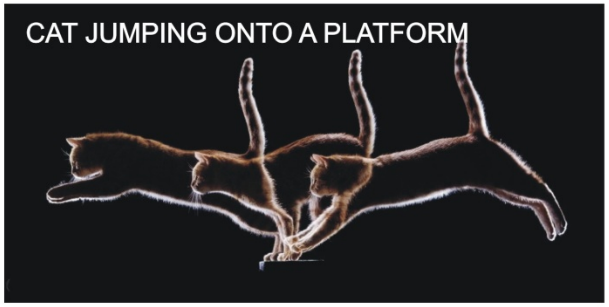
WHAT MAKES WALKING BEHAVIOR 'NATURALISTIC'? FEEDBACK SIGNALING THE RATE OF CHANGE OF FORCE (dF/dt) IN SERIALLY HOMOLOGOUS LEGS OF INSECTS.

S. N. ZILL[1] , C. J. DALLMANN[2], S. S. CHAUDHRY[1], N. S. SZCZECINSKI[3].

[1] Biomed. Sciences/Anatomy, J.C. Edwards Sch. Med., Huntington, WV;
[2] Physiol. and Biophysics, Univ. of Washington, Seattle, WA;
[3] Mech. and Aerospace Engin. West Virginia Univ., Morgantown, WV

ABSTRACT - Animal behaviors can be remarkably fluid and graceful. We have studied how signals from sense organs that monitor forces contribute to feedback control of walking in insects. Sensory activities of receptors that encode forces via strains in the exoskeleton (tibial campaniform sensilla, CS Groups 6A and 6B) were recorded extracellularly. Forces were applied to the front legs of stick insects using conventional and 'naturalistic' waveforms (joint torques calculated from experiments in freely walking animals, including steps with variance from the mean). These studies have shown that discharges of front leg 6B sensilla 1) most closely follow increases in the rate of change of force (dF/dt) rather than the force magnitude and 2) show substantial hysteresis to transient force decrements. Firing of 6A sensilla, which can signal large force decreases in middle and hind legs, was longer in duration during front leg stepping, in part due to the smaller forces generated by front legs. Discharges of receptors in front legs, therefore, form a continuum monitoring force variations in walking, and potentially in other behaviors such as tactile exploration. We are currently also characterizing the sensitivities of front leg CS by using waveforms that increase gradually (exponentially) to a level and include transient perturbations: studies to date have confirmed the sensitivities of tibial sensilla to transient force increments and decrements in dF/dt. We have also used these data in tests of a mathematical model of the receptors and replicated the findings for front leg receptors. The model results support the notion that the recorded discharge patterns result from the comparison between one fast- and one slowly responding component in the system. Dynamic properties such as discharge adaptation in response to constant force and responses to decreasing forces emerge from this single mechanism. Overall, our biological data and modeling studies show that tibial campaniform sensilla in all legs monitor the rate of change of force (dF/dt) and support the idea that these signals can be used to adjust muscle contractions to aid in generating the smooth accelerations and decelerations characteristic of 'naturalistic' movements that occur in walking. Support: NSF CRCNS 2113028, NSF 2015317

