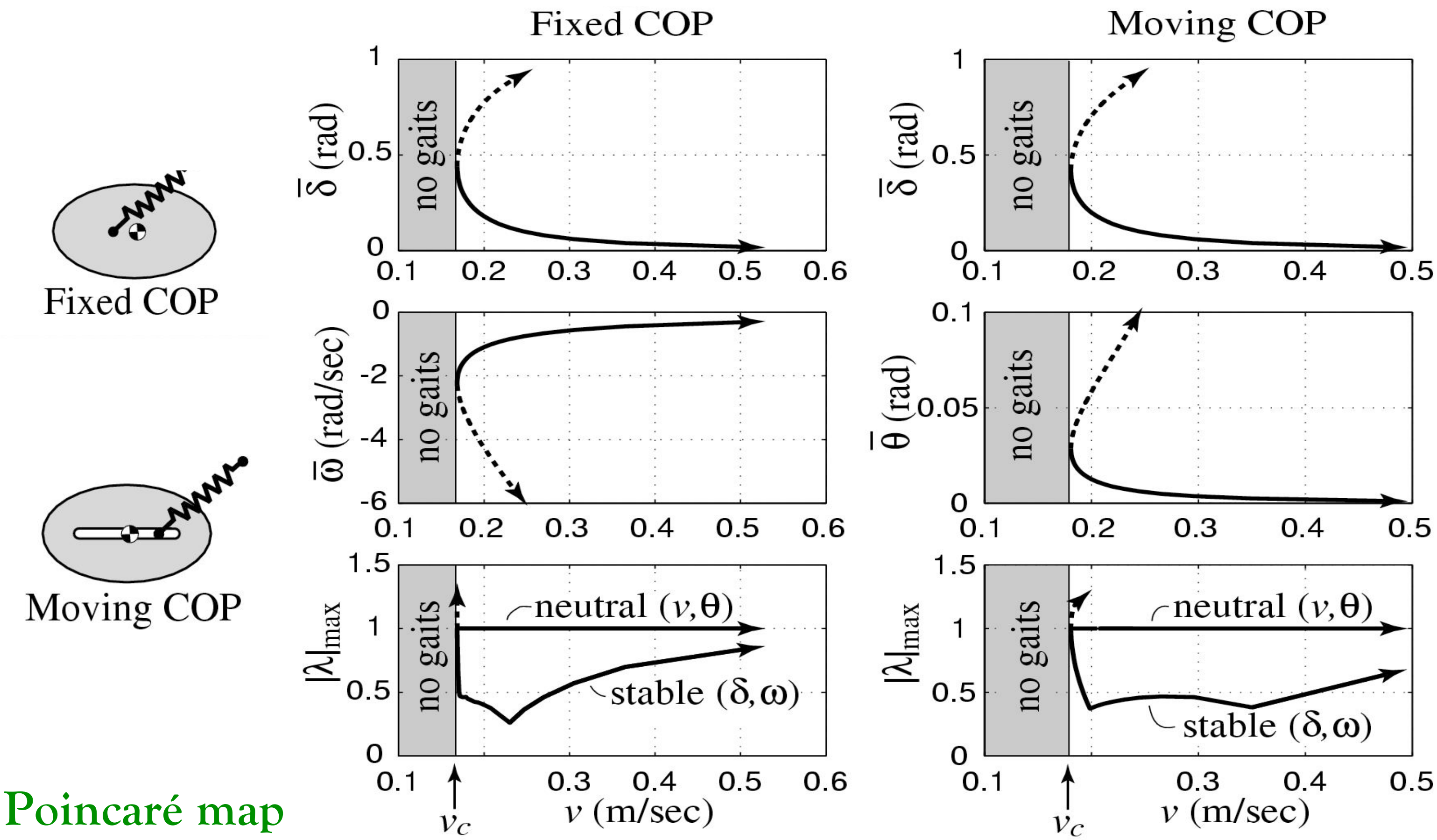
$L_F = m\zeta^2\dot{\psi} \pm I\dot{\theta}$ = AM about stance foot conserved ⇒ **reduces to two dof.**

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

Preflexes -- partial asymptotic stability for a conservative system:

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**.

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

Piecewise holonomic constraints & partial asymptotic stability:

Classical **holonomically-constrained** mechanical systems have symplectic phase spaces, so cannot exhibit asymptotic stability. Linearized systems have eigenvalues occurring in pairs:

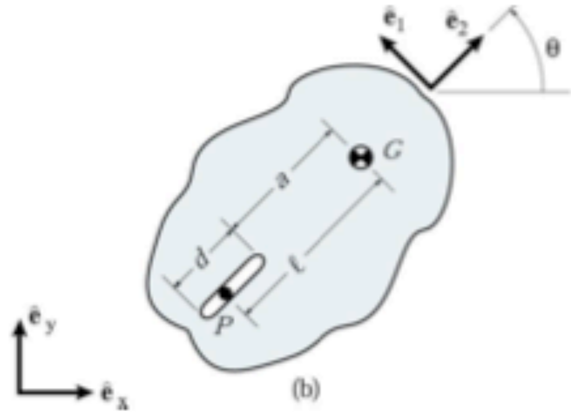
$$\dot{\mathbf{x}} = \mathbf{JDH}(\mathbf{x}) \;\Rightarrow\; \pm\lambda, \text{ or } \lambda, 1/\lambda \text{ for Poincaré map.}$$

So if one direction is **stable**, another is **unstable**. But **nonholonomic** systems can exhibit exponential stability: e.g., the Chaplygin sled or ice-skater (see Neimark-Fufaev). A. Ruina invented a **piecewise holonomic** sled. Successive peg insertions transform angular momentum to linear momentum, so straight running is **partially asymptotically stable**.

Example: Peg-leg walker:

$$\begin{pmatrix} \theta_{n+1} \\ p_{\theta_{n+1}} \end{pmatrix} = \begin{bmatrix} 1 & B \\ 0 & A \end{bmatrix} \begin{pmatrix} \theta_n \\ p_{\theta_n} \end{pmatrix}, \; A = \left[\frac{ma(a+d)+I}{m(a+d)^2+I}\right]$$

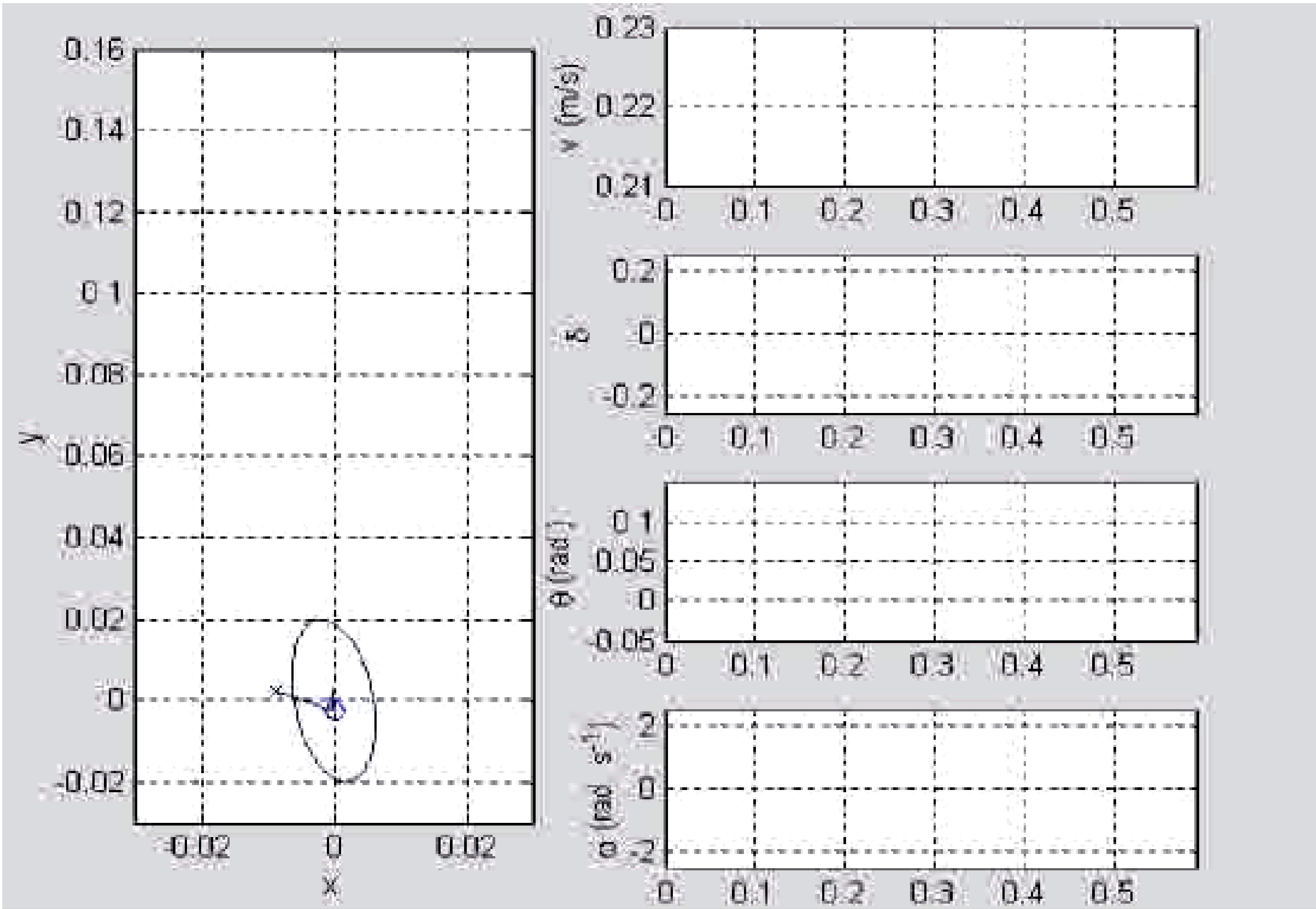
Angular momentum balance about peg insertion point.



