A neuromechanical model for the neuronal basis of curve walking in the stick insect

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Knops S, Tóth TI, Guschlbauer C, Gruhn M, Daun-Gruhn S. A neuromechanical model for the neuronal basis of curve walking in the stick insect. J Neurophysiol 109: 679–691, 2013. First published November 7, 2012; doi:10.1152/jn.00648.2012.—The coordination of the movement of single and multiple limbs is essential for the generation of locomotion. Movement about single joints and the resulting stepping patterns are usually generated by the activity of antagonistic muscle pairs. In the stick insect, the three major muscle pairs of a leg are the protractor and retractor coxae, the levator and depressor trochanteris, and the flexor and extensor tibiae. The protractor and retractor move the coxa, and thereby the leg, forward and backward. The levator and depressor move the femur up and down. The flexor flexes, and the extensor extends the tibia about the femur-tibia joint. The underlying neuronal mechanisms for a forward stepping middle leg have been thoroughly investigated in experimental and theoretical studies. However, the details of the neuronal and mechanical mechanisms driving a stepping single leg in situations other than forward walking remain largely unknown. Here, we present a neuromechanical model of the coupled three joint control system of the stick insect’s middle leg. The model can generate forward, backward, or sideward stepping. Switching between them is achieved by changing only a few central signals controlling the neuromechanical model. In kinematic simulations, we are able to generate curve walking with two different mechanisms. In the first, the inner middle leg is switched from forward to sideward and in the second to backward stepping. Both are observed in the behaving animal, and in the model and animal alike, backward stepping of the inner middle leg produces tighter turns than sideward stepping.

CPG; intrasegmental coupling; locomotion; sensory feedback

LOCOMOTION OF VERTEBRATES and arthropods alike is based on the coordinated movement of leg joints. The movement of the leg can be subdivided into two phases. The phase during which the leg has ground contact is the stance phase and allows propulsion of the body. The other phase is the swing phase, where the leg is lifted off the ground to move it to the new starting position for the next stance phase. During stepping, the different leg joints have to be controlled by the nervous system, and the movements of the legs have to be coordinated. The neuronal and muscular mechanisms involved in arthropod locomotion have been thoroughly studied in the stick insect (Carausius morosus; Bässler and Büschges 1998; Büschges et al. 2008, 2011; Dürr et al. 2004; Orlovsky et al. 1999; Ritzmann and Büschges 2007). The neurophysiological data available provide insight into the interactions between central networks and sensory organs. These interactions are essential for the processing of sensory feedback signals. Leg joints are driven by their individual pattern generating networks (CPGs; Akay et al. 2004; Büschges 1995, 2005; Daun-Gruhn 2011; Ekeberg et al. 2004), which can be controlled by sensory input, for example, by load signals from the campaniform sensilla (Borgmann et al. 2011; Daun-Gruhn et al. 2011; Zill et al. 2004, 2009, 2011; for a review, see Büschges and Gruhn 2008). The coordination between leg joints has been investigated on the behavioral level (Cruse 1990; Graham 1972; von Buddenbrock 1921; Wendler 1965, 1978) as well as on the neuromuscular level by recording EMG activity and intracellular and extracellular electrical activity of motoneurons (MNs; Büschges 1995; Büschges et al. 2004, 2008; Ritzmann and Büschges 2007; Rosenbaum et al. 2010). However, the details of the neuronal and mechanical mechanisms that produce the muscle activity of a stepping single leg in situations other than forward walking remain largely unknown. In an earlier neuromechanical model, we demonstrated how rhythmic electrical CPG activity might be converted into mechanical leg movement (Toth et al. 2012). We examined forward and backward walking and the switching between forward and backward walking for two of the three main leg joints of the stick insect’s middle leg: the thorax-coxa joint (ThC-joint) at which the protractor coxae and the retractor coxae (henceforth protractor-retractor) muscle pair moves the coxa forward and backward, and the coxa-trochanter joint (CTr-joint) at which the levator trochanteris and the depressor trochanteris (henceforth levator-depressor) muscle pair moves the femur up and down.