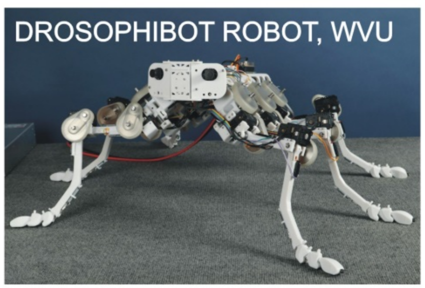
INCORPORATING MECHANISMS OF CONTROL OF ANIMAL MOVEMENTS INTO ROBOTIC MACHINES

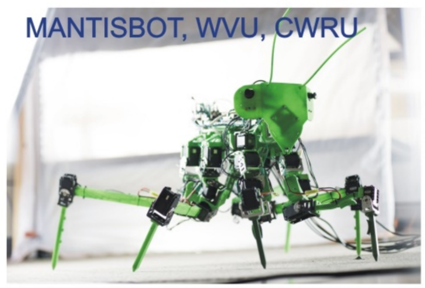

CAT JUMPING ONTO A PLATFORM

PRAYING MANTIS CATCHING A FLY IN MIDAIR

STICK INSECT CLIMBING

APPLICATIONS IN ROBOTICS


DROSOPHIBOT ROBOT, WVU

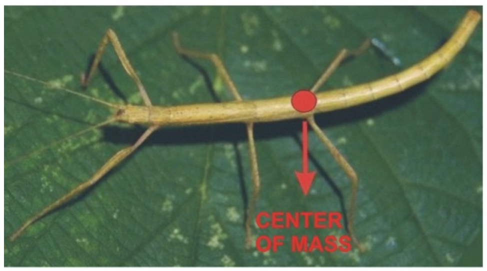

MANTISBOT, WVU, CWRU


SURGERY FULLY CONTROLLED BY COMPUTER

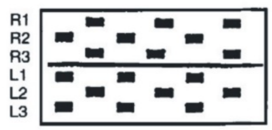
The behaviors of many animals are remarkably graceful. Recent work in robotics has demonstrated advantages in replicating many of these characteristics in the design and control of robotic arms and walking machines.

FLEXIBILITY IN USE OF FRONT LEGS IN STICK INSECTS

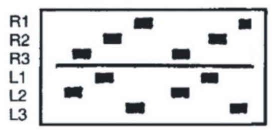
WALKING



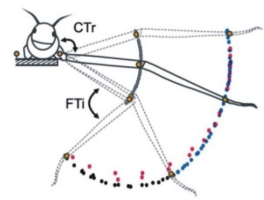
TRIPOD GAIT



METACHRONAL GAIT



SEARCHING

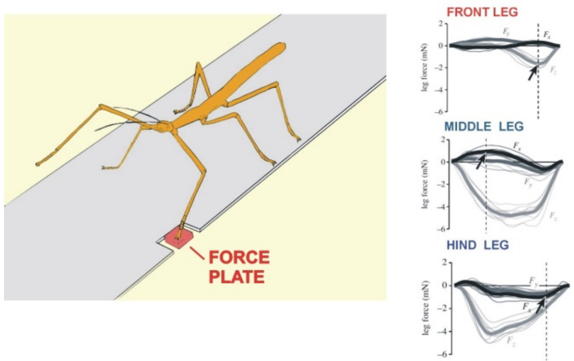


Berg E, et al. 2015,
Curr. Biol. 25:2012-7

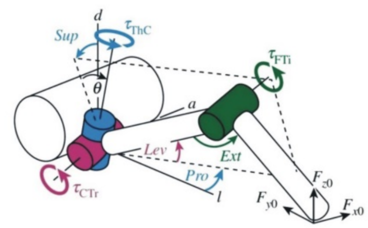
We have studied front legs of stick insects, which are designed for flexibility in use. The center of mass of stick insects is located near the attachment of the hind leg. This effectively unloads the front legs and permits them to be used in both walking and searching movements, without the constraints of support of body weight.

FORCES EXERTED BY FRONT LEGS VARY WIDELY

GROUND REACTION FORCES IN WALKING: SMALLER IN FRONT LEGS

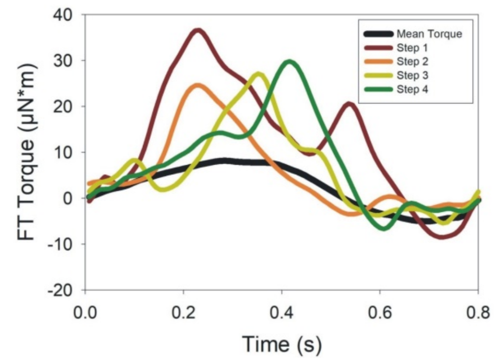


JOINT TORQUES CALCULATED BY INVERSE DYNAMICS



CHRIS DALLMANN,
JOSEF SCHMITZ,
BIELEFELD UNIV.