LLS has no impacts: conserves energy, but trades ang. mom. step to step.

Simple models -- LLS

Partial asymptotic stability via geometry & piecewise holonomy:



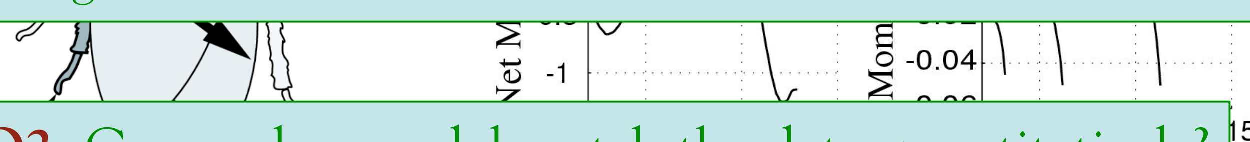
Simple models - LLS

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

LLS Model:

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.**



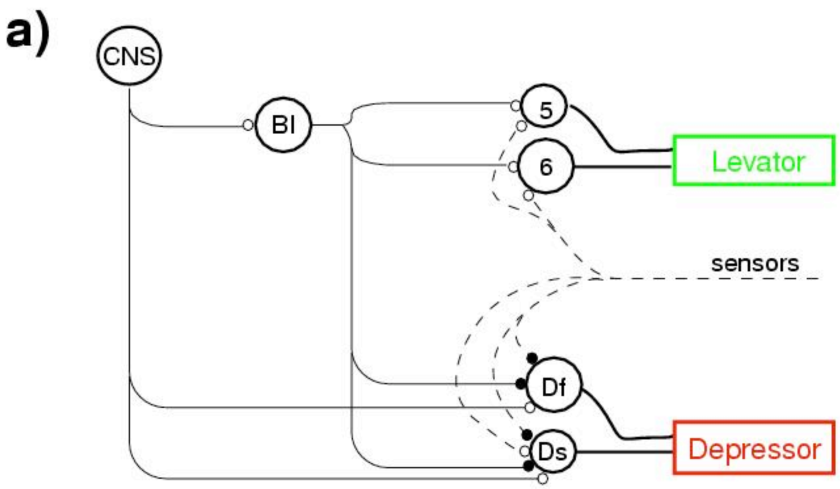
Q2. Can such a model match the data quantitatively?

Not with 2 legs.

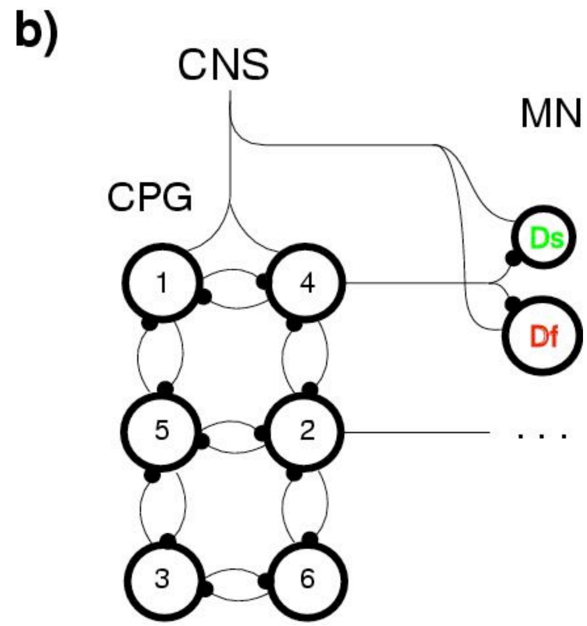
In stanc … net
forces.

Hexapedal models - CPG and muscles

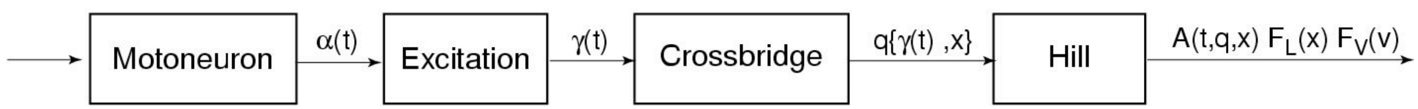
CPG + motoneurons + muscles



Pearson, 1972.



Muscle



+ Hill type muscle model
(coming later)

Ghigliazza & H, SIAM J Appl. Dyn. Sys. 3, 636-670 & 671-700, 2004.

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

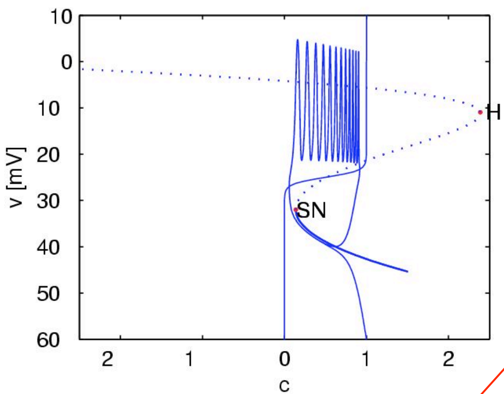
$$
\begin{aligned}
C\dot{v} &= -[I_{\mathrm{Ca}} + I_{\mathrm{K}} + I_{\mathrm{KCa}} + \bar{g}_{\mathrm{L}}(v - E_{\mathrm{K}})] + I_{\mathrm{syn}} + I_{\mathrm{ext}}\,, \\
\dot{m} &= \frac{\epsilon}{\tau_m(v)}\,[m_\infty(v) - m]\,, \qquad\qquad \delta \ll \epsilon \ll \frac{1}{C}\,. \\
\dot{c} &= \frac{\delta}{\tau_c(v)}\,[c_\infty(v)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

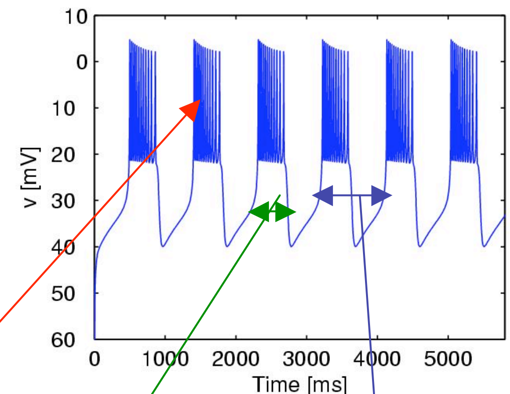
$$
I_{\mathrm{Ca}} = \bar{g}_{\mathrm{Ca}} n_\infty(v)(v - E_{\mathrm{Ca}})\,, \quad I_{\mathrm{K}} = \bar{g}_{\mathrm{K}} m \cdot (v - E_{\mathrm{K}})\,, \quad I_{\mathrm{KCa}} = \bar{g}_{\mathrm{KCa}} c \cdot (v - E_{\mathrm{KCa}})\,.
$$

Synaptically coupled via I_{syn}:

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

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





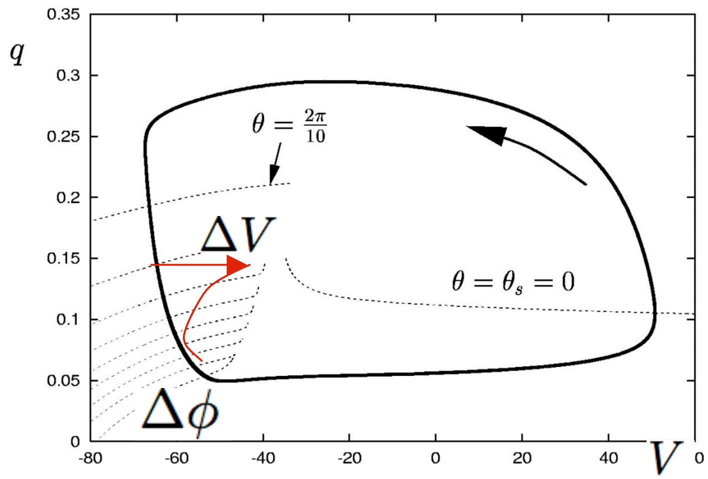
$$I_{\mathrm{syn}} = \bar{g}_{\mathrm{syn}} s(v - v_{\mathrm{syn}})\,.$$

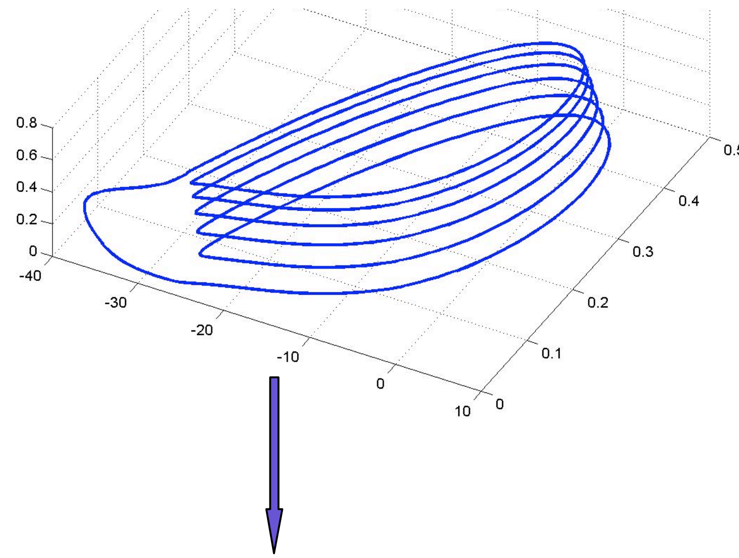
Key output params: Spiking freq. Duty cycle Stepping freq. Need to understand how input currents and conductances tune them.