In the present study, we extend our existing model (Toth et al. 2012) by including the femur-tibia joint (FTi-joint) about which the tibia is flexed or extended by the flexor tibiae and the extensor tibiae (henceforth flexor-extensor (FE) muscle pair). The resulting model will describe a forward stepping middle leg, which can be switched to perform backward or sideward stepping. First, we introduce the equation of motion for the isolated FTi-joint and then we will consider the coupled three-joint system, in which the coupling between the neuromuscular systems is done via sensory feedback signals. The coupling is implemented such that the protraction is switched to retraction, and extension is switched to flexion when the angle in the CTr-joint, representing a lumped sensory signal that integrates ground contact, load, and movement, falls below a threshold value. Furthermore, extension is switched to flexion when a threshold angle at the FTi-joint, representing extension signals is exceeded. We shall provide reasons for the use of a lumped sensory input signal in the model.

In appropriate experimental conditions, one can induce a switch between forward and backward stepping or forward and sideward stepping of the middle leg of the stick insect. We present a partly hypothetical neuronal mechanism that can perform both types of switches by changing essentially a
central neuronal input signal in the model. Finally, using this mechanism, we shall show how the model can produce two different kinds of curve walking in concert with a contralateral forward walking middle leg.

METHODS

Experiments

Animals. Experiments were performed on adult female stick insects (Carausius morosus) at 20–22°C. The animals were reared in the animal facility of our institute at 22–24°C under a 12:12-h light-dark cycle and fed blackberry leaves ad libitum. The kinematic experiments were set up in a darkened Faraday cage and performed in a darkened room. The anatomical measurements were carried out on a table with a fiber illuminator C-FI230 (Nikon, Tokyo, Japan) on it. Preparation and experimental procedure. For kinematic measurements, the animals were glued (two-component glue, ProTempII; ESPE, Seefeld, Germany) ventral side down onto a balsa stick that was thinner than the width of the insect (3 × 5 × 100 mm, W × H × L). The right hind leg was removed by pinching the coxa of the leg to induce autotomy (Schmidt and Grund 2003). The right middle leg was fixed at the level of the coxa at a right angle to the body axis, allowing, however, free up and down movement of the leg. The position of the animal was adjusted at −8–10 mm above the slippery surface, which corresponds to the height during free walking. Stepping was elicited as optomotor response on a slippery surface setup as described in Gruhn et al. (2006) or through a tactile stimulus to the abdomen with a paint brush.

To obtain detailed anatomical data on the extensor and flexor muscles, the following surgical procedures were performed. First, the right middle leg was amputated at mid-coxa level and fixed with three insect pins in a sylgard dish to determine the position of femoral muscle tendons (apodemes). The femur was opened by cutting a window into the lateral cuticle. Muscle fibers damaged as a consequence of cutting the window into the femoral cuticle, the tracheae, the femoral chordotonal organ (ICO) and its tendon, the retractor unguis I muscle and its tendon, the nervus cruris, and the F2 nerve were removed.

FTI-angle and angular velocity. The walking SURFACE and TARSAL CONTACT. The animals performed stepping movements on a highly polished, black nickel-coated brass plate. Slipperiness was ensured using a glycerine/water mix at a ratio of 95% glycerine and 5% saturated NaCl solution to allow conductivity of the lubricant for electric monitoring of single-leg tarsal contact on the metal plate. To determine the exact moment of switch between swing and stance phase, we measured the time of tarsal touch down and lift off. This was achieved by using the leg as a switch to close an electric circuit between the plate and a lock-in amplifier as described previously (Gruhn et al. 2006). Thus between touch down and lift off of the tarsus onto and from the slippery surface, respectively, electrical current could flow from the plate through tarsus and tibia into the copper wire. The output signal of the amplifier was fed into an AD converter (Micro 1401, II; CED, Cambridge, UK), digitalized using Spike2 (Vers.5.05, CED) and stored together with the trigger signal for the camera to allow frame by frame correlation with the tarsal contact trace.

OPTICAL RECORDING AND DIGITAL ANALYSIS OF LEG MOVEMENTS. For the precise digital analysis of leg movements, we recorded walking sequences from above with a high-speed video camera (Marlin F-O33C, Allied Vision Technologies, Stadtruda, Germany) at 100 frames/s as described previously in Gruhn et al. (2006) and additionally through a mirror positioned at a 45° angle to the walking surface at the rear of the animal. The right middle leg was marked at the distal end of the femur and the tibia, respectively. An additional marker was set at the center of the thorax between the mesothoracic legs. We used orange fluorescent pigments (Dr. Georg Kremer Farbmittel, Aichstetten, Germany) as markers, which were mixed into small portions of two-component glue. During the recording of walking sequences, the animal was illuminated with blue LED arrays (12-V AC/DC, Conrad Electronic). A yellow filter in front of the camera lens was used to suppress the short wavelength of the activation light. The video files were analyzed using motion tracking software (WINanalyze, Vers. 1.9; Mikromak Service, Berlin, Germany). Leg angles were measured between the marker positions on the leg and the base of the middle leg at the coxa. A representative example of the FTI angle γ and the corresponding angular velocity is displayed in RESULTS (see Fig. 5, A and B).

