PAPER

Neuromechanical model of praying mantis explores the role of descending commands in pre-strike pivots

To cite this article: Nicholas S Szczecinski et al 2015 Bioinspir. Biomim. 10 065005

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3	1	Neuromechanical Model of Praving Mantis Explores the Role of Descending Commands in
4	2	Pre-Strike Pivots
5	3	
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18	10	
19	13	Abstract
20	14	Praying mantises hunt by standing on their meso- and metathoracic legs and using them
21	15	to rotate and translate (together, "pivot") their bodies toward prey. We have developed a
22	16	neuromechanical software model of the praying mantis <i>Tenodera sinensis</i> to use as a platform
23	17	for testing postural controllers that the animal may use while hunting. Previous results showed
25	18	that a feedforward model was insufficient for capturing the diversity of posture observed in the
26	19	animal (Szczecinski et al., 2014). Therefore we have expanded upon this model to make a
27	20	flexible controller with feedback that more closely mimics the animal. The controller actuates 24
28	21	joints in the legs of a dynamical model to orient the head and translate the thorax toward prey. It
29	22	is controlled by a simulation of nonspiking neurons assembled as a highly simplified version of
30 31	23	networks that may exist in the mantid central complex and thoracic ganglia. Because of the
32	24	distributed nature of these networks, we hypothesize that descending commands that orient the
33	25	mantis toward prey may be simple direction-of-intent signals, which are turned into motor
34	26	commands by the structure of low-level networks in the thoracic ganglia. We verify this through
35	27	a series of experiments with the model. It captures the speed and range of mantid pivots as
36	28	reported in other work (Yamawaki, Uno, Ikeda, & Toh, 2011). It is capable of pivoting toward
37	29	prev from a variety of initial postures, as seen in the animal. Finally, we compare the model's
38	30	ioint kinematics during pivots to preliminary 3D kinematics collected from <i>Tenodera</i>
39 40	31	jour minimus contrag priots to promining 52 minomatics concered nom remoteria.
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1 Introduction

Praying mantises use visual feedback to orient their heads toward prey while keeping their feet stationary using a highly mobile neck, mesothorax-prothorax joint, and legs. When pivoting (i.e. rotating and translating their bodies and heads) toward static prey, mantises actuate their body segments (Yamawaki et al., 2011) and legs (Cleal & Prete, 1996) in coordinated ways to locate prey in the center of their visual field before striking. Early cybernetic models described the control system that converts an error signal, the distance of the prev from the center of the visual field, into precise head saccades that center the target (Laessig & Kirmse, 1972; Mittelstaedt, 1957). However, these models did not address the types of commands that are necessary to coordinate all the joints in each leg into a coordinated motion.

Coordinating legs and body segments is a complicated task, requiring that descending commands be sent from higher command centers that process vision to the legs to rotate or translate the body. In other insects, the central complex (CX) plays a role in sensory-guided motion, such as locomotion speed (Bender, Pollack, & Ritzmann, 2010), the orientation of the body during walking and climbing (Guo & Ritzmann, 2013), measuring distance in the visual field (Wessnitzer & Webb, 2006) and navigation (Vitzthum, Muller, & Homberg, 2002).

We are interested in the structure of insects' central nervous systems (CNS) and how they use structures like the central complex (CX) to guide movement via descending commands to local control networks. Some animals appear to use task-level control to generate joint commands for a complicated task, such as placing one's foot in a particular position (Ting et al., 2009). By feeding back information about the error in the task-level goal (in this example, foot position) into the joint controllers and applying additional constraints about posture, a unique motor program can be produced. In contrast, insects in an active walking state use the active reaction (AR) during stance phase to control redundant joints (Hellekes, Blincow, Hoffmann, & Büschges, 2011). The AR applies positive feedback control to particular joints, allowing them to move when acted upon by the ground or other joints. This is an effective solution for controlling redundant joints in a computationally inexpensive way and has been tested in simulations (Schmitz, Schneider, Schilling, & Cruse, 2008). Yet another proposed solution is to use an internal body model to exploit the mechanical properties of the body. Imagine pulling a marionette by a single string attached to the head; the passive motion of the puppet's legs can be calculated and used as control inputs to the joint controllers (Schilling, Paskarbeit, Schmitz, Schneider, & Cruse, 2012). When this model is implemented as a recurrent neural network, joint motion can be quickly calculated that moves the body in the desired direction, as dictated by the marionette's "string." Mechanisms like these that reduce the dimensionality of control may enable the CX to use relatively simple descending commands to control posture.

Making a model of a nervous system can be a useful tool for gaining insight into system function or generating hypotheses for filling gaps in knowledge (Ritzmann, Quinn, Watson, & Zill, 2000). Past models have used finite state machines (Ekeberg, Blümel, & Büschges, 2004) or artificial neural networks (Beer, Chiel, & Sterling, 1989; Cruse, Kindermann, Schumm, Dean, & Schmitz, 1998) to model the causality or connectivity observed in nervous systems. However, models that additionally include the dynamics of neurons and synapses potentially reveal more about system function than those that do not. Much of the prior work in legged animal nervous system modeling that utilizes dynamical neuron and synapse models focuses on oscillator

in this work.

structure of insect nervous systems.

coordination for inter- or intra-leg coordination, and generally omits the details of how any

Quinn, & Ritzmann, 2013). However, the scope of the present research is to examine what

acting on the body and the role of mechanical feedback in muscle control.

mechanisms might lead to precise posture adjustments, requiring that we consider the forces

particular joint's motion is controlled (Daun-Gruhn & Tóth, 2010; Szczecinski, Brown, Bender,

Walknet uses artificial neural networks and more recently recurrent neural networks (Schilling,

coordination of stick insects. The network structure is heterarchical, meaning that networks with

model the components (i.e. neurons and synapses) and connectivity of insect neural systems. We

elect to use conductance-based neuron models (Equation (3)) rather than static neurons because

their dynamics are more similar to those in animals, and may be important to how they control

motion. In addition, we model the neural system as a single, continuous network, mimicking the

This requires that we use animal data regarding network topology and dynamics. A

wealth of knowledge is available explaining how insects perceive joint motion (Bucher, Akay,