FT JOINT TORQUES: MEAN AND INDIVIDUAL STEPS



The forces generated by the front legs have been studied by Dallmann et al. (2019). Ground reaction forces and joint angles were measured in freely moving animals permitting calculation of joint torques. In walking on a horizontal surface, the forces exerted by the front legs and mean torques at the femoro-tibial joint were much smaller than the middle or hind legs. However, considerable variability occurred and animals showed more equivalent forces when climbing a vertical surface (Cruse, 1976). We have studied how these forces are encoded by force receptors (campaniform sensilla) of the front legs. Responses were tested to forces in the waveforms of joint torques obtained in freely moving animals.

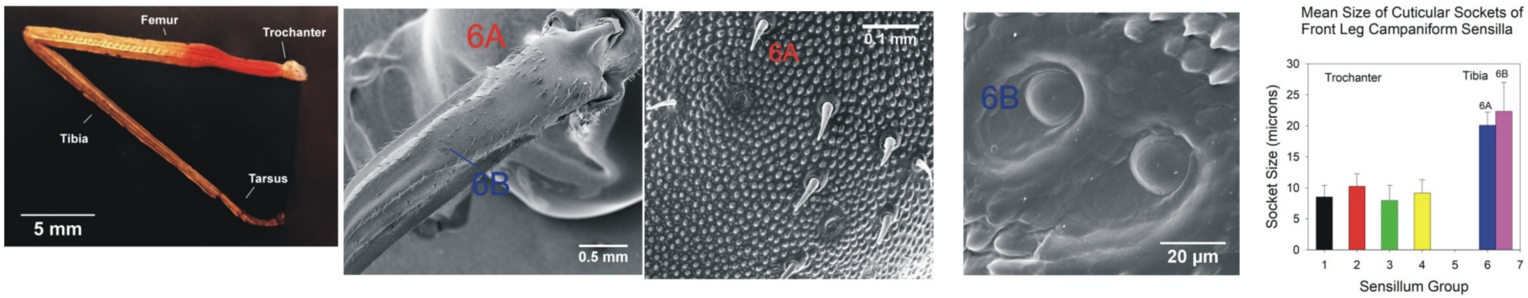
QUESTIONS ADDRESSED IN THIS STUDY:

1) WHAT SPECIFIC PARAMETERS ARE SIGNALLED BY FORCE RECEPTORS (CAMPANIFORM SENSILLA) OF FRONT LEGS IN FREE WALKING ANIMALS?

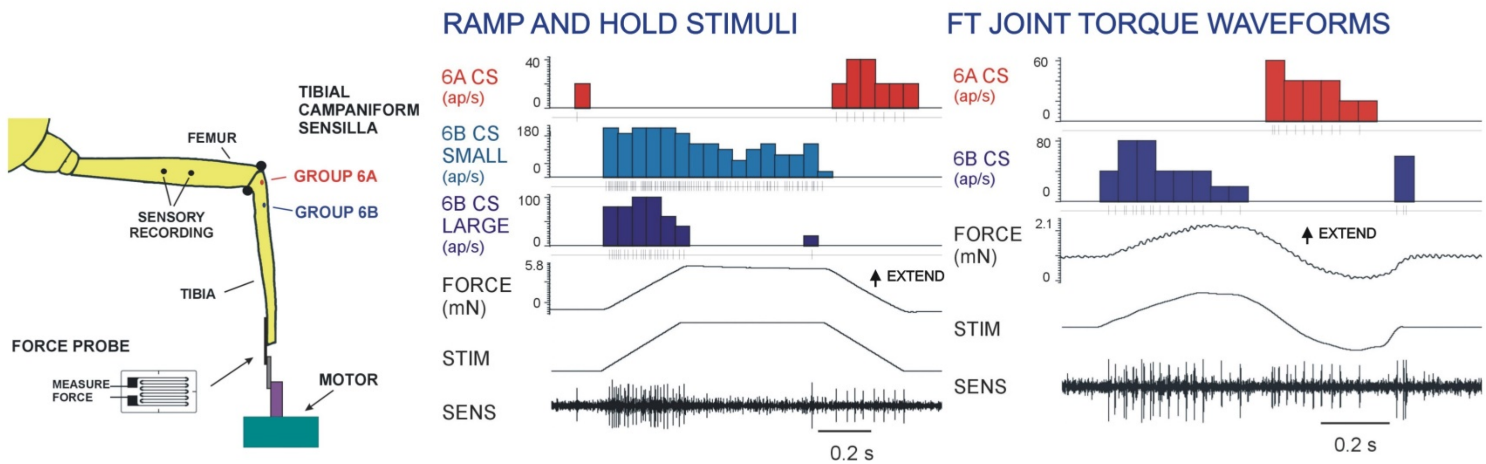
2) CAN THESE CHARACTERISTICS BE EMULATED BY A MATHEMATICAL MODEL OF THE SENSE ORGANS?