Anatomical measurements on the extensor and flexor muscles. To calculate the pennation angles of femoral fibers, the distance from the extensor tibiae tendon to the dorsal cuticular edge of the femur and the distance from the flexor tibiae tendon to the ventral cuticular edge of the femur were determined using a measurement ocular at a 25-fold magnification. These edges were easily identifiable by a row of hairs (setae) that is localized on the ridge. Measurements were taken in the proximal part of the femur (at ~35% of the entire femur length) and in the medial part of the femur (at ~50% of the entire femur length) because the number of histochemically identified fast fibers generating most of the muscle force decreases from proximal to distal [for the extensor tibiae: Bäsßler et al. (1996), and for the flexor tibiae: Godlewsk (2012)]. Length measurements were carried out at the following FTI-joint angles: 0° ± 3° (tibia maximally extended), 90 ± 3° (tibia perpendicular to the longitudinal axis of the femur), and 150 ± 3° (tibia maximally flexed). The preparation was constantly kept wet with saline (Weidler and Diecke 1969). To improve discrimination of tissues, the contrast was enhanced by application of either Fast Green (Sigma, St. Louis, MO) solution or methylene blue (Merck, Darmstadt, Germany) solution for a few minutes. The measurement ocular was calibrated using a piece of standard millimeter paper (Selecta, Germany). The data were analyzed in OriginPro8.5.0 (OriginLab, Northampton, MA) and were plotted as box-whiskers diagrams showing minimum and maximum, 25 and 75 percentiles, the median and the mean. A one-way ANOVA was performed comparing the means by a post hoc Tukey test.

The Model

The protractor-retractor (PR) and levator-depressor (LD) neuromechanical systems, which carry out the forward/backward and upward/downward movements of the leg, respectively, and their interactions have already been described and analyzed in detail in Toth et al. (2012). By including the FE system, we have obtained an extended model comprising all three main leg joints. The neuron and muscle models, as well as the neuromuscular coupling for the FE system have remained the same as for the two other neuromechanical systems. However, the equation of mechanical motion differs from those in the PR and LD systems because of the different anatomical and geometrical conditions (see below). Here, we also investigated the effect of the mechanical coupling between the femur and the tibia. Using the Principle of Least Action, we calculated the Euler-Lagrange equations for the coupled femur-tibia system and solved them numerically. The effect of the mechanical coupling was small (not illustrated). This is in good agreement with experimental findings by Hooper et al. (2009), who demonstrated that in the stick insect the passive mechanical coupling between the joints is negligible. We thus neglected the mechanical coupling between the movements of the femur and tibia in the following. However, we took the increased moment of inertia into account as described in Modified moment of inertia in the PR and LD mechanical systems. Then, detailed consideration of the FE neuromechanical system will follow.

Modified moment of inertia in the PR and LD mechanical systems. The preceding arguments enabled us to treat the three mechanical systems at the individual leg joints independently. However, when the
tibia is present in the model, the moment of inertia to be overcome by the PR or LD muscles is larger than without the tibia. To take the mechanical effect of the tibia into account, we computed an “effective” moment of inertia to be used in the equations of motion in the PR and LD systems. The basic idea is first to compute the moment of inertia of the femur-tibia mechanical system (coupled rods) about the axis of rotation of the femur at a constant value of the flexion angle \( \gamma \) and then to average over the range of the \( \gamma \) angles that occur during stepping. That is we obtained for a given \( \gamma \)

\[
\hat{I}_F(\gamma) = I_F + I_t + m_F l_F^2 + m_T l_T \cos \gamma
\]

(1)

where \( I_F = m_F l_F^2 / 3 \) and \( I_t = m_T l_T^2 / 3 \) are the moments of inertia of the femur and tibia, respectively, with the corresponding masses \( m_F \) and \( m_T \), and lengths \( l_F \) and \( l_T \). The range of the \( \gamma \) angles extended from \( \gamma_{\text{min}} = \pi / 4 = 45^\circ \) to \( \gamma_{\text{max}} = 1.92 = 110^\circ \). Thus the effective value \( I_{FT} \) of the moment of inertia that was used in the computations is

\[
I_{FT} = \frac{1}{\gamma_{\text{max}} - \gamma_{\text{min}}} \int_{\gamma_{\text{min}}}^{\gamma_{\text{max}}} \hat{I}_F(\gamma) d\gamma
\]

(2)

\[
I_{FT} = I_F + I_t + m_F l_F^2 + m_T l_T \sin \gamma_{\text{max}} - \sin \gamma_{\text{min}}
\]

(3)

Its numerical value together with those of the masses and lengths, all being our own measurements, is given in Table 1.