DiCaprio, & Büschges, 2003; Field & Matheson, 1998; Hess & Büschges, 1999), how those

signals are transduced into neural signals (Büschges & Wolf, 1995; Wolf & Büschges, 1995),

and the gains and filter properties of the control system-muscle-limb loop (Bässler, Büschges,

resistance reflex (Büschges & Gruhn, 2007), as well as loading information (Zill, Schmitz, &

Büschges, 2004) and body height (Cruse, Riemenschneider, & Stammer, 1989; Cruse, Schmitz,

Braun, & Schweins, 1993). These data are used to produce the joint control network topologies

This paper presents an improvement over our previous neuromechanical model for

studying prey targeting behavior (Szczecinski, Martin, Ritzmann, & Ouinn, 2014). It encodes

task-level controllers for body height, translation, and rotation into a network of conductance-

dimensionality control signal, possibly originating in the CX, sent to the thoracic leg control

networks. The low-level muscle control networks process this information to produce motion

translations) that orient the body toward prey from a variety of initial postures. The control

the direction of some joints' motion depending on the context without additional descending

commands. Finally, we make a comparison to preliminary 3D kinematics collected from a

mantis, and discuss how to improve the model going forward.

that corrects the error in body rotation and translation. Our model produces pivots (rotations and

network, though static, reproduces bifurcations in joint motion observed in the animal, changing

based nonspiking neuron models. This task-level feedback is represented by a low-

Meditz, & Bässler, 1996). In addition, insects maintain posture while standing using the

different functions are swapped in and out to control different motions, such as stance or swing

phase. Walknet is certainly capable and represents the most complete insect neuromechanical

model that currently exists. For the work in this paper, however, we chose to more directly

Hoinville, Schmitz, & Cruse, 2013; Schilling, Paskarbeit, et al., 2013) to mimic postural and

locomotory behaviors seen in stick insects. Many tools exist for training artificial neural

networks, and as such Walknet is trained to replicate the posture, reflexes, and walking

The most complete insect model that does examine posture control in detail is Walknet.



Figure 1 – A. Body segments and joints of the praying mantis *Tenodera sinensis*. Segments are indicated by cyan pointers, and joints are indicated by magenta. Leg joints are indicated on cut-aways of the metathoracic (T3) legs. Axes of rotation drawn as dashed lines lie in the plane of the paper. In all, 27 body joints are actuated in this model (6 per 4 legs, 3 body joints). B. A screenshot from the simulation, showing the model standing on its hind four legs. C. Table showing segment names, their mass in the simulation, and their length and radius. Radii marked with an asterisk (*) are maximum radii of tapered segments. Values replaced by a dash (-) are either nonexistent (i.e. head length) or not meaningful metrics of size.

1 Methods

2 Modeling components

All modeling was performed in AnimatLab 2 (Cofer et al., 2010). The mantis body is modeled as 28 rigid bodies connected by 27 hinge joints. The hind and middle legs have six joints each, as observed in the animal: three Thorax-Coxa (ThC) joints, a Coxa-Trochanter (CTr) joint, a Trochanter-Femur (TrF) joint, and a Femur-Tibia (FTi) joint (Figure 1A). The front legs have all of these except the TrF joint, which is nearly fused (Corrette, 1990). The prothorax and mesothorax are connected by two hinge joints, one that allows the prothorax to pitch with respect to the mesothorax, and one that allows yaw. Finally, a single hinge neck joint allows the head to vaw. This is a simplification of the animal's flexible neck (Levereault, 1938), but is sufficient to study prey targeting in the horizontal plane. All joints have friction, because dissipative forces are known to play a large role in the control of insect posture (Zakotnik, Matheson, & Dürr, 2006). The front legs are held off the ground against the prothorax, as in preparation for a prey strike, and do not participate in any pivots (and are not counted in the model's degrees of freedom, Figure 1B). Segment lengths, joint locations, and range of motion were taken from the body of a dead male from our colony. Each segment has the average density of the animal, computed by dividing its total mass by its total volume (Figure 1C).

The model stands freely on a flat plane. Only friction keeps its feet from sliding, whereas insects actively grip the substrate they stand on to keep their feet in place (Bässler, 1983). This simplification requires that we set the static and sliding coefficients of friction to 5 to prevent slipping. The legs are only mechanically decoupled if one raises off the ground, or if ground friction is reduced.

An antagonistic pair of linear Hill muscles actuates each joint, with attachments based on cockroach anatomy (Carbonell, 1947), justified by their evolutionary proximity (Svenson & Whiting, 2004). The linear Hill muscle model is comprised of four elements: a contractile actuator, spring, and damper all in parallel, placed in series with another spring. The time derivative of the tension *T* in the muscle can be expressed as:

$$\frac{dT}{dt} = \frac{k_s}{c} \left(k_p x + c \dot{x} - \left(1 + \frac{k_p}{k_s} \right) \cdot T + Act \right) \quad (1)$$

31 where k_s is the stiffness of the series spring, k_p is the stiffness of the parallel spring, c is the 32 damping of the muscle, x(t) is the length of the muscle, and *Act* is the activation, a sigmoid:

$$Act(V_{MN}) = A \cdot \left(1 + \exp\left(B \cdot (C - V_{MN})\right)\right)^{-1}$$
(2)

where *A*, *B*, and *C* describe the amplitude, steepness, and input voltage offset of the sigmoid, respectively, and V_{MN} is the voltage of the innervating motor neuron. More details about the model can be found in (Shadmehr & Arbib, 1992).

Neurons are modeled as leaky conductance-based models with no ion-specific channels. The neurons do not spike, and as such resemble nonspiking neurons known to exist throughout motor control systems in insects (Büschges & Wolf, 1995) or the average activity of a population of spiking neurons. The neuron's membrane voltage V changes according to:

$$C_{mem}\frac{dV}{dt} = G_{mem} \cdot (E_{rest} - V) + \sum_{i=1}^{n} G_{syn} \cdot (E_{syn} - V) + I_{app} \quad (3)$$

in which *C* is capacitance, *G* is conductance, and *E* is a static reference voltage (i.e. reversal
potential). The subscripts *mem* stand for membrane, *syn* stand for synaptic, and *app* stand for

applied. The summation is over all of the *n* incoming synapses for one neuron. Neurons
 communicate via synapses by changing their conductance according to:

$$g_{syn} = \begin{cases} 0 & V < E_{lo} \\ G_{\max} \frac{V - E_{lo}}{E_{hi} - E_{lo}} & V \ge E_{lo} \text{ and } V \le E_{hi} \\ G_{\max} & V > E_{hi} \end{cases}$$
(4)

where E_{lo} is the synaptic threshold, E_{hi} is the synaptic saturation, g_{syn} is the instantaneous conductance of the synapse, and G_{max} is the maximal conductance of the synapse.