CAMPANIFOM SENSILLA OF FRONT LEGS

SEM: Annalie Exter, Josef Schmitz, Bielefeld Univ.

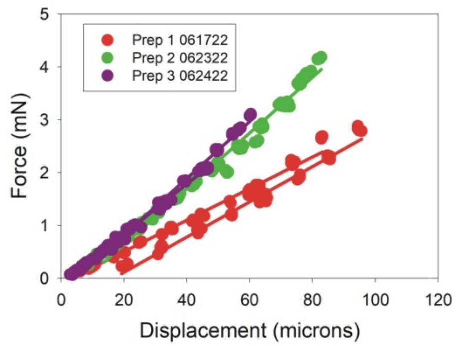


SENSORY RESPONSES IN FRONT AND HIND LEGS OF THE SAME ANIMAL

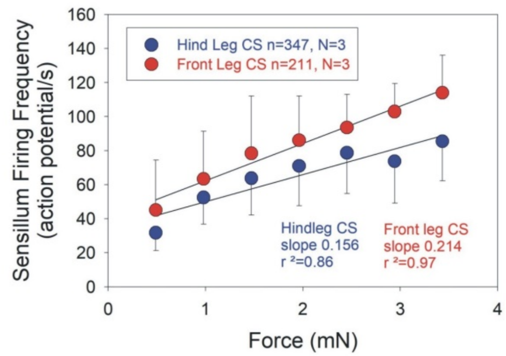


The tibial sensilla of front legs are organized in two subgroups (6A and 6B), similar to other legs. Sensory activities were recorded extracellularly to application of forces using ramp and hold stimuli and femoro-tibial (FT) joint torque waveforms Forces applied in the direction of joint extension (mimicking flexor muscle contractions) produced firing of 6B sensilla to force increases and 6A receptors to force decreases.

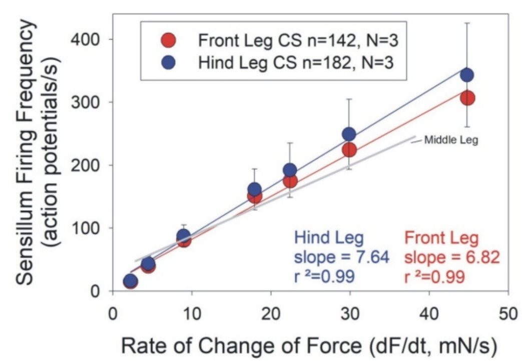
LEG STIFFNESS VARIES BUT IS SIMILAR IN FRONT AND HIND LEGS OF INDIVIDUAL ANIMALS



TONIC SENSITIVITIES ARE SOMEWHAT HIGHER IN FRONT LEGS



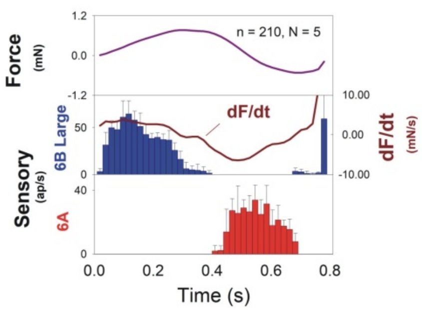
DYNAMIC SENSITIVITIES (dF/dt) ARE SIMILAR IN ALL LEGS



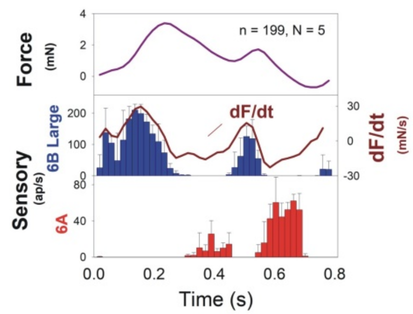
To determine response sensitivities, we compared sensory activities in front and hind legs of the same animals (compensating for variability in cuticular properties). Tonic sensitivities were slightly higher in front legs but all legs showed similar strong encoding of the rate of change of force.