**FE system integrated in the full model.** Figure 1 shows the three neuromechanical systems in the model of the stick insect’s leg, coupled through sensory signals. They are (from top to bottom) the PR, the LD, and the FE system. All have the same structure but differ in the values of their parameters, and, in addition, in the description of their mechanical movement. The core of each of the systems is a CPG, which controls the activity of the MNs via a layer of interneurons (INs). The reason behind the network structure used is described in detail in Daun-Gruhn et al. (2011) and Toth et al. (2012). Considering the FE system, the conductances \( g_{\text{app}} \) and \( g_{\text{app}6} \) represent inputs to the CPG that are supposed to originate in higher brain regions. Both the CPG neuron C6 and the interneuron IN11 receive excitatory input from interneuron IN12 and both inhibit C5. IN12 receives sensory input from peripheral sense organs. The sensory pathway is analogous to that of the LD network, the latter having been constructed using data from Borgmann et al. (2011) (Daun-Gruhn et al. 2011). The muscle model as well as the neuromuscular coupling are the same as in Toth et al. (2012). The coupling between the three systems associated with the three joints is implemented through the angles \( \beta \) and \( \gamma \) at the leg joints. The sensory input represented by the angle \( \beta \) is a combination of load, motion, and ground contact signals. The coupling is implemented such that the switch from protraction to retraction and the one from extension to flexion is triggered at a critical value of the angle \( \beta \). The intra-leg coupling through sensory feedback signals in the stick insect has been described in qualitative terms by Büschges (2005). The coupling through the angle \( \gamma \) represents a stabilizing intrajoint coupling mediated through position signals from the fCO. All neurons in the network were modeled according to the Hodgkin-Huxley formalism (Hodgkin and Huxley 1952). The CPG neurons and the INs are nonspiking, while the MNs are spiking neurons (cf. Daun et al. 2009; Daun-Gruhn and Toth 2011).

**Equation of the mechanical motion of the FE system.** Figure 2A shows a frontal view sketch of the stick insect’s middle leg. The horizontal part is the femur, where the flexor and extensor muscles are located. These muscles control the movement of the tibia (vertical part). The geometrical arrangement is shown in Fig. 2B. The tendon of the extensor, \( T_E \), and the flexor, \( T_F \), are fixed to the tibia at the points \( A \) and \( B \). The rotation axis of the tibia is at \( O \), perpendicular to the plane of Fig. 2. It is known (Guschlbauer et al. 2007; Guschlbauer 2009) that \( AO = d \) and \( BO = 2d \). The tendons are moved by contraction of the muscle fibers, one of their ends fixed to the tendon, the other one to the cuticle (oblique lines between \( C_E \), \( T_E \), and \( C_F \) and \( T_F \), respectively). The zero position of the angle \( \gamma \) is when the femur and the tibia are collinear, i.e., at outstretched leg. In Fig. 2C, a single muscle fiber is schematically displayed. The distance between tendon and cuticle is \( E = h \). The fiber is fixed to the tendon at \( C \), and to the cuticle at \( C \). In this position, it has length \( l_t \), and its angle with the tendon is \( \phi_t \). If the muscle contracts (with a force \( F_{\text{mus}} \)), point \( C \) of the muscle fiber at the tendon will be shifted to \( D \) due to the force \( F_L \) parallel to the tendon. The angle between tendon and fiber at \( D \) is \( \phi \). The angle \( \beta \) between femur and tibia is thus determined by the movement of the tendon.

Our experiments revealed that the variation of \( h \) at different angles \( \gamma \) in different muscle parts in both the extensor (Fig. 3A) and the flexor (Fig. 3B) was negligible. The Tukey test showed a significant difference (\( P < 0.05 \)) between the tendon positions of the proximal flexor at \( 90^\circ \) and \( 150^\circ \), only. We therefore consider the distance \( h \) between the tendon and the cuticle to be constant during contraction. The mean value of this distance is \( h_F = 0.34 \) mm for the extensor, and \( h_F = 0.42 \) mm for the flexor.