Simplify again: reduce each oscillator state to a single phase angle:

Hexapedal Models - CPG

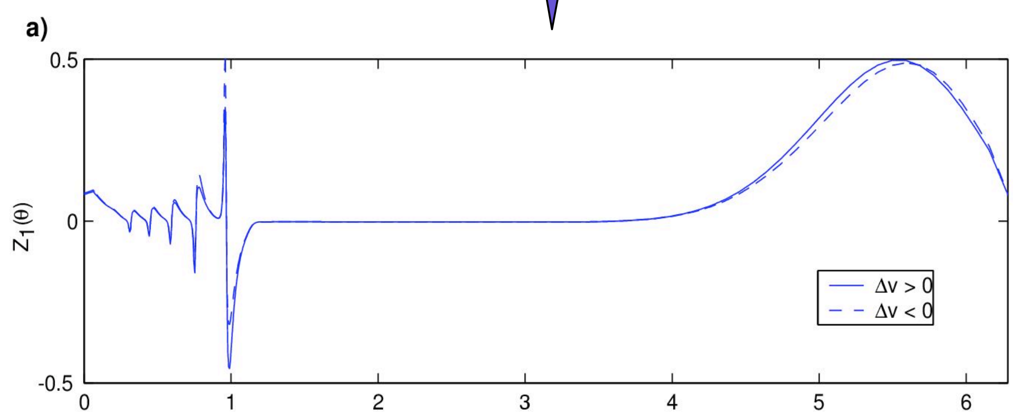
Good coordinates! Phase response curves (PRC) for periodically bursting cells:





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

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

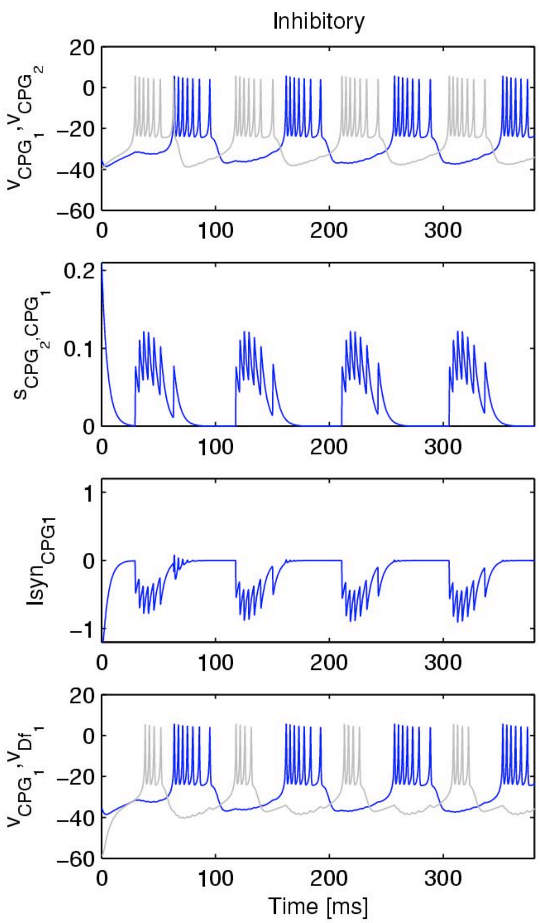


PRC tells how phases shift as a function of input phase, explain coordination.

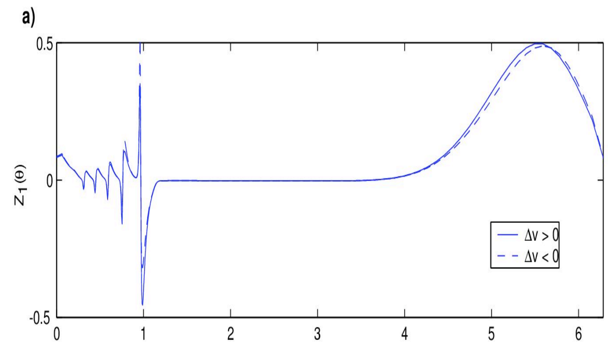
Simplify further: average over the step period:

Hexapedal models - CPG and muscles

Towards the CPG circuit: Analyze coupling effects via **Phase Response Curve** $Z(\phi)$ [Malkin, Winfree, Ermentrout]. For a pair of oscillators:

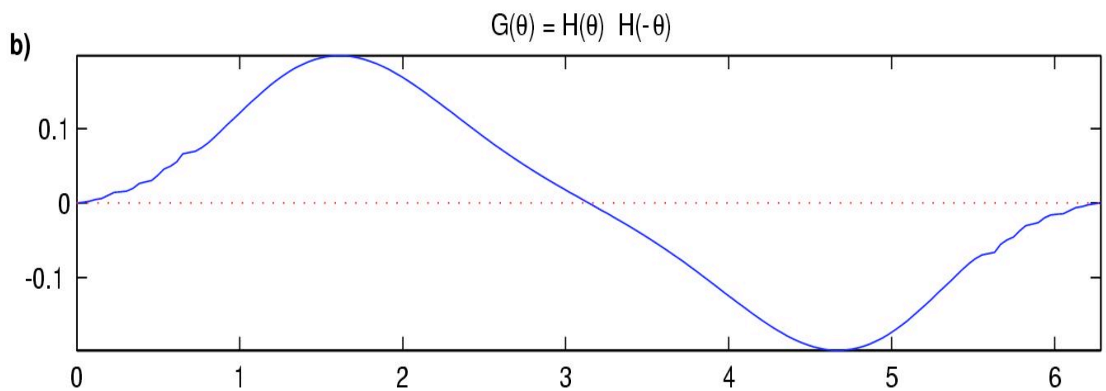


$$\dot{\phi}_1 = \omega_0 + \alpha_{21} Z(\phi_1) f(\phi_1, \phi_2)$$
$$\dot{\phi}_2 = \omega_0 + \alpha_{12} Z(\phi_2) f(\phi_2, \phi_1)$$
$$\phi_j = \omega_0 t + \psi_j \, .$$



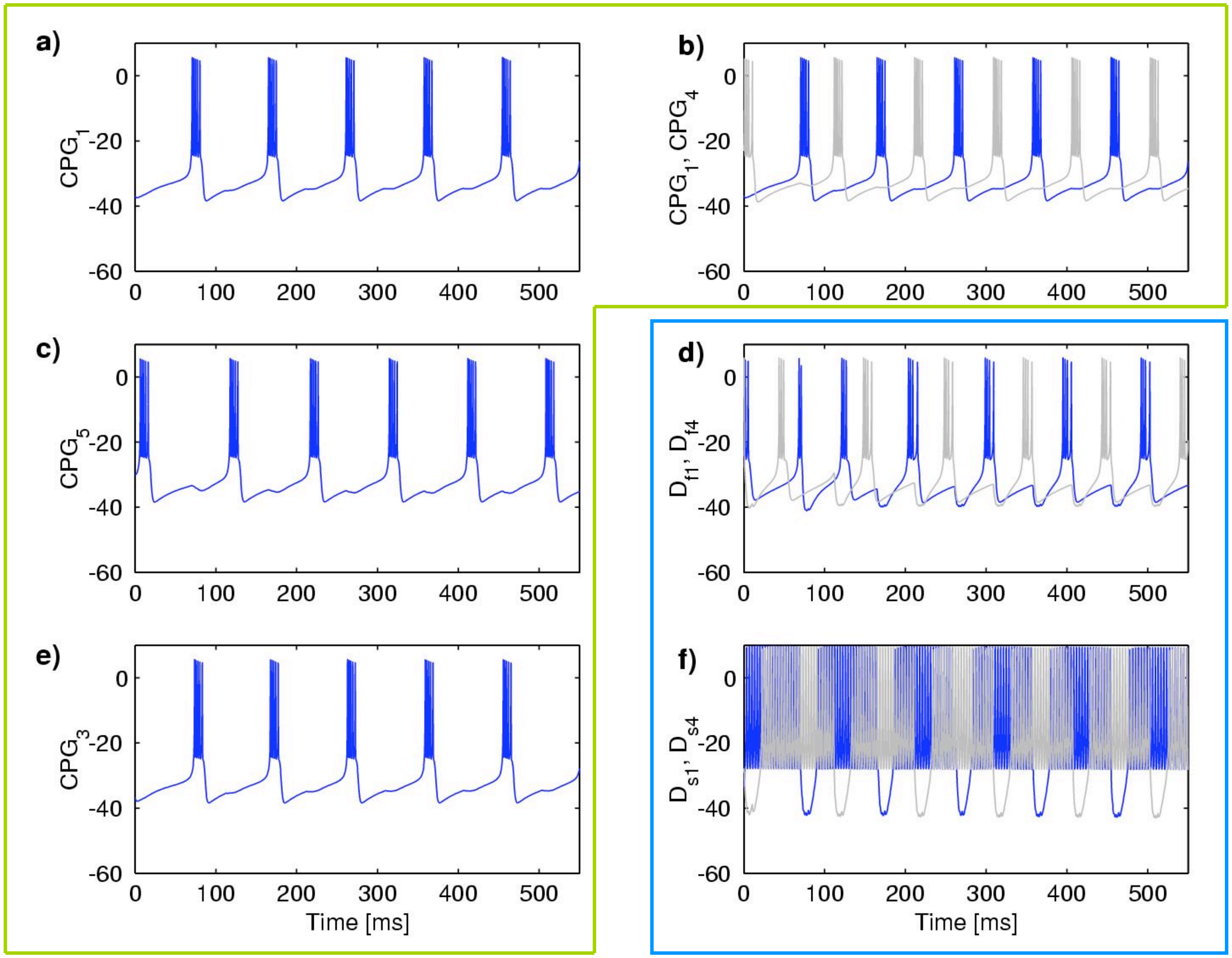
Average over fast time t:

$$\dot{\psi}_1 = \alpha_{21} H(\psi_1 - \psi_2) \, , \qquad \Rightarrow \quad \dot{\psi}_1 - \dot{\psi}_2 = G_\alpha(\psi_1 - \psi_2) \, .$$
$$\dot{\psi}_2 = \alpha_{12} H(\psi_2 - \psi_1) \, ;$$



Hexapedal models - CPG, motoneurons, and muscles

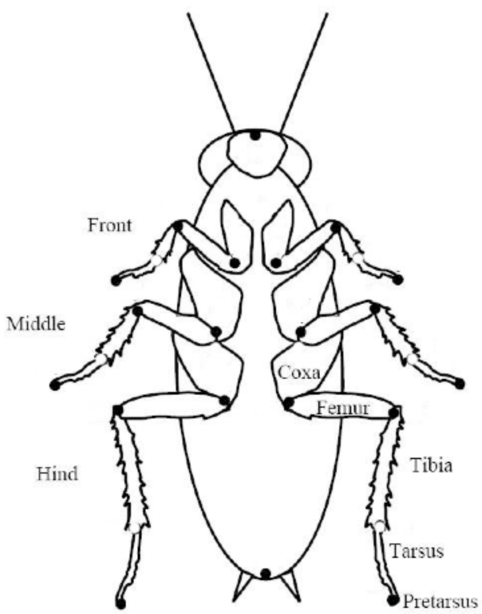
CPG and motoneuron outputs: correct phasing for double tripod gait

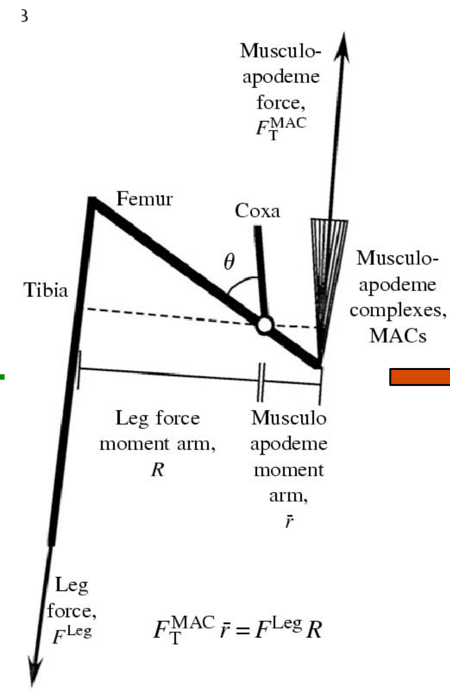


Part III: Towards an integrated neuromechanical model:

Hexapedal models - jointed legs

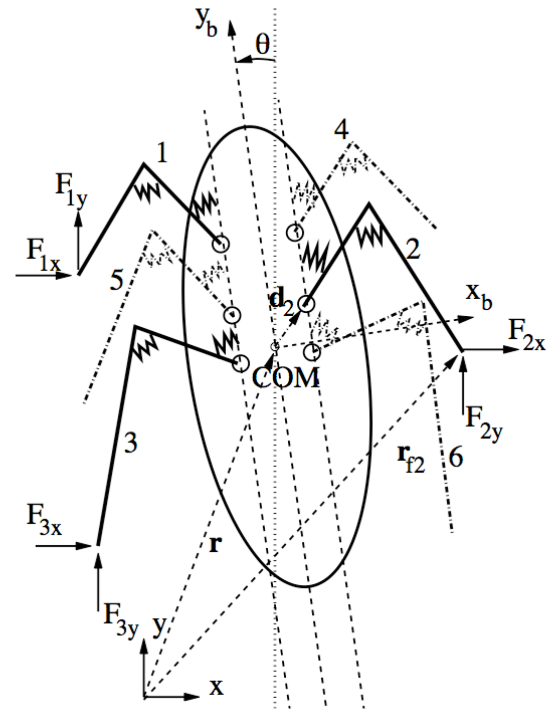
Now we want to integrate the CPG and motoneurons with simplified muscles and jointed limbs, thus moving towards neuromechanics. Start with actuated springs at the two major leg joints for horizontal plane motions:





R. J. FULL AND A. N. AHN

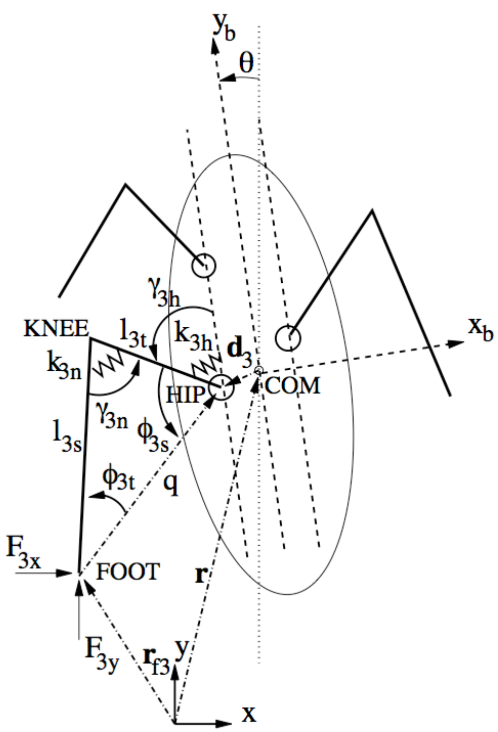
The Journal of Experimental Biology **198**, 1285–1298 (1995)



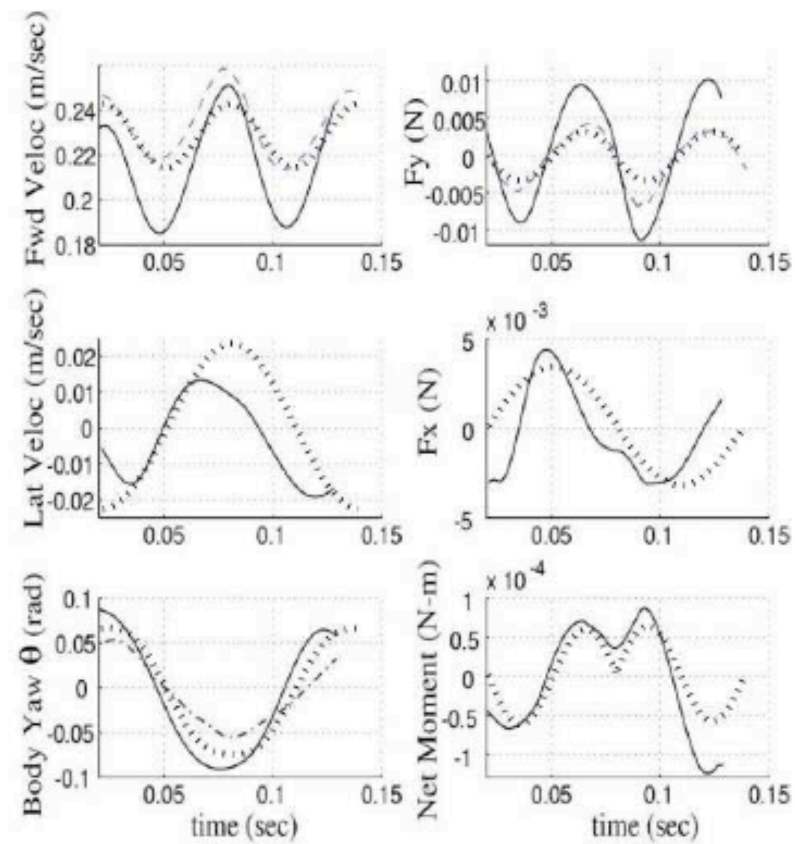
Seipel, H, Full, Biol. Cybern. 91, 76-90, 2004.
Ghigliazza & H, Reg. Cha. Dyn. 193-225, 2005.
Kukillaya & H, Biol. Cybern. 97, 379-395, 2007.

Hexapedal models - jointed legs

First we build an mechanical model with realistic leg geometry and actuated torsional springs at the joints. Given insect foot forces and COM motions, we solve an inverse problem to derive feedforward inputs to joint angles that yield joint torques and foot forces that match the data.