SENSORY ENCODING OF JOINT TORQUES IN WALKING

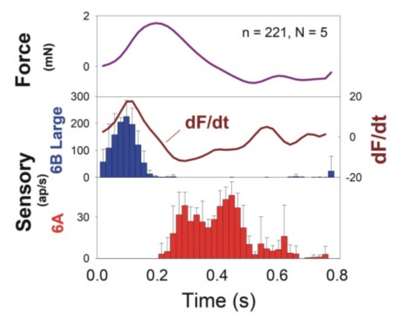
MEAN TORQUE



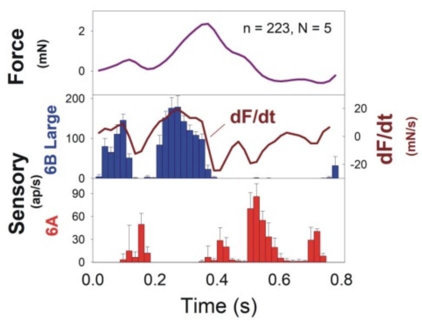
STEP 1 TORQUE



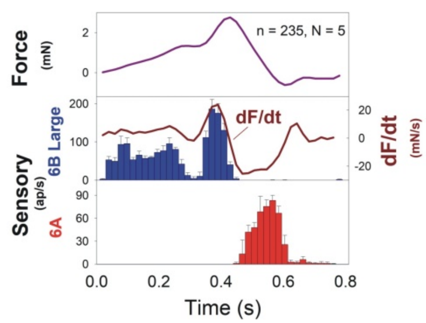
STEP 2 TORQUE



STEP 3 TORQUE

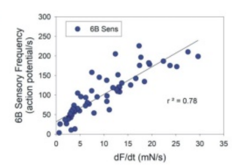


STEP 4 TORQUE

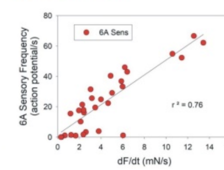


RECEPTORS ENCODE FORCE DYNAMICS IN WALKING

6B VS dF/dt



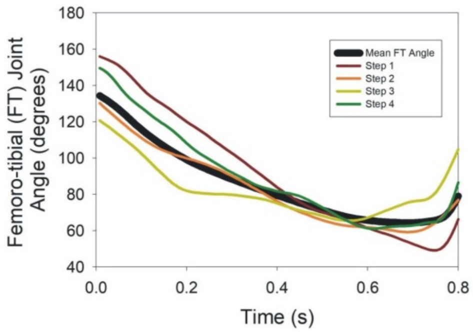
6A VS dF/dt



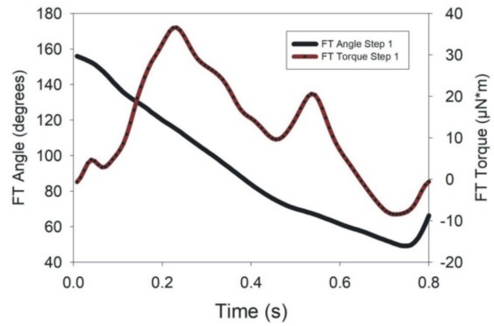
Sensilla fired in intermittent bursts to forces applied using FT joint torque waveforms. All discharges more closely reflected the rate of change of force rather than the force level. Firing to force decreases was prolonged in the front legs as force magnitude was low and discharges to force decrements are maximal near zero offset.