The equation of mechanical motion (Newton’s second law of motion for torques) reads

\[
I_t \ddot{\gamma} = F_{\text{Fp}} \cdot 2d \sin \gamma - F_{\text{pE}} \cdot d \sin \gamma + M_v
\]

(4)

with the moment of inertia \( I_t \), the parallel forces \( F_{\text{Fp}} \) and \( F_{\text{pE}} \) in the flexor and the extensor muscles, and the distances \( 2d \) and \( d \) from the rotation point of the FTi-joint. \( M_v \) is the torque due to viscosity, which is produced by two force components acting on the lever:

\[
M_v = 2d F_E v_E + d F_E \dot{v}_E
\]

\[
= -2d b_E v_E - d b_E \dot{v}_E
\]

\[
= -d b_E \dot{v}_E
\]

\[
= -5 d b_E \dot{v}_E
\]

(5)

since the viscosity force is proportional to, and counteracts the velocity. The viscosity constant \( b_E \) is set to be the same for both muscles. Hence, the equation of motion reads

\[
\ddot{\gamma} = \frac{d}{I_t} [(2 F_{\text{Fp}} - F_{\text{pE}}) \sin \gamma - 5b_E d \dot{v}_E]
\]

(6)

The forces \( F_{\text{Fp}} = F_{\text{pF}}(l_F) \) and \( F_{\text{pE}} = F_{\text{pE}}(l_E) \) are the projections of the corresponding muscle forces on the direction of movement of the tendon:

\[
F_{\text{Fp}} = F_{\text{mF}} \cos \phi_F
\]

(7)

\[
F_{\text{pE}} = F_{\text{mE}} \cos \phi_E
\]

(8)

where \( \phi_F = \phi_F(l_F) \) and \( \phi_E = \phi_E(l_E) \) are angles between the fibers and tendons in the respective muscles and depend on the fiber length. According to findings by Guschlbauer et al. (2007) and Guschlbauer (2009), the muscle forces are quadratic functions of the muscle length:

\[
F_{\text{mF}} = k_F (l_F - l_{\text{mus}})^2
\]

(9)

\[
F_{\text{mE}} = k_E (l_E - l_{\text{mus}})^2
\]

(10)

Table 1. Parameters of the tibia segment used for the simulation

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimal angle</td>
<td>45°</td>
</tr>
<tr>
<td>Maximal angle</td>
<td>110°</td>
</tr>
<tr>
<td>Femur mass</td>
<td>0.006 g</td>
</tr>
<tr>
<td>Femur length</td>
<td>12 mm</td>
</tr>
<tr>
<td>Tibia mass</td>
<td>0.002 g</td>
</tr>
<tr>
<td>Tibia length</td>
<td>12 mm</td>
</tr>
<tr>
<td>Momentum of inertia of the tibia</td>
<td>0.096 g mm²</td>
</tr>
<tr>
<td>Corrected value of the momentum of inertia</td>
<td>0.288 g mm²</td>
</tr>
</tbody>
</table>

Parameter values in this table are our own measurements and calculations. For further explanations, see METHODS.
\[ F_{mE} = k_E(l_E - l_{E\text{min}})^2 \] (10)

\( l_{E\text{min}} \) and \( l_{E\text{min}} \) are the minimal lengths of the fibers, i.e., when the fibers are unstrained. Since the muscle fibers are arranged in parallel, the spring constants \( k_F \) and \( k_E \) of the entire muscles are the sum of the spring constants of the individual fibers. The fiber length is calculated by using the cosine theorem

\[ l_F(\gamma) = \sqrt{l_{F0}^2 + s_F^2(\gamma) - 2l_{F0}s_F(\gamma)\cos\phi_{F0}} \] (11)

\[ l_E(\gamma) = \sqrt{l_{E0}^2 + s_E^2(\gamma) - 2l_{E0}s_E(\gamma)\cos\phi_{E0}} \] (12)

with \( \phi_{F0} = \sqrt{1 - (h_F/h_{E0})^2} \) and \( \phi_{E0} = \sqrt{1 - (h_E/h_{E0})^2} \) and the shifts \( s_F(\gamma) = -2d \sin \gamma \) and \( s_E(\gamma) = d \sin \gamma \). The \( l_{F0} \) and \( l_{E0} \) are fiber lengths at \( \gamma = \gamma_0 = 90^\circ \). In the simplified muscle model used here, we neglect the force velocity relation in the muscle, since stepping movements in the stick insect are usually slow. In addition, an increased damping torque, which is also velocity dependent, can partly compensate for the lack of the force-velocity relation in the model.