Joint controller design

A proportional controller was designed for each joint to provide position feedback to the muscles based on muscle control structures thought to exist in the animal. In the animal, each joint must provide different torques depending on its position along the leg and its orientation. Therefore each controller-muscle actuator loop was designed according to the torque requirements and range of motion of that joint. Rather than merely optimizing some or all of the parameters to produce the desired motion for this study, we used network topology and animal data to solve for parameters that give the model basic capabilities (e.g. supporting its own weight in a variety of poses, etc.). The design process is described here.

18 The feedback controller is shown in Figure 2A. Shape- and color-coded sections of the 19 network were tuned separately and then assembled to produce the desired behavior. These 20 sections will be described according to the flow of information: the desired and actual joint angle 21 are compared, generating an error signal; this error signal activates the motor neurons, which 22 stimulate the muscles to generate tension; muscle tension causes motion, which is registered by 23 sensors and converted into the current joint angle for comparison to the desired value.

The basic component of a feedback loop is a network that can compare the actual and desired system state, in this case, the joint angle. It is known that nonspiking interneurons (NSIs) in the thoracic ganglia of insects provide excitatory and inhibitory input to motor neurons in the leg (Wolf & Büschges, 1995). These NSIs exist in parallel, antagonistic pathways, and some show activity that correlate with leg position. We used these results to inspire the design of a network capable of computing the difference between the actual and desired joint angle of each joint. For each joint, extension is encoded in the NSI labeled Actual in Figure 2A. When the joint is fully flexed, Actual sits at its resting potential. Extending the joint will proportionally depolarize Actual, to a maximum 20 mV above rest when fully extended. If the joint is more extended than the desired position, the flexor motor neuron Flx MN should be excited to correct the error, and the extensor motor neuron Ext MN should be inhibited. This is accomplished via the Too Ext NSI, which along with the Too Flx NSI carry position information in parallel antagonistic pathways to the motor neurons.

39 Steady state analysis shows how this structure generates an error signal for stimulating 40 the motor neurons. Solving Equation (3) for steady state $\left(\frac{dV}{dt} = 0\right)$ yields 41 $V^{SS} = \frac{G_{mem} \cdot E_{rest} + \sum G_{syn} \cdot E_{syn} + I_{app}}{2}$ (5)

$$SS = \frac{G_{mem} + \Sigma c_{syn} + \Sigma G_{syn} + G_{app}}{G_{mem} + \Sigma G_{syn}} \quad (5)$$

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3	1	Applying this to the <i>Too Ext</i> NSI in the network in Figure 2A,
5	2	$V_{\text{SS}}^{\text{SS}} = = \frac{G_{mem} \cdot E_{rest} + g_{Desired} \cdot E_{Desired} + g_{Actual} \cdot E_{Actual}}{(6)}$
6	2	$G_{mem} + g_{Desired} + g_{Actual}$
7	3	In which $V_{Too Frt}^{SS}$ is the steady state voltage of the <i>Too Ext</i> NSI. Lower case gs are synaptic
8	4	conductances (not maximum synaptic conductances; see Equation (4)), and upper case Gs are
9	5	constant conductances. The subscripts <i>Desired</i> and <i>Actual</i> correspond to parameters of the
10	6	synapses leaving these neurons, respectively, and synapsing onto $Too Ext$. As long as V_{Actual} and
12	7	V_{prime} are within the bounds specified in Equation (4), a_{prime} is linearly proportional to
13	8	$V_{\rm restrict}$ and $q_{\rm restrict}$ is linearly proportional to $V_{\rm rest}$. Our joint rotation encoding (see previous
14	9	naragraph) guarantees this allowing us to express the "middle" case in Equation (4) in a simpler
15	10	form:
16	10	a = a V + b (7)
17	11	$g_{Desired} = u \cdot v_{Desired} + b (7)$
18	12	$g_{Actual} = u \cdot v_{Actual} + b (8)$
20	13	a and b are constants calculated with E_{lo} and E_{hi} from Equation (4). In our system, $a = 0.05$ and
21	14	b = 3. We can now make some substitutions that simplify analysis by constraining some
22	15	parameter choices. Let
23	16	$G_{mem} = 1 (9)$
24	17	$F = \frac{1}{2} \cdot (F_{2} + F_{1} + F_{2})$ (10)
25	17	$\frac{L}{2} = \frac{2}{2} \frac{(L_{Desired} + L_{Actual})}{2}$
20 27	18	$\Lambda F = \frac{1}{2} \cdot (F_{\rm p} + F_{\rm res} + F_{\rm res}) (11)$
28	10	$\frac{dE}{2} = \frac{2}{2} \left(\frac{D_{Destrea}}{2} - \frac{D_{Actual}}{2} \right)$
29	19	Combining Equations (10) and (11) shows that
30	20	$E_{Desired} = E + \Delta E (12)$
31	21	$E_{Actual} = E - \Delta E$ (13)
32	22	Note that this requires that the synapse from <i>Desired</i> is excitatory and that from <i>Actual</i> is
33	23	inhibitory. We can substitute Equations (9-13) into Equation (6)
34 35	24	$E_{rest} + (a \cdot V_{Desired} + b) \cdot (E + \Delta E) + (a \cdot V_{Actual} + b) \cdot (E - \Delta E) $ (14)
36	24	$V_{Too Ext}^{OO} =$
37	25	Collecting terms
38		$E_{rest} + (a \cdot (V_{Desired} + V_{Actual}) + b) \cdot E + a \cdot (V_{Desired} - V_{Actual}) \cdot \Delta E$
39	26	$V_{Too Ext}^{33} = \frac{1}{(V_{Too Ext} + a) + b} $ (15)
40 11	27	Δ dditionally we define the error between <i>Desired</i> and <i>Actual</i>
42	27	Additionally we define the effor between <i>Destred</i> and <i>Actual</i> $a = V_{a} + v_{b} + v_{c}$ (16)
43	20	$e = v_{Desired} + v_{Actual}$ (10)
44	2)	1
45 46	30	$V = \frac{1}{2} \cdot \left(V_{Desired} + V_{Actual} \right) (17)$
47	31	Substituting Equations (16-17) into Equation (15)
48 49	32	$V_{Too Ext}^{SS} = \frac{E_{rest} + 2(a \cdot V + b) \cdot E + (a \cdot e + b) \cdot \Delta E}{C + 2(a \cdot V + b)} $ (18)
50	22	$G_{mem} + 2(a \cdot v + b)$
51	33 24	If we require that E, the mean of the synaptic potentials coming into $100 Ext$ (Equation (10)), is
52	34 25	equal to E_{rest} , define the sum of the conductances of these synapses
53 54	35	$g = 2(a \cdot v + b) (19)$
55	36 27	and define
56	37	$U_{Too Ext}^{33} = V_{Too Ext}^{33} - E (20),$
57	38	we obtain
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$$U_{Too \ Ext}^{SS} = \frac{a \cdot \Delta E}{1+g} \cdot e = k_{pos} \cdot e \quad (21)$$