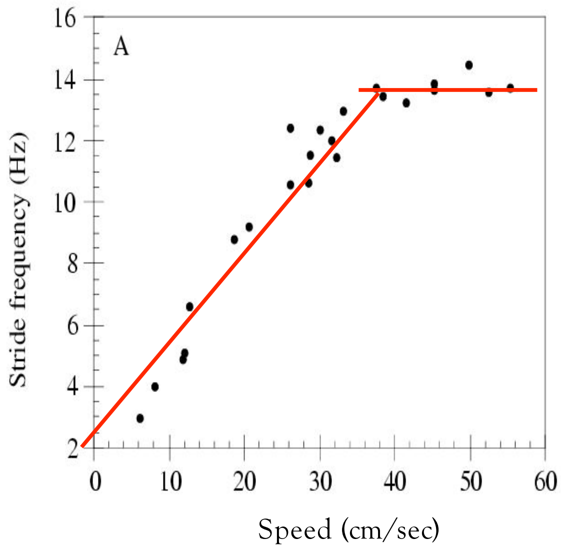


Solid: expt.
Dashed: model



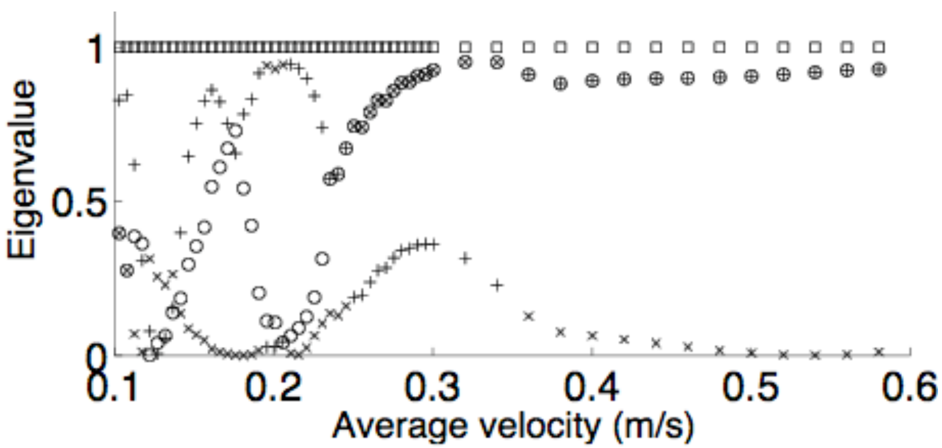
Hexapedal models - jointed legs

With appropriate leg cycle frequency and stride length variations, we find branches of stable gaits over the physiological speed range. Again we use stride-to-stride Poincaré map analysis:



Black: expt.

Red: model.



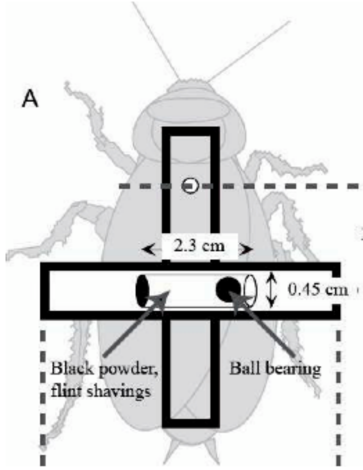
Eigenvalue dependence on speed.

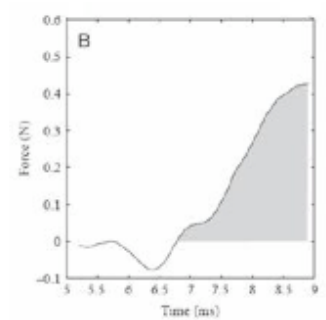
L. H. TING[1], R. BLICKHAN[2] AND R. J. FULL[1],
J. exp. Biol. **197**, 251–269 (1994)

Kukillaya & H, Biol. Cybern. 97, 379-395, 2007.

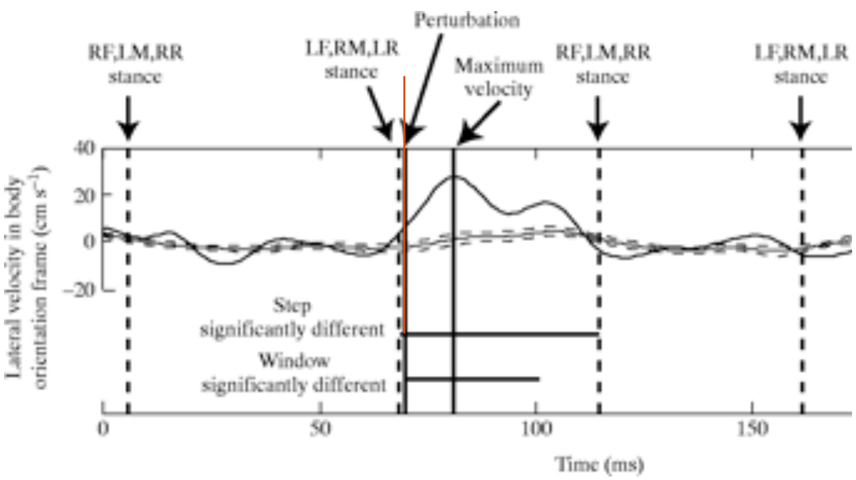
Experimental evidence for preflexive (mechanical) stabilization:

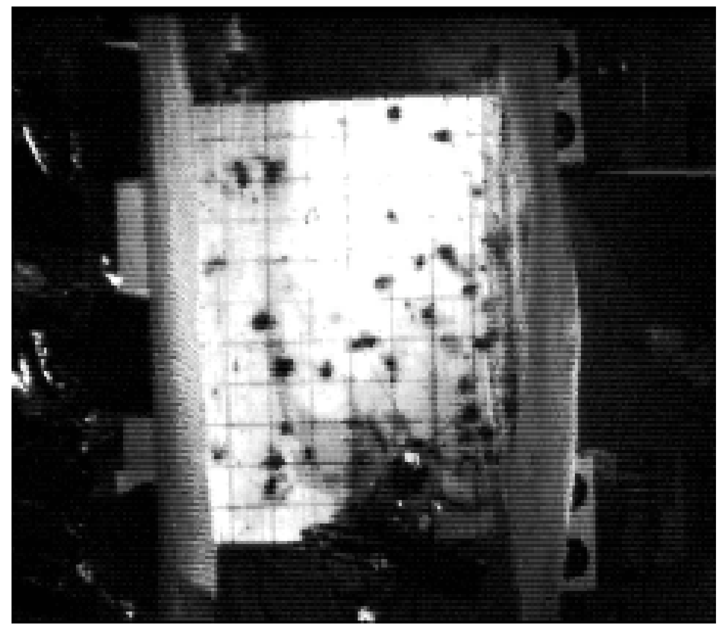
A Rapid Impulse Perturbation, and its consequences.





Force impulse





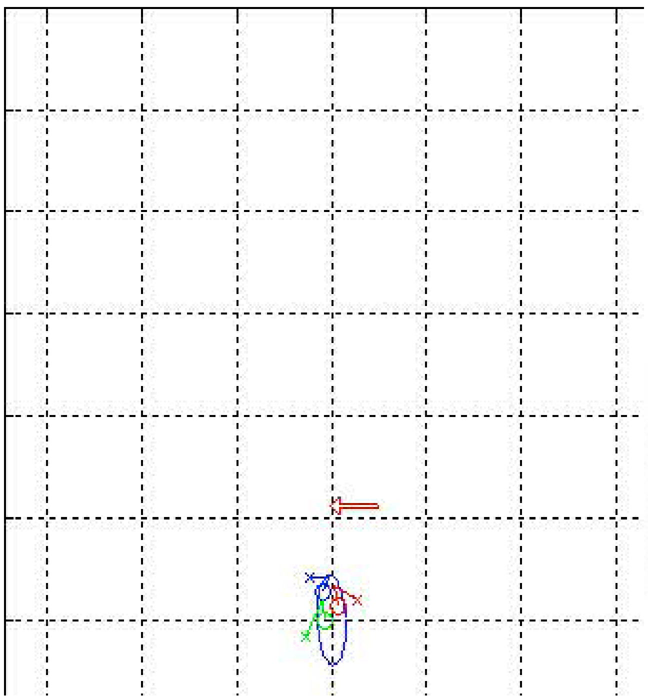
Recovery within 1 stride: 15-35 msec. Too fast for neuromuscular corrections via proprioceptive sensory system!