We define the switch conditions between flexion and extension and vice versa, like it is done in Toth et al. (2012). That is \( \gamma \) and \( \gamma \) vanish at the switch points, and we get the following relation for the spring constants from Eq. 6:

\[ a = \frac{k_F}{k_E} = \frac{1}{2} \left( \frac{l_E - l_{E\text{min}}}{l_E - l_{E\text{min}}} \right)^2 \] (13)

The lengths \( l_F \), \( l_E \), and angles \( \phi_F \), \( \phi_E \) are functions of the angle \( \gamma \). Since we have two extreme angles (maximum flexion and maximum extension), we obtain two different values for \( a \): one for the flexion and one for the extension. To determine the absolute values of the spring constants, we have, however, to resort to computer simulations.

**Implementation of the Model**

The coupled system consists of 72 equations, 66 for the 24 neurons, and 2 each for the 3 mechanical systems. The program implementing this system was written in C. The numerical integration was performed by using the CVODE software package (Cohen and Hindmarsh 1996). The integration over a period of 9 s took on average 15 s.

**RESULTS**

First, we studied the mechanical properties of the model of a single and standalone FTi-joint. Only after having obtained satisfactory results with this system did we integrate it into the existing PR-LD-neuromuscular model. First, we report on the tests carried out with the model of a single FTi-joint.

**Fig. 1. Topology of the network of one leg consisting of a protractor-retractor (PR; top), a levator-depressor (LD; middle), and a flexor-extensor (FE) network (bottom).** CPG, central pattern generator (encased in a box); MN, motoneurons; IN, interneurons; INCS, interneuron receiving sensory input from campaniform sensilla. Empty triangles: excitatory synapses; filled circles: inhibitory synapses. \( g_{app1}, g_{app2} \) and \( g_{app6}, g_{app7} \) are central excitatory inputs to the CPG neurons; \( g_{INCS}, g_{INCS}, g_{INCS}, g_{INCS}, g_{INCS} \) and \( g_{INCS} \) inhibitory inputs to the INs; \( g_{appCS} \) excitatory input from the campaniform sensilla (CS). Pro. m., Ret. m., Dep. m., Lev. m., Ext. m., and Flex. m.: protractor, retractor, levator, depressor, extensor, and flexor muscles, respectively, in the model innervated by the corresponding MNs. \( \beta \)-Hexagon in the LD system: combined sensory signal originating in the LD system and conveyed to the PR and FE system; \( \gamma \)-hexagon in the FE system: inhibitory signal from the femoral chordotonal organ counteracting the excitatory signal from the LD system.
Neuronal and Mechanical Properties of the Single, Isolated FE System

The parameter values used in the simulation of the mechanical movement of the tibia at the FTI-joint are listed in Tables 1 and 2. The fiber lengths and angles ($l_{Emin}$, $l_{Fmin}$, $l_{EO}$, $l_{FO}$, and $\phi_{EO}$, $\phi_{FO}$), the distance between tendon mounting point and rotation axis ($d$ and $2d$), and the distance between tendon and cuticle ($h_E$, $h_F$) were measured in experiments (cf. Guschlbauer et al. 2007; Guschlbauer 2009, and Fig. 3), or estimated on the basis of experimental data. The absolute values of the spring constants $k_E$ and $k_F$ and the viscosity constant $b$, were determined in computer simulations the same way as described in Toth et al. (2012). In addition, we directly measured the mass and the length of the tibia of the stick insect and listed the data in Table 1.

Our experimental results show high variability in the values of the extreme leg positions, hence in the angular range for $\gamma$ ($\gamma_{EAF} \in [100^\circ, 130^\circ]$ and $\gamma_{EAF} \in [40^\circ, 60^\circ]$). The choice of $\gamma_{max} = 110^\circ$ and $\gamma_{min} = 45^\circ$ was made to approximate natural stepping. At the extension end position, $\gamma = \gamma_{min} = 45^\circ$, we have $a = a_E = 0.0136$, and at the flexion end position, $\gamma = \gamma_{max} = 110^\circ$, $a = a_F = 0.5809$.