in which k_{pos} is the gain (or amplification) of the comparator. This shows that the change in the membrane potential of *Too Ext* from its resting potential is proportional to the difference between the membrane potential of *Desired* and *Actual*. This is the basic requirement for a feedback comparison between a desired and actual state, and depends on the parallel antagonistic structure of the network (Figure 2A, red rectangles). This analysis can be repeated for *Too Flx*, with the same result as long as the synaptic potentials $E_{Desired}$ and E_{Actual} are swapped, establishing parallel antagonistic pathways.

10 These pathways innervate the motor neurons (Figure 2A, blue hexagons), which activate 11 the muscles. Each muscle's activation (*Act* in Equation (1)) is a sigmoidal function of its motor 12 neuron's voltage (Equation (2)). An important observation is that changing the baseline 13 activation of the motor neurons changes the stiffness of the controller acting on the joint. 14 Stiffness, *k* is defined as the partial derivative of the applied control torque, τ with respect to the 15 deflection from the commanded position, θ . For the case of a proportional controller, this yields:

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$$\tau = k \cdot \theta \rightarrow k = \frac{\partial \tau}{\partial \theta} \quad (22)$$

In a neuromuscular system, the torque depends not only on the muscle activation, but also on the
gain of the comparator (Equation (21)). Assuming small joint rotation and using the chain rule,
we obtain:

$$k = \frac{\partial \tau}{\partial \theta} = \frac{\partial \tau}{\partial A} \cdot \frac{\partial A}{\partial \theta} \quad (23)$$



Generating muscle tension produces motion, which must be registered by the nervous system for comparison to the desired position. One mechanism by which insects encode joint rotations is the stretch of chordotonal organs (CO) that span joints (Field & Matheson, 1998). Each CO innervates dozens of neurons with sensitivity to joint extension and velocity. Our model simplifies this; each joint possesses a network that maps the extensor muscle length to the joint rotation via a layer of neurons (Figure 2A, yellow ellipses). To tune the map, a network with extensor length as the input and joint rotation as the output with a single hidden layer, initially with only one node, is designed. Muscle attachments and joint kinematics are used to calculate the extensor length as a function of the joint angle and used to train all synaptic properties (see parameters in Equation (4)) with a genetic algorithm (GA). Once the GA is complete, the most successful parameter combination is refined by a quasi-Newton optimizer until the steady state network activity matches the expected value as closely as possible. A quasi-Newton optimizer minimizes a function in a sequential fashion like a Newton optimizer, but only computes the gradient explicitly. It uses subsequent gradient calculations to approximate the Hessian matrix, reducing the problem from $O((n^2+3n)/2)$ to O(2n) (Dennis & Schnabel, 1983). Such a gradient-based method guarantees the local optimality of the synaptic parameters of the mapping network (Dennis & Schnabel, 1983). If the resulting map is not accurate enough, an additional neuron is added to the hidden layer and the process is repeated until the network encodes the joint angle accurately enough.

After designing the feedback pathways, muscle properties are calculated. Joint torques are approximated by calculating the manipulator Jacobian of each leg and multiplying by ground wrenches (Murray, Li, & Sastry, 1994). For each joint, the most extended pose of the distal joints is found via a quasi-Newton optimizer. Then, the body weight is applied in the direction perpendicular to both that joint's axis and the joint-to-foot vector. Using the joint geometry and muscle attachments, the maximum muscle force can be calculated by ensuring that the worst case torque can be applied even when the muscle has its lowest mechanical advantage about the joint.

The series stiffness k_s in Equation (1) represents that of the apodeme (tendon), which is very stiff, and is calculated by finding the stiffness required to resist the maximal muscle force when stretched over its entire range of motion. Other modeling studies have made tendons stiffer (Ekeberg & Pearson, 2005), but in an attempt to better condition the simulation, the stiffnesses were reduced. Lower stiffnesses produce smaller accelerations. This reduces the risk of an unsuccessful end of the simulation with a zero-divide and the simulation can run with a larger step size and, therefore, faster. The parallel stiffness is set to 20% of the series stiffness. Muscle damping is approximated based on expected maximal joint rotation speeds and joint torques. The damping is set such that when each joint is moving at its maximum expected speed, the tension from the damping is equal to half of the muscle's maximum force output, at which point the joint would be at its stiffest.

The result of this design process is evident in a Bode plot of the joint's response (Figure 2C). Joints were designed to operate at a maximum of 8 Hz, which is a preferred running speed for cockroaches (Bender et al., 2011), and on the correct order for rapid (roughly 125 ms)

posture adjustments that mantises make (Yamawaki et al., 2011). The graph shows that the
 resonant frequency of the joint controller is approximately 8 Hz, above which the gain decreases.