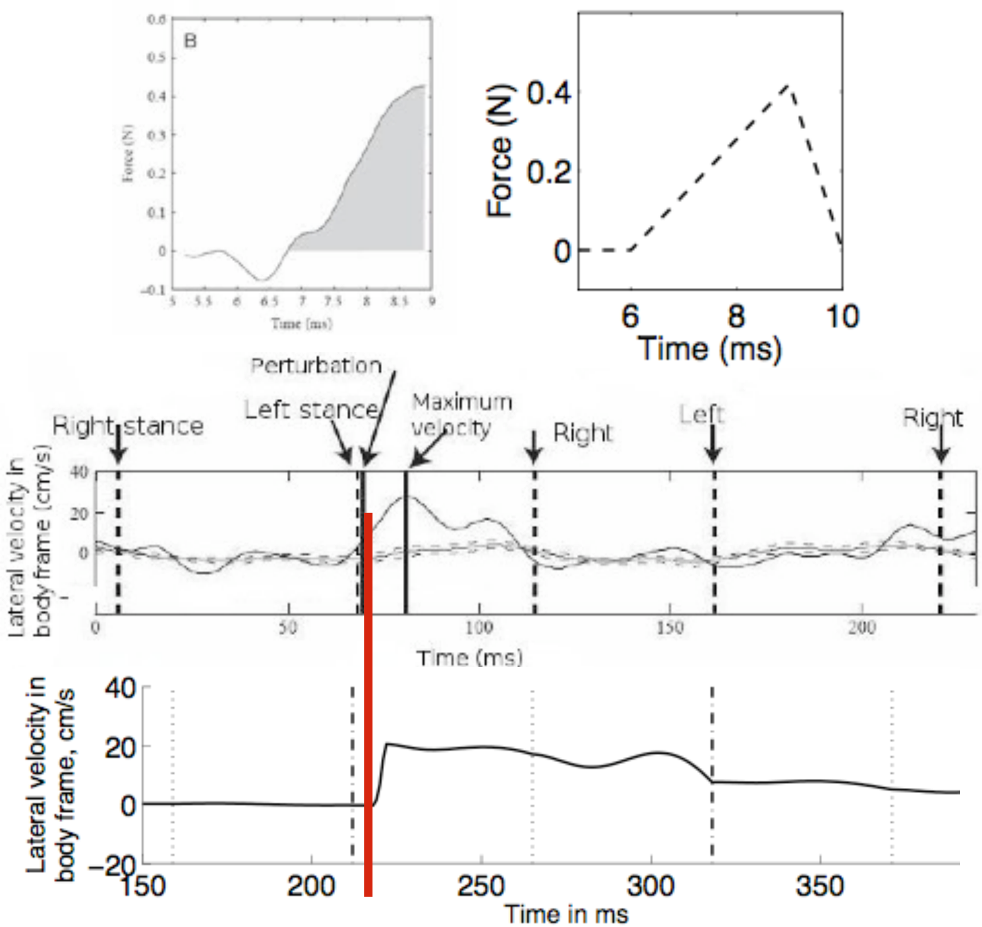
Jindrich & Full, J Exp. Biol. 205, 2803-2823, 2002.

Hexapedal models - jointed legs

We perform the RIP on the model, without corrective steering.

* The purely feedforward actuated system is also preflexively stable. *

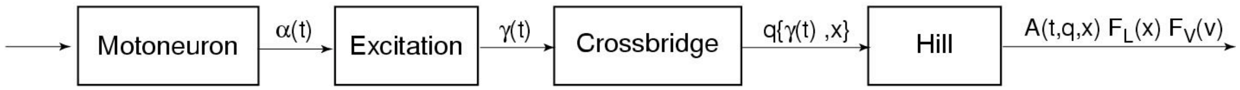


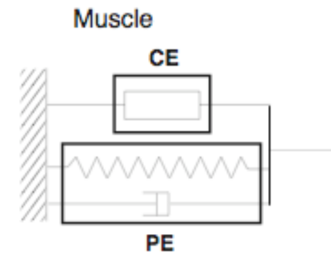


We have an good mechanical model, but can we incorporate the CPG and muscles?

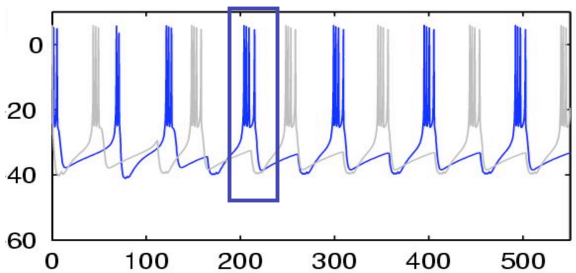
Integrated CPG-muscle-hexapedal models

A model for muscles (after A.V. Hill):





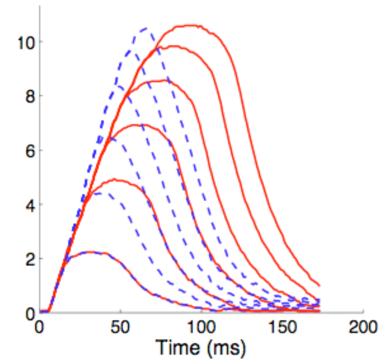
Calcium release dynamics:



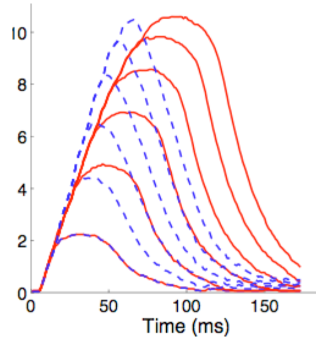
+

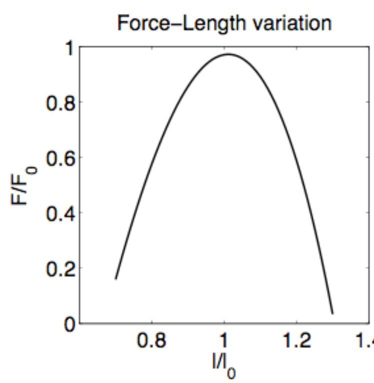
$$\ddot{\beta} + c_1\dot{\beta} + c_2\beta = c_3 u(t),$$
$$\ddot{\eta} + c_4\dot{\eta} + c_5\eta = c_6\beta(t),$$

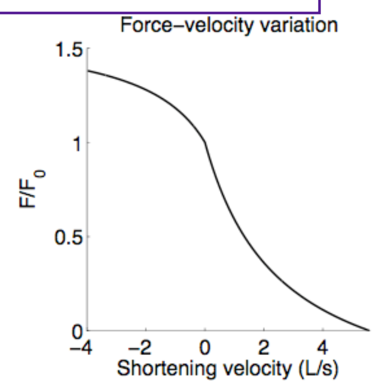
$$A(t) = \frac{a_0 + (\rho\eta)^2}{1 + (\rho\eta)^2}.$$



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



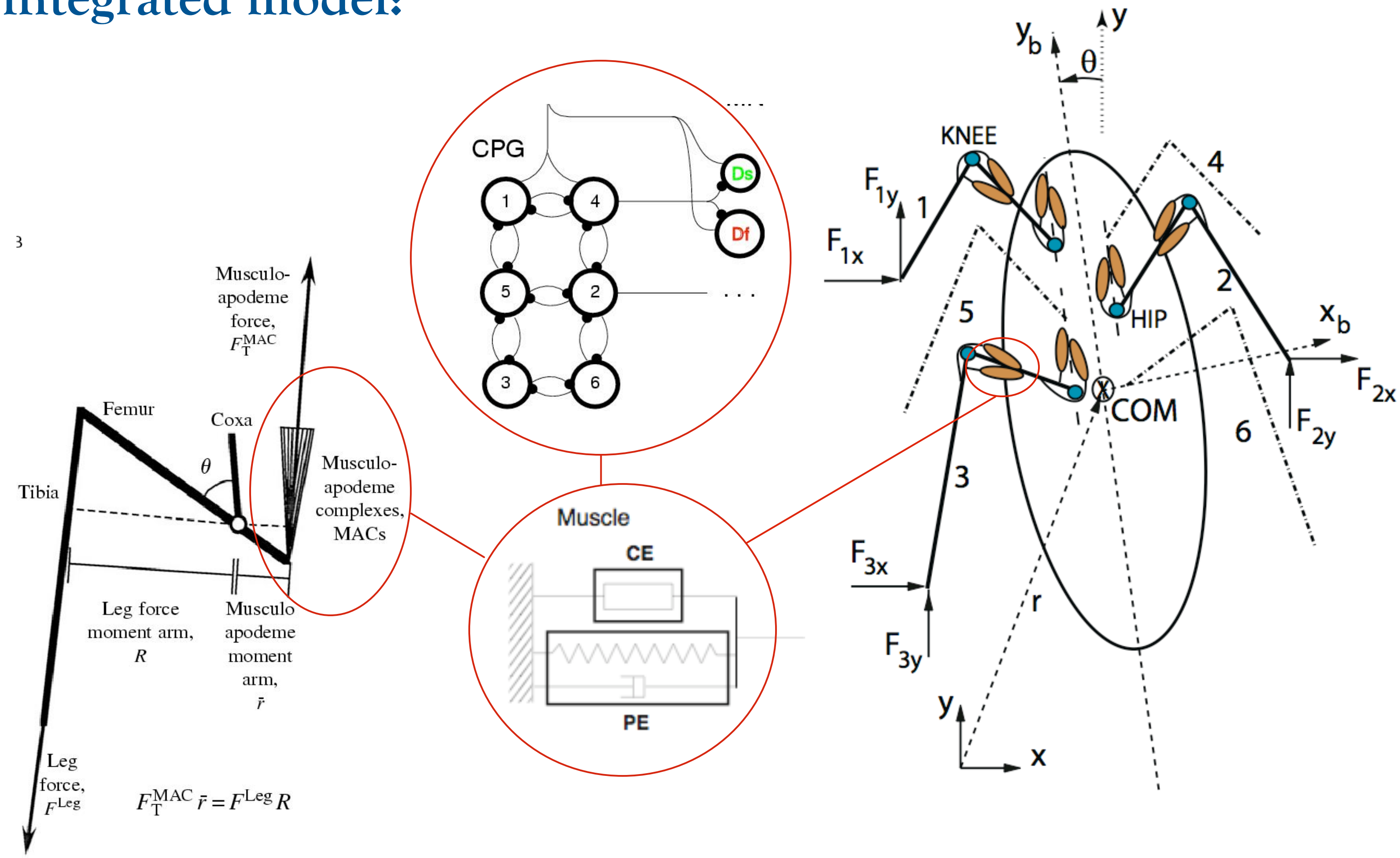




Match isolated EMG, isometric & const. veloc muscle data from Ahn, Meijer & Full, 1998-2006.