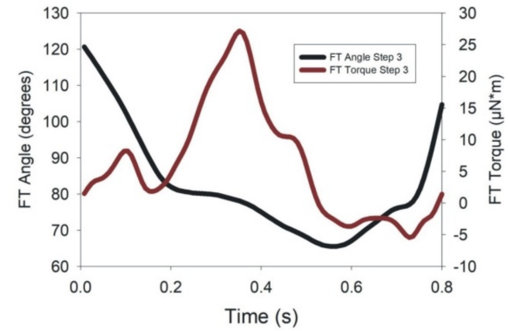
JOINT MOVEMENTS ARE RELATIVELY CONSTANT: FORCE FEEDBACK COULD STABILIZE MOVEMENTS

FT JOINT ANGLE ALL STEPS



JOINT ANGLE AND TORQUES IN INDIVIDUAL STEPS





In contrast to the intermittent and variable force feedback, joint movements in these steps were relatively constant. This suggests that force feedback may stabilize the distal leg joint to force variations due to gait (timing of stance in other legs) to generate smooth joint movements.

A MATHEMATICAL MODEL OF CAMPANIFORM SENSILLA PREDICTS FORCE ENCODING

DYNAMICAL DESCRIPTION OF SENSORY RESPONSES

Sensory discharge = tonic response + adaptation + offset

$y = b*u + a*(u-x) + c$

Adaptive threshold

$\tau \, dx/dt = \mathrm{sign}(u-x) \, |u-x|^d$

y – sensory discharge frequency
u – applied force
x – applied force low pass filtered
c – offset
Constants a, b, c and d are determined by genetic algorithms

METHOD: USE EVOLUTIONARY (GENETIC) ALGORITHMS TO CREATE MODEL

1. CREATE CANDIDATE MODELS - Apply evolutionary (genetic) algorithm using data of median step.

2. 'GENETIC' RECOMBINATION - Recombine models to produce new models which better fit the data.

3. GRADIENT BASED OPTIMIZATION - Best model is used to create optimization routine to improve accuracy.

We have developed a model of force encoding by campaniform sensilla (Szczecinski et al. 2020, 2021). The model calculates the discharge frequency of the receptors as an adaptive function (initial force minus force after a delay) and a function reflecting tonic sensitivity (adjusted by an offset). Characteristics of the campaniform sensilla, such as rate sensitivity and hysteresis, are not specifically determined as variables but, instead, are emergent properties of the model. The model is tuned using data in the median step by selecting values for the constants that minimized the error between the experimental data and the model's response. Only the median step was used in tuning the model (it was not re-tuned for other steps).

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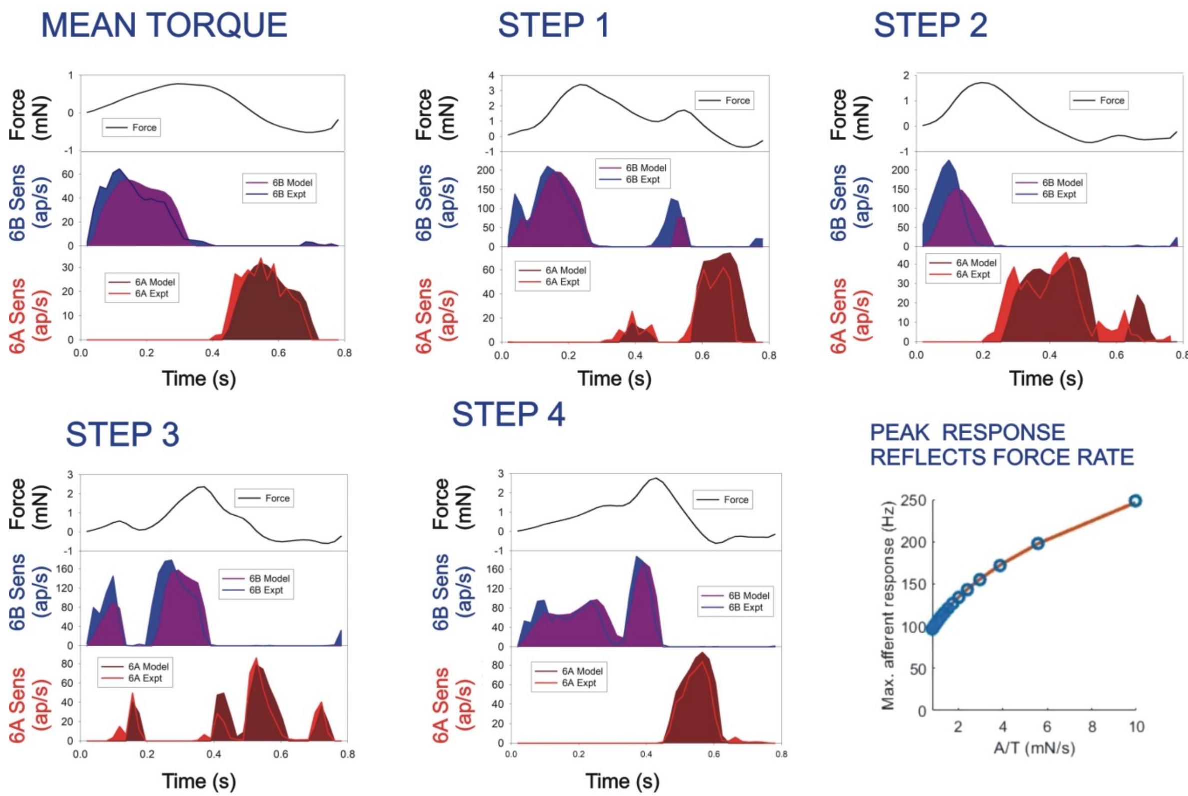
The model was generated by: 1) An Evolutionary (Genetic) Algorithm created a "population" of candidate models, each with a "genome" consisting of random parameter values. The "reproductive fitness" was calculated as the goodness of fit to the experimental data. 2) 'Genetic' recombination - Models were "mated" with other models. Each genome was cut at a random location and the second segment was swapped between individuals (called crossover). 3. Gradient based optimization - An optimization routine was applied to confirm there is not a combination of parameter values that will better fit the data.