4 Generating Model Posture – Feedback Model

5 In our previous work, we developed a model that issued feedforward commands to the 6 leg joints to execute prey-orienting pivots (Szczecinski et al., 2014). We observed the animal and 7 identified leg joints that appeared to play the largest role in pre-strike pivots. We then solved an 8 inverse kinematics problem for each leg, using a quasi-Newton optimizer to minimize the 9 distance between the position of the foot and the position required for a particular pivot, as a 10 function of the joint angles. The required joint angle commands for a given body translation and 11 rotation were then encoded in a mapping network, as described in Joint controller design.

This method had two drawbacks. The first is that when watching the animal, it is clear that it can orient itself toward prey from many different starting leg postures. The feedforward model, however, commands joint angles in a one-to-one fashion for given body translation and rotation. Therefore it lacks the basic adaptability of the animal's control system, and the model presented in this paper addresses this shortcoming. The second drawback of the feedforward model is that it was not a good predictor of the animal data we collected. The animal data, in the form of the change of each joint's angle as a function of the change in the body's rotation and position, was very noisy, likely because the animal can pivot from many different starting postures, and the nonlinearities inherent in leg kinematics obscured any trends that may exist.

The model presented in this paper uses feedback loops to produce posture (networks shown in Figure 3 and Figure 4), eliminating the feedforward absolute joint position descending commands. Instead, it sends more abstract descending commands encoding the deviation in body rotation, translation, and altitude from desired values. These descending commands specify joint flexion or extension with muscle force proportional to the error of the head orientation. This descending command is fused with joint angle data at the thoracic level, and a new position command is sent to the joint. This is not the same as sending a descending command that is as simple as a joint angle. Consider the torque produced by a proportional controller, τ , like that implemented in this model:

$\tau = k \cdot (\theta_{Desired} - \theta) \quad (24)$

In which k is the feedback gain and θ is the joint angle at this instant, and $\theta_{Desired}$ is the desired rotation. The descending command in our model is the difference between the head's rotation in the horizontal plane and a desired rotation, which represents the location of the prey in the visual field. This defines the orientation error *e*. Fusing *e* with the joint angle at the thoracic level produces the controller input:

38
$$\theta_{Desired} = e + \theta$$
 (25)
39 Substituting this into Equation (24) yields the joint torque output
40 $\tau = k \cdot (e + \theta - \theta) = k \cdot e$ (26)

This means that in our model, descending commands can cause the leg joints to produce torque to take corrective action and orient the head toward prey, regardless of their current position. Of course, this will not be the case if a joint is at the limit of its range of motion. Our observations and previous studies in locusts (Zill & Frazier, 1992) suggest that when the end of the range of motion is reached, the insect will take a single step to move joints to a more favorable position, a scenario beyond the scope of this work.

A diagram of the orientation network is shown in Figure 3. The actual and desired absolute rotation of the head in the horizontal plane is used as an abstraction of a visual prey signal. It is known that mantises use visual information to orient toward prey (Mittelstaedt, 1957), so our model registers the rotation of its head as well as a target value (i.e. where the prev is) (Figure 3, gray shading, "lobula"). In arthropods, the CX receives highly processed signals from contralateral head sensors, suggesting that this is a candidate of where the signals from visual centers are compared to one another (Strausfeld, 2012), and the command to turn left or right toward the prev is produced. Our model implements this behavior via a series of comparators (Equation (22) and Figure 2A), one for each body segment (Figure 3, violet shading, "central complex"). Each comparator's output is sent to a different body segment. In the model's thoracic ganglia, the descending command to turn is integrated with the proprioceptor for that segment, as described by Equation (26) (Figure 3, orange shading, "thoracic ganglia"). To control the legs, trends of joint motion when the animal pivots (Cleal & Prete, 1996; Szczecinski et al., 2014) were encoded via connections to the middle legs' FTi and ThC3 joints and the hind legs' CTr joints. These trends are listed in the table in Figure 3.

Unlike our previous, feedforward model (Szczecinski et al., 2014), the descending commands discussed so far do not maintain the model's body height and position. Therefore another controller is necessary to monitor its body height, lateral position, and longitudinal position to produce muscle forces that maintain a baseline upright posture. The joint torques necessary to counter external forces can be calculated by multiplying the leg's Jacobian matrix transposed times the external forces and moments (Murray et al., 1994). Biological data, however, suggests that this problem may be solved without such a complicated body model (Lévy & Cruse, 2008b). It is known that stick insects use their CTr joint to servo their body height (Cruse et al., 1989). This observation makes sense because the CTr's orientation requires it to support much more of the animal's weight than the ThC or FTi joints. Using this same logic, our model uses its middle legs' CTr joints, as well as the ThC3 joints on the hind legs, to control the body's height. The ThC3 joint is included because like the stick insect's CTr joint, its orientation forces it to support the body's weight. Data from cockroaches performing an escape behavior show that lateral body movements are directed by the middle legs' FTi joints, and longitudinal movement is propelled by the hind CTr and FTi joints (Nye & Ritzmann, 1992). Because of the similarities in these insects' leg morphologies, our model also controls translation in the horizontal plane via its middle FTi joints and hind CTr joints. Of course other joints could be selected, but we chose to control these because of the data available from related insects. Figure 4 shows a diagram like Figure 3 that details these connections.

The model's static posture is the result of all of these control networks sharing control of the leg joints. Therefore even the initial posture before executing a pivot is not explicitly commanded. To generate reproducible data, a startup routine was established. The model begins suspended above the ground, with all body posture servo loops (Figure 3 and Figure 4) disabled.



Figure 3 – Diagram of our feedback based orienting model. Regions of the nervous system in which analogs to our simplified systems may reside are highlighted. Neurons from the local reflex network in Figure 2 are the same color and shape for comparison. Neural data from the trial in Figure 5C illustrates network function. Prior to 1500 ms, the prey and head angle activate the Too Right neuron. The Vis/Prop Fuse neuron combines the Too Right activation with the joint's current angle, the T2 R FTi Angle neuron. This combination then produces new joint commands for the T2 R FTi Des. Angle neuron. The difference between the current angle and the new joint command specify the torque output, illustrated by the shaded areas in the plot. The negative torque ($\tau < 0$) is due to corrections made by the network in Figure 4. Leg joint pivot coordination rules are summarized in the table at the bottom.