Integrated CPG-muscle-hexapedal models

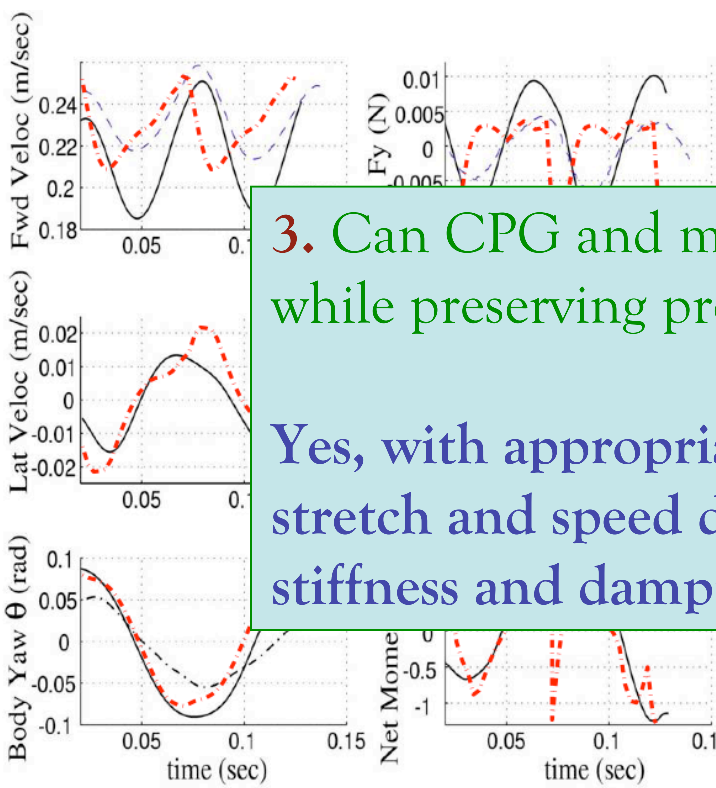
Inserting extensor-flexor muscle pairs at each joint, we produce an integrated model:



R. Kukillaya, work in progress, 2008.

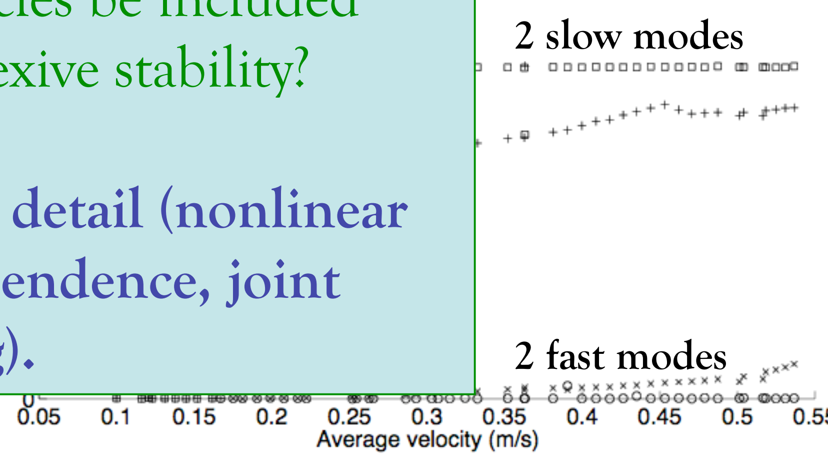
Integrated CPG-muscle-hexapedal models

Let the beast run! We obtain a good quantitative match to data, and stability over the physiological speed range.



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

Yes, with appropriate detail (nonlinear stretch and speed dependence, joint stiffness and damping).



Gait at preferred speed

Expt. (black, dashed), model (red)

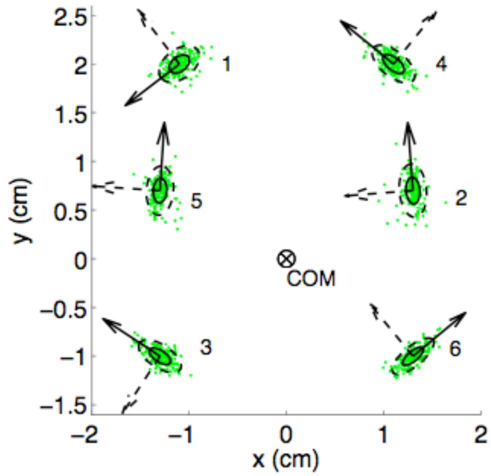
Eigenvalues over speed range

R. Kukillaya, work in progress, 2008.

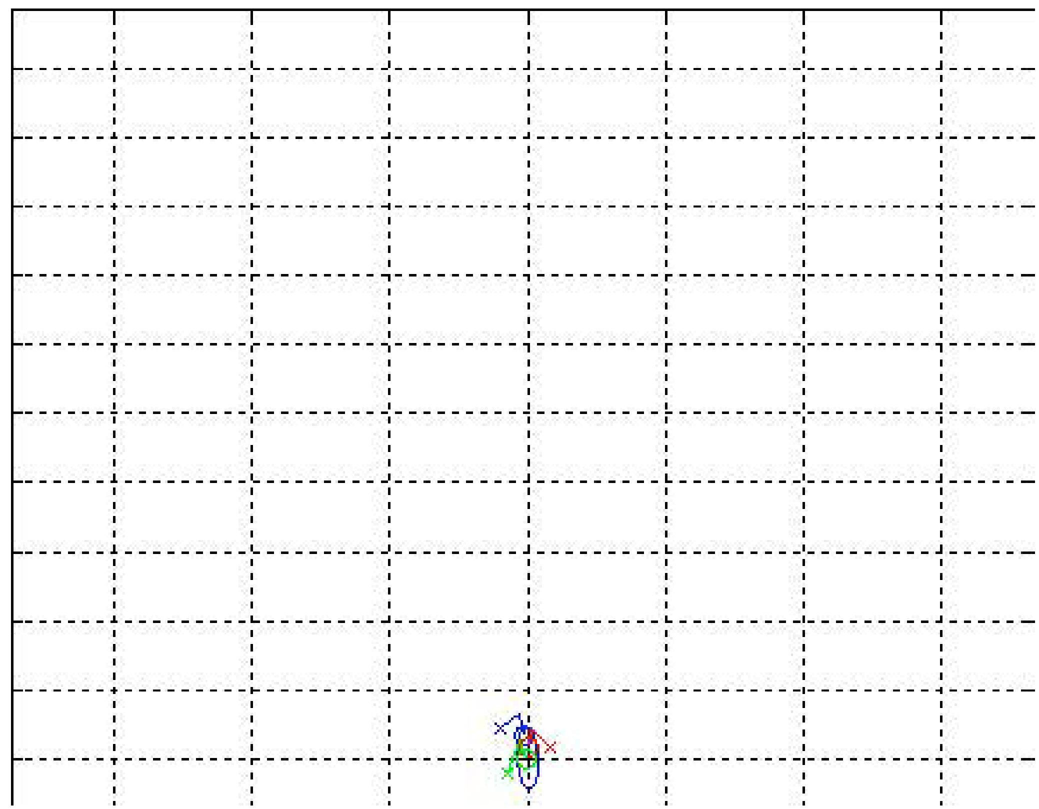
Integrated CPG-muscle-hexapedal models

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

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.

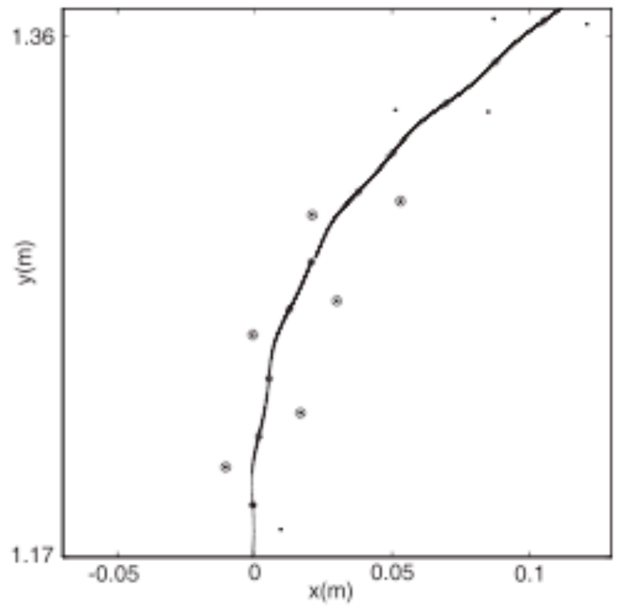


Fast eigenvalues filter out high frequencies, leave slow heading changes.
Also robust to variable neural spikes and foot touchdown & liftoff timing.