Figure 4 shows the mechanical and neuronal signals that occur in the model at the FTI-joint during forward stepping of the middle leg. The time course of $\gamma$ and the corresponding angular velocity are displayed in the first and second trace from the top. The third, fourth, and fifth rows show the electrical activities of the flexor and extensor MNs and those of the CPG neurons, respectively. It can be seen that the flexing movement (i.e., that from $45^\circ$ to $110^\circ$) commences shortly after the flexor MN becomes active. Similarly, the activity of the extensor MN triggers the extension movement. It is known from data obtained in the stick insect (see review in Büschges 2005) that the phase relation between flexion and extension in a forward stepping middle leg is $\sim 1:1$. In the model, this is achieved by setting $g_{appF} = 0.2095$ nS and $g_{appE} = 0.1000$ nS. Also, in agreement with experimental observations, the duration of one step is set to be $T_{per} = 500$ ms (Graham 1972). The spring constants and the viscosity constant were chosen such that the motion reaches a steady state at the switch points (see 2nd row in Fig. 4).

Our experimental data revealed that the ratio between the flexion and extension phases is strongly different from 1:1 in a sideward stepping animal: the extension phase became shorter and the flexion longer. A typical example is shown in Fig. 5, A and B. We adjusted our model to the experimental data by setting the conductances of the input currents to the CPG to $g_{appF} = 0.1895$ nS and $g_{appE} = 0.1200$ nS. With this choice, the simulations (Fig. 5, C and D) satisfactorily reproduced the experimental data of sideward stepping in the stick insect (Fig. 5, A and B). Note that the values of all other parameters of the FE network were left unchanged.

Neuromechanical Control in the Integrated Three-Joint Model

We have so far considered the properties of the model of the single, isolated FTI-joint and found that it satisfactorily mimics the neuromechanical behavior of its biological counterpart. Here, we integrate this model into that of the previously existing neuromechanical model of the PR and LD systems (Toth et al. 2012). We establish the connection between the FE model and the PR-LD model by introducing an excitatory connection from the latter to the former one (to IN12, cf. Fig. 1). This excitatory connection will be activated, exerting a sufficiently high synaptic current on IN12, if the angle $\beta$ falls below a threshold value. This value is set to $\beta_{thrFE} = 50^\circ$ in the model. Increasing the threshold causes the flexion to begin earlier. As in our earlier model (Toth et al. 2012), the levation angle $\beta$ represents a combination of signals from peripheral sense organs, such as ground contact, load on the leg, and
position. These sensory signals crucially affect the intra-segmental coordination of leg movements during locomotion (cf. Büschges 2005). At the same time, the actual value of $\beta$ reflects them in a natural way: the leg position is mainly determined by $\beta$; the sensory signals of ground contact and load occur at a well-defined value of $\beta$. The use of the angle $\beta$ in the model, as a representative of the combined sensory signals is therefore satisfactorily justified.

Video records of freely walking stick insects (Grabowska et al. 2012) show that the switch from flexion to extension often occurs in the middle of the stance phase, which is also supported by EMG recordings from intact walking animals tethered above a slippery surface (Rosenbaum et al. 2010). To account for this observation in our model, we introduced a second synaptic connection to the FE system (IN12). This synaptic connection is related to the angle $\gamma$. It is inhibitory and thus counteracts the excitatory influence from the LD system (cf. Fig. 1). It can be interpreted as sensory input from the fCO, which measures angular change of the femur (Büschges 2005). If the angle in the FTi-joint exceeds a certain value, which is $\gamma_{thrFE} = 90^\circ$, IN12 will undergo inhibition. This connection causes a shortening of the duration of flexion and mildly distorts the 1:1 phase ratio in the FE system.