The joints are commanded to positions that produce plausible leg posture for a mantid. The model is then dropped onto the ground, and the body position control network (Figure 4) is activated. The model then stands upright and orients itself forward. Once it finds equilibrium, the head orienting control network (Figure 3) is activated, and the model tracks a prey signal. In this study, we are primarily interested in how the animal coordinates its leg joints when pivoting. Therefore the neck and body joints were made immobile in all of the data shown. They can be unlocked, and mimic the coordination seen in mantids when pivoting toward static prey (Yamawaki et al., 2011).



Figure 4 – Diagram of our feedback based posture model. Descending commands that enable body height servoing (*Servo Body Height*) and set the intended body height (*Desired Body Height*) activate the system, which compares the height of the attachment point of each leg to the desired value. As noted in the text, the ThC3 joint controls height in the hind legs, and the CTr joint controls height in the middle legs. Neurons from the local reflex network in Figure 2A are the same color and shape for comparison. Rules for rejecting perturbations in the horizontal plane are also provided; they are implemented via analogous networks.

1 3D Tracking Animal Experiments

The food-deprived freely-walking adult animals were positioned in the center of an open-top clear acrylic box (40 cm x 40 cm x 15 cm) and three cockroach nymphs were placed into the corner of the arena. Two nearly-orthogonal cameras (A602f, Basler AG, Ahrensburg, Germany) were positioned beneath the base of the acrylic arena and video was recorded at 100 frames per second. The joint and body segments during each discrete movement were aligned on each video and digitized using the DLT script for Matlab provided by Tyson Hedrick (Hedrick, 2008). A total of twenty eight points were manually located on the animal during the digitizing process in both synchronized videos to calculate joint angles in a three-dimensional space. These measurements allowed us to locate the tarsus, tibia and femur, as well as the location of the tarsus-tibia, FTi and CTr joints. From these data the FTi and CTr angles could be approximated

Results

13 Postural Tuning and Stability

We first tuned the dynamics of the model to match those of a mantis pivot. We are primarily interested in the coordination of the legs that produces pivots, so in all of our simulation trials, the neck and body joints are locked. Motor commands to pivot are generated by the networks in Figure 3 and Figure 4, in the form of joint torques proportional to the rotation or translation error (Equation (26)). Therefore increasing the feedback gain of the comparators in these networks will increase the torque applied by the joints, and in turn the speed of the motion. This is accomplished in our model by increasing the maximum conductivity of the synapses in the first shaded columns of Figure 3 and Figure 4. Published data from Tenodera show that the duration of the pivot correlates with the rotation that the thorax undergoes (Yamawaki et al., 2011), at about 700 ms per radian. Thus we adjusted the feedback gain of the comparators until the model produced pivots of comparable speed. A sweep of ten pivots (linearly spaced from 3 to 30 degrees) with our model reveals a mean rotation rate of 1011 ms per radian, with a standard deviation of 239 ms per radian, putting the model's speed on the same order of magnitude as that of the animal.

The feedback gain that produced the animal-like pivot speeds caused the model to overshoot the target and oscillate around it or destabilize. Therefore we introduced a "tolerance" to each feedback loop, that is, a range around the desired state that evoked no corrective response. This was implemented by hyperpolarizing the neurons in the comparator networks (Too Low, Too High, etc.) in Figure 3 and Figure 4. The impact of this addition is shown in Figure 5. Introducing a moderate tolerance to the rotation (+/- 2 degrees), longitudinal translation (+/- 1.5 mm), and height (+/- 1 mm) control networks greatly improved the stability of the model while allowing for mantis-like speeds. These values were selected by sweeping tolerance values for each control loop and comparing the model's performance, as shown in Figure 5.

39 Leg Kinematics of Pivots

40 Since the posture and orientation controllers do not explicitly specify position commands 41 for the joints, we analyzed the leg motion during pivots generated by this control system. We 42 observe that the animal can pivot itself toward prey from a variety of initial leg postures, so our 43 model must capture this adaptability. To test model performance, we generated families of 44 curves in which one joint's initial rotation was modified in increments of 10% of its range of 45 motion. The model was then allowed to achieve equilibrium due to the body position control network in Figure 4, and then commanded to rotate the thorax 30 degrees, roughly the largest
 pivot we observed in the animal.
 3

The model is sensitive to some initial T2 FTi joint rotations, as shown in Figure 6. When the contralateral, or pushing leg's FTi angles were varied, the model rotated to within 10% of the target rotation from 55% of starting positions. The trials in which it did not succeed were those in which the leg began from an already extended pose; the leg effectively run out of range of motion. When the ipsilateral, or pulling leg's FTi angles were swept, the model rotated to within 10% of the target rotation from 82% of starting positions. The model failed to pivot properly when the FTi began too flexed, not allowing it to flex any further and pull the body laterally. However, this was only a limitation when the joint began within 10% of its most flexed position. Observing the animal reveals that it may take single steps with one leg if it reaches its range of motion, but modeling such an action is outside the scope of this model. Overall, the



model was successful in 15 of 22 initial T2 FTi joint rotations.

The T2 CTr starting angle was not varied in this way because in our model, it only receives feedback about body height, not body rotation. However, one can see that the CTr

extends when the FTi becomes too flexed or extended to maintain body height, as seen in other
insects (Bucher et al., 2003; Cruse et al., 1989). These data also qualitatively agree with
previously reported two-dimensional data collected from striking mantids, in which the
contralateral T2 CTr joint extends significantly during most pivots, while the ipsilateral T2 CTr
shows comparatively less motion (Cleal & Prete, 1996).

Sweeping the T3 CTr joint rotations yielded similar success rates, shown in Figure 7. Overall the model pivoted successfully in 14 of 22 initial postures. When the CTr was started in a very flexed position (dark traces, Figure 7), the tarsus of that leg could not reach the ground, and the model could not support itself. When the joint was free to rotate, the leg then had to extend toward the ground and first lift the body, then pivot. Not surprisingly, these pivots were rarely accurate, apparently because the FTi joint ran out of range of motion (Figure 7, left column). When the contralateral CTr was started in an extended position, the model hit the limits of its range of motion and failed to rotate accurately. In a few cases, individual legs did not maintain ground contact, causing the legs to move freely through the air rather than moving the body toward the target. Insects use their tarsi to grip the substrate and prevent their feet from lifting (Bässler, 1983). Our current model, however, does not include tarsal gripping, leading to occasional out-of-ground-plane motions. In spite of this shortcoming, the model's control system is flexible enough to succeed in most, but not all, starting postures.