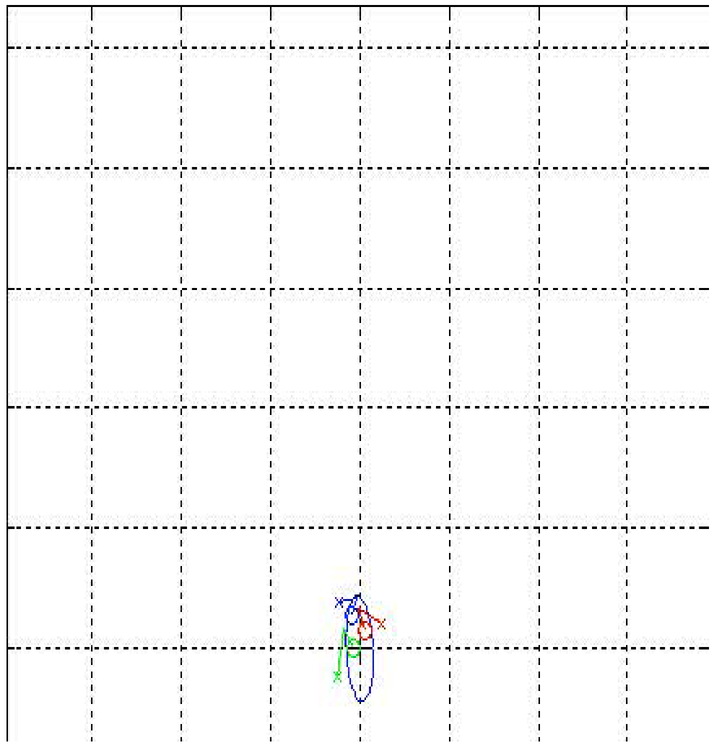
Hexapedal models - jointed legs

Steering by adjusting foot positions at TD for 2-4 strides to use unstable dynamics (still feedforward control):

Simple LLS model: to turn right, move COP forward on left TD for 2-4 steps

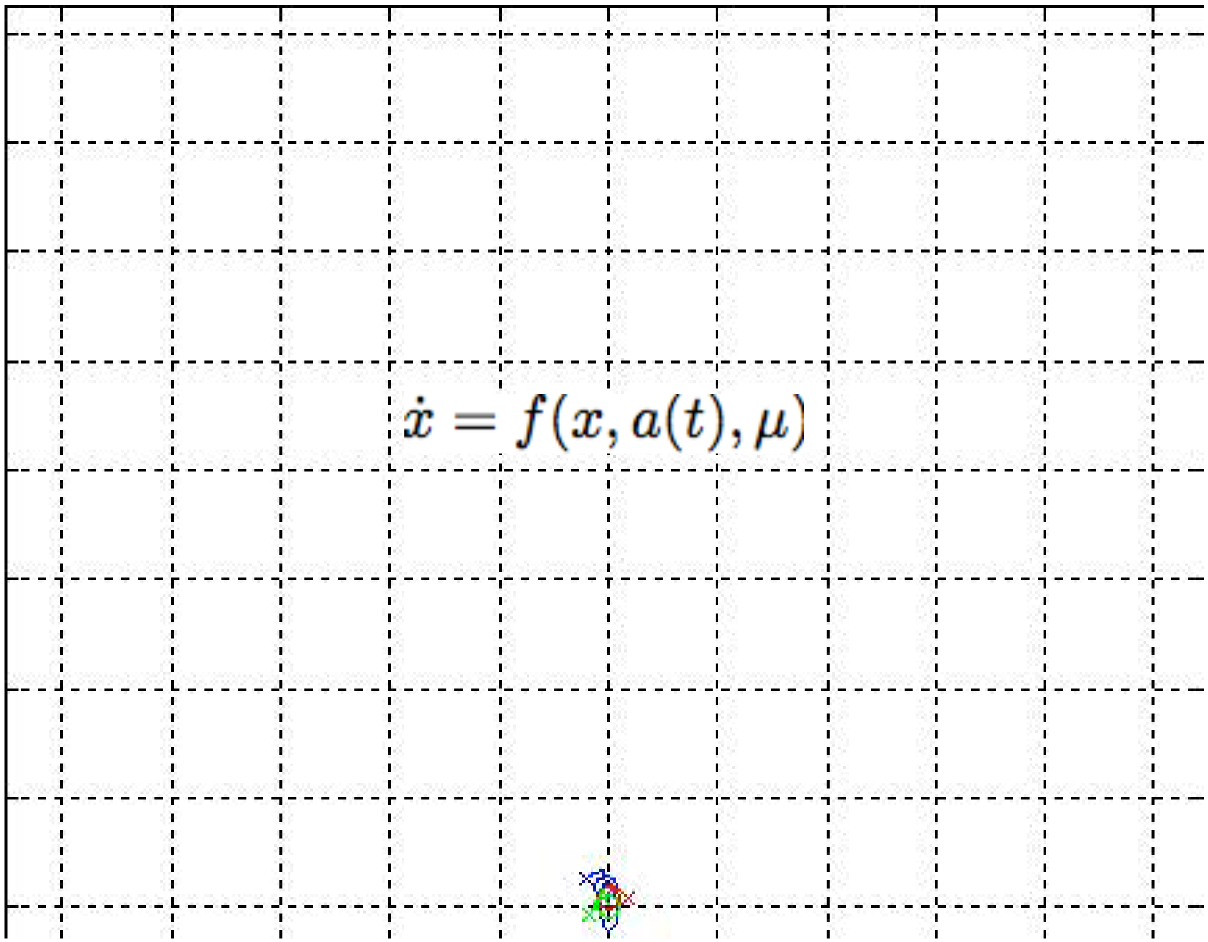


Hexapod with random perturbations



Proctor & H, Reg & Cha. Dyn., 13 (4), 267-282, 2008.

The end of la cucaracha
(the perils of instability)



$$\dot{x} = f(x, a(t), \mu)$$

Summary

1. Passive springy legs + biped geom + intermittent stance phases can stabilize: preflexes beat reflexes on short timescales! But bad forces & moments.

2. Bursting neuron CPG model, phase reduction, control parameters.

3. Actuated hexapedal models get forces right, incorporate muscles, preserve preflexive stability, will allow integration of CPG and sensory feedback.

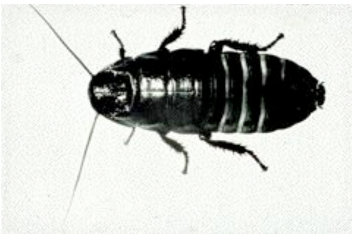
4. Persistent question: How much detail do we need?

5. Math tools: deterministic & stochastic dynamical systems, control theory,

Open Problems: Add sensory feedback; develop theory and numerical methods for hybrid dynamical systems, ...

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

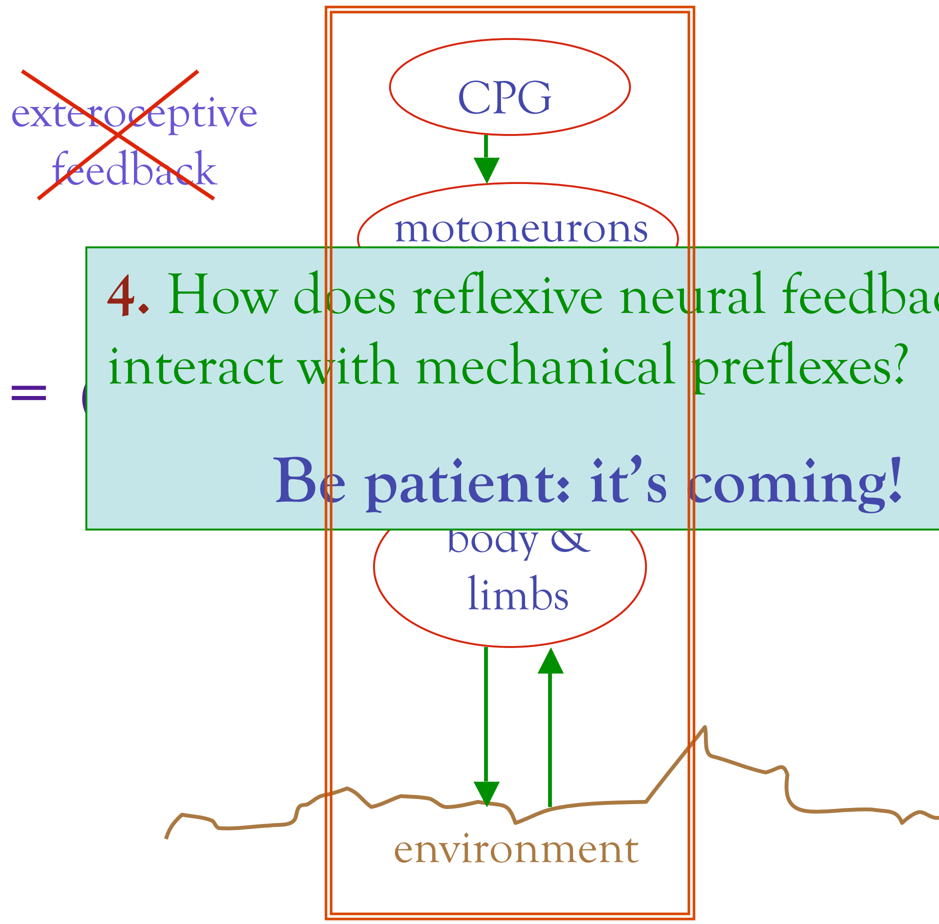
A moral: Integrative biology needs mathematics and mechanics: molecules & cells don't explain everything!



Integrated CPG-muscle-hexapedal models

So, what do we have to show after 10 years?

=



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

Be patient: it's coming!