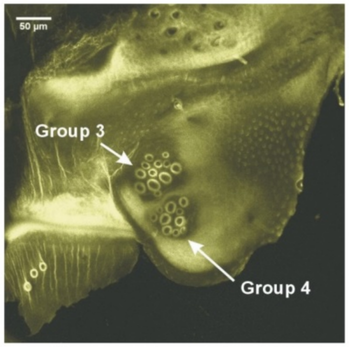
MODEL REPRODUCES ENCODING OF JOINT TORQUES IN WALKING



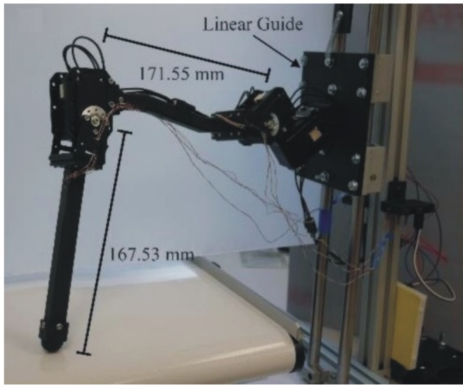
Application of the model in tests of all front leg joint torques showed that it accurately replicated sensory discharges in walking.

CURRENT AND FUTURE WORK

STICK
INSECT
TROCHANTERAL
CS



ROBOTIC
LEG WITH
TIBIAL AND
TROCHANTERAL
SENSORS:
WILL ZYHOWSKI,
WVU



We plan to extend our biological studies to examine responses of the trochanteral campaniform sensilla in walking. Our results are also being tested in a robotic leg (work of Will Zyhowski) for potential incorporation into the control of a walking machine.

CONCLUSIONS:

1) SENSORY SIGNALS IN FRONT LEGS MORE CLOSELY REFLECT THE RATE OF CHANGE OF FORCE (dF/dt) THAN THE LEVEL OF FORCE.

2) THESE DISCONTINUOUS SIGNALS COULD AID IN ADJUSTING MOTOR OUTPUTS TO GENERATE SMOOTH JOINT MOVEMENTS.

3) WHAT MAKES WALKING BEHAVIOR 'NATURALISTIC"? WORKING HYPOTHESIS: SMOOTH MOVEMENTS ARE STABILIZED BY DYNAMIC SIGNALS OF FORCE RECEPTORS.

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