21 Effect of Body Translation on Leg Kinematics

These data were collected from trials in which the model maintained its longitudinal (i.e. forward and backward) position. The animal, however, often moves forward or backward while executing a pivot. As observed in escaping cockroaches as they pivot, executing a different motion may require drastically different leg motion. For instance, some joints change their range of motion, or even change direction, when stimulus is applied at different angles (Nye & Ritzmann, 1992). Is this change the result of a totally different signal from the higher command centers, or can these unique motions be produced by the same control network, whose connectivity is never modulated?

We hypothesized that the structure of our control system did not need to be varied by descending commands to produce the same kind of drastic kinematic changes seen in the animal. To test it, the model was made to perform a variety of different rotations while moving forward the same amount, or vice versa. Based on previous data collected in cockroaches (Nye & Ritzmann, 1992) and mantids (Cleal & Prete, 1996), we expected to see two changes in joint motion. The first is that the ipsilateral T3 CTr joint should change from flexion to extension as the model translates further forward during a pivot. Second, the contralateral T2 FTi joint should switch from flexing to extending as the model rotates further for the same forward translation.

The results from these experiments are shown in Figure 8. The first column shows that
the ipsilateral T3 CTr joint changes direction as the model's forward translation is varied from 0
mm to 10 mm while executing a 0.25 radian pivot. This is qualitatively consistent with
observations in animals. The second column shows that the contralateral T2 FTi joint changes
from flexion during forward translation to extension when translating and pivoting
simultaneously. This effect is not as dramatic as the T3 CTr, likely because the ThC joints
contribute to both translation and rotation control in our model. However, these data show that

degree of mechanical coupling.

this single network with unchanging connectivity is capable of producing the bifurcations in leg

rotation controller in Figure 3 and posture controller in Figure 4. Figure 8 shows that these are

However, removing this mechanical coupling (that is, removing the ground) does cause the feet

to move at different rates, meaning that the coordinated motion of the model depends on some

joint kinematics observed in the animal due to the combination of feedback from the body

actively commanded and are not simply the result of mechanical coupling between the legs.



Figure 6 – Data showing head rotation and T2 leg joint rotation when the T2 FTi joint is started from different positions. The head and prothorax were locked with respect to the mesothorax, meaning that only the legs could rotate the head toward the target at 0.5 radian. In 82% of starting T2 FTi joint angles, the model oriented within 10% of the target, plus the tolerance (red bar). The T2 CTr joint angles also vary, because this joint controls body height, and must compensate for the change in FTi angle. The model fails to accurately pivot when its joints reach their range of motion, that is, when the contralateral leg fully extends its FTi joint, or when the ipsilateral fully flexes it.

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Figure 8 – Kinematic data from trials showing that joints may change their direction of travel for the same rotation or translation, not based on descending commands, but based on the accompanying translation or rotation, respectively. (left) The model was made to rotate 0.25 radian while sweeping 10 mm of possible translation. The T3 CTr joint changes from flexion to extension as the forward translation of the model increases for the same body rotation. (right) The model was made to translate 10 mm while sweeping 0.4 radian of possible rotation. The T2 FTi joint changes from flexion to extension as the model increases its rotation for the same translation. The bottom row shows data from the Visual-Proprioception Integration neurons in the center shaded columns of Figure 3 and Figure 4. When their activation is above the dashed line, the joint is actively commanded to extend. When their activation is below the dashed line, the joint is actively commanded to flex. These data

0.4

2.5

0.5

2.0

0.5

-40

-70

millivolts

radian

radian

millimeters

radian

 show that the extension and flexion of the joints are the result of descending commands, not the mechanical coupling of the legs.

1 Compo

Comparison to 3D kinematics from the animal

Preliminary three-dimensional kinematics were collected from mantises as they pivoted, tracking prey in an open arena. As the method is improved, more data will be collected, but here we present data from a single trial for comparison to the model. The starting joint angles for the model were made as close to the animal's as possible. The model was then commanded to execute a pivot and translation of the same magnitude as the animal. Data in Figure 9 shows that while the model and animal are not in total agreement, many of the same trends are captured. For instance, joints in the ipsilateral T2 leg flex to rotate the body. Joints in the ipsilateral T3 leg largely remain stationary, acting as a pivot point, while those in the contralateral T3 leg extend a small amount to push the animal or model forward and to the left. Much more data will need to be collected to make definitive conclusions about how the leg joints are used to propel the body.



Discussion

We present a hypothetical posture controller for modeling praying mantis pre-strike postural adjustments built upon joint controllers based on details of insect neurobiology. The control system is built from realistic models of muscles and neurons, forcing us to address details

of how such networks function. The low-level controller has structures analogous to those known to exist in animals (Field & Matheson, 1998; Wolf & Büschges, 1995), and exhibits the same filtering properties as those in other insects (D. Bässler et al., 1996). As a result, our posture control networks and the form of descending commands in our model are more thorough hypotheses than one could produce with a simpler model, and suggest as-yet unexamined mechanisms that may be found in the animal. Examples in this study include feedback tolerances to avoid overshoot due to body inertia (Figure 5), and the incorporation of local proprioceptive information with simple descending commands to produce joint torque commands (Equation (26), Figure 3, and Figure 4).

11 Low-level networks

By modeling low-level circuits, we were able to show how simple descending commands might interact with local control networks to produce adaptive posture control. Starting with a detailed model of insect joint control will also allow us to explore different behaviors in the future. Optimizing controller parameters to produce a single behavior (Zakotnik et al., 2006) would limit the possibility of extending this model. The animal does not have a nervous system tuned for a single behavior, and for this reason we have built a model based on what is known about insect feedback control of muscles (D. Bässler et al., 1996; Wolf & Büschges, 1995), and calculated parameters based each joint's function and capability (i.e. range of motion, speed, and torque).

Making such a detailed model also required deliberate consideration of the nature of descending commands that would be necessary for the animal to produce pivoting motions. In the real world the animal must orient toward prey from many different foot positions, making it unlikely that it sends descending commands in the form of joint positions. Instead, we combine local proprioception with simple descending commands to produce more adaptive and flexible targeting motions, within the bounds of what is known about insect joint control. This feedback-based model can rotate the thorax as much as we see in the animal from many different starting configurations, not because of complicated descending commands, but instead by processing descending commands with the local control networks. By constructing a control system with a topology like that of insects, we were able to hypothesize how descending commands affect local controllers to produce the adaptable posture we observe in mantises.

Our low-level controller model is also important to consider because of the compliance it offers. Joints may produce torques that resist one another, but the passive forces in the muscles allow the system to overcome these small discrepancies and execute the pivots without locking up or moving the feet. This is an especially important lesson in robotics, in which such elasticity is not common (although it is becoming more common: Paskarbeit, Schilling, Schmitz, & Schneider, 2015; Spröwitz, Ajallooeian, Tuleu, & Ijspeert, 2014; von Twickel, Hild, Siedel, Patel, & Pasemann, 2011).

42 Task Level Control of Pivots

43 Our results show how one control system, without descending commands to change
44 connectivity, may produce joint kinematics that are markedly different under minimally different
45 circumstances. Instead of the animal executing a discrete type 1 or type 2 pivot (Cleal & Prete,
46 1996), the brain may instead simply send commands to translate and rotate some amount in the

course of tracking prev. Our model suggests that this signal need not be complicated; the local networks in the thoracic ganglia could be programmed, in the form of static connections that fuse local proprioception with descending commands, to automatically convert intended body motion into joint motion. This idea is an application of task-level control, in which one or more higher level goals (e.g. appendage location in 3D space, etc.) are used to produce control signals for multiple joints (Ting et al., 2009). Such a control strategy often has an infinite number of solutions, and thus depends on constraints to find a unique course of action. In our controller, each T2 leg actively controls four degrees of freedom, and each leg receives feedback from three feedback loops: leg attachment height, head rotation, and forward translation. However, synergies are also present that reduce the dimensionality: the FTi and ThC3 joints work in unison to rotate the body, and the FTi and ThC1 joints work in unison to move the body forward. The animal, however, may have more flexible strategies for reducing dimensionality that let it exploit the extra degrees of freedom to accomplish other tasks.

This redundancy is further complicated by the fact that the environment may impose more constraints on motion. For instance, when more than one leg is in contact with the ground at once, it can be very difficult to produce joint output that does not violate the constraint that no feet move. One biological solution, called the active reaction, is to control extra joints with positive velocity feedback, which amplifies the motion imposed on a joint by the ground or other joints (Lévy & Cruse, 2008a; Schmitz et al., 2008). This method has also been tested in simulation and on a robot; Walknet uses leg-level feedback loops like those in this paper to control body height with one joint per leg, and the rest of the joints use the active reaction while walking (Schmitz et al., 2008). The active reaction may improve the pivots described in this paper by reducing or eliminating scenarios in which joints repel one another. For instance, joints on the T2 legs that currently control forward translation could instead be controlled by the active reaction, and move in response to pushing from the T3 CTr joints, which are known to produce thrust in other insects (Full, Blickhan, & Ting, 1991).

Another way to ensure joints do not resist each other is to use an "internal puppet" for kinematic planning to achieve high-level goals (Schilling, Hoinville, et al., 2013). Joint motions that satisfy the principle of least action can be calculated by pulling a passive model of the body in the intended direction of travel, letting the joints move subject to constraints imposed by the world (or a simulation of it). This technique is capable of solving complicated inverse kinematics problems and can be used for motion planning (Schilling, Paskarbeit, et al., 2013), but requires that the modeler construct a kinematic model of the animat and encode it within the controller. It is unknown whether insects possess such detailed internal models, and our work has not needed one so far. However, it is possible that replicating more complicated hunting behaviors in the future may require an internal model for planning, at which point we will implement one.

Comparison to Animal Data, and Related Future Work

41 We will need to continue to collect 3D kinematic data of mantis pivots to better 42 understand how it uses its legs to orient toward prey. The feedback loops that make up the 43 posture and orientation control networks in this work were based on observations of mantises 44 and other insects (Cleal & Prete, 1996; Cruse et al., 1989; Nye & Ritzmann, 1992), the 45 orientation of leg joints (i.e. the leg Jacobian), and experimentation. They do not represent loops 46 that must be present in the animal, or the only possible combination of them. Previous studies

have used thorough 3D kinematics to better inform network connectivity and improve the
 accuracy of similar models (Bender, Simpson, & Ritzmann, 2010; Szczecinski et al., 2013), and
 improved 3D data, specifically of the ThC joints, would also benefit this model.

This lack of ThC data was likely responsible for much of the disagreement between model and animal data in Figure 9. When attempting to start the simulation from the starting posture of the animal, placing all four feet on the ground was impossible without ThC knowledge. Collecting these data in the future will allow us to make a more detailed comparison with the animal, and better tune the model's high-level network parameters, such as the strength of descending commands to each joint controller. This has the benefit not only of producing a more effective model of the animal (Cruse et al., 1998), but represents an opportunity to disprove elements of our hypothetical model that cannot replicate animal behavior, even when tuned as well as possible.

14 Conclusions

We present a neuromechanical model of a praying mantis that we use to explore preyorienting stationary pivots (i.e. rotations and translations) seen in the animal. Building such a detailed model enables us to make detailed hypotheses, specifically that descending commands from the CX that control visually-guided pivots could be as minimal as a direction and magnitude to pivot the body. These signals, when combined with proprioceptors from the leg joints, are capable of producing a wide range of pivots from many different starting configurations.

22 Acknowledgments

This work was supported by a NASA Office of the Chief Technologist's Space
Technology Research Fellowship (Grant Number NN12AN24H). Further funding was provided
by DARPA M3 (Grant Number DI-MISC-81612A), AFOSR (Grant Number FA9550-10-10054), and NSF (Grant Number IOS-1120305). Also, the authors would like to thank Alexander
Hunt for many thoughtful discussions during the preparation of this manuscript, as well as two
anonymous reviewers for their thoughtful suggestions.

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