**Switch from forward to backward stepping in the middle leg.**

As we showed earlier (Toth et al. 2012), the model consisting of the PR and LD systems, only, was already capable of performing forward and backward stepping, and switching between them. This property of the earlier model is preserved in the present, extended one. Figure 6 shows the time course of the three main joint angles. The simulation record begins with forward walking. Then, the model is switched to perform backward stepping at $t = 6000$ ms. Finally, a switch back to forward stepping takes place at $t = 9250$ ms. Arrows in the top trace in Fig. 6 indicate the switches. As in the animal (Rosenbaum et al. 2010), during backward stepping, the protractor MN and muscle are active in the stance phase, and the retractor MN and muscle in the swing phase. Moreover, the activity patterns of the LD and FE muscle pairs remain the same, both in the animal and the model, irrespective of the walking direction. In Toth et al. (2012), we propose a potential mechanism of the switch between forward and backward stepping. It is based on experimental data by Rosenbaum et al. (2010). The underlying neuronal network is displayed in Fig. 7. An excitatory input to the cell SB induces backward, and one to the cell SF forward stepping via presynaptic inhibition to the “parallel” and “cross” connections from the CPG to the INs IN1 and IN2. Thus changing a single variable in the model suffices to produce the switch between forward and backward stepping (for details see Toth et al. 2012). In Supplement Video S1, an animation illustrates these switches in the middle leg (Supplemental Material for this article is available online at the J Neurophysiol website).

**Switch from forward to sideward stepping in the middle leg.**

Sideward stepping in the stick insect middle leg could be achieved by stiffening the ThC-joint, i.e., fixing it at a certain stationary angle $\alpha_0$. We implemented this in the model by inhibiting both interneurons SF and SB at the same time in the network that controls forward and backward stepping (Fig. 7). Since both interneurons were kept at their resting potential or below due to the inhibition, the presynaptic inhibition to all of the four excitatory connections from the CPG neurons to the interneurons IN1 and IN2 was inactivated. Hence, these connections became simultaneously active. Accordingly, the interneurons IN1 and IN2 became permanently active, too, and suppressed the activity of the protractor and retractor MN irrespective of the oscillatory phase of the CPG (Fig. 8). Depending on the point of time at which the switch was initiated, i.e., SF and SB inhibited, stationary angles at several discrete values could be attained. For example, we had $\alpha_0 = 28^\circ$ when the switch command occurred at the end of the period of protractor MN firing; $\alpha_0 = 102^\circ$ when the switch command arrived just after the beginning of the active retractor phase; and $\alpha_0 = 128^\circ$, when the switch was triggered at the end of it. The asymmetry in the stationary values of $\alpha$ is due to the asymmetric properties of the two muscles, which we assume...
on the basis of the findings by Guschlbauer (2009) with regard to the extensor and flexor tibiae muscles. In the simulations to follow, sideward stepping was evoked at the stationary angle $\theta_0 = 102^\circ$. As mentioned earlier (cf. Neuronal and Mechanical Properties of the Single, Isolated FE System), the extension phase became shorter and the flexion longer during sideward stepping. Accordingly, the oscillatory properties of the CPG in the FE system were changed by changing the values of the conductances $g_{app5}$ and $g_{app6}$ of the input currents to the CPG as described in Neuronal and Mechanical Properties of the Single, Isolated FE System. The motion of the CTr-joint, however, remained unchanged during sideward stepping in accordance with our experimental data. The threshold angle for the sensory coupling from CTr to FTi, too, was kept constant. A Supplemental Video S2 shows the switch from forward to sideward stepping of a single middle leg.

Curve Walking

Experimental findings related to curve walking have shown that stick insects use two main methods for turning depending on curvature applied (Cruse et al. 2009; Dürr and Ebeling 2004; Gruhn et al. 2009; Jander 1982, 1985; Rosano and Webb 2007). One way to perform curve walking is to shorten the stride length of the inner middle leg (Dürr and Ebeling 2004; Gruhn et al. 2009; Jander 1982, 1985). This is done by reducing the angular range in the PR system; in the extreme case the ThC-joint is fixed and the inner leg is restricted to sideward stepping. Another possibility is to change the walking direction of the inner middle leg from forward to backward (Gruhn et al. 2009).

To test whether our neuromechanical system of the three leg joints could produce the required intra-leg coordination, we carried out “pseudodynamical” simulations with our model using the software package Open Dynamic Engine (ODE) (Smith 2006) as a visualization tool, only. This means that we used the angular movements obtained from the kinematic model and fed them into ODE as input signals. Importantly, ODE did not modify any of the kinematic input signals during the simulations. We also wanted to compare the two turning strategies in detail. To do that, we used two “active” middle legs whose movements were governed by the angular signals produced by our model and fed into ODE as input signals. These legs were attached to the thorax of a simulated stick insect body, as were four additional “passive” ones that did not

<table>
<thead>
<tr>
<th>Parameters in the muscles used in the simulation</th>
<th>Extensor</th>
<th>Flexor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimal length of the fiber</td>
<td>$l_{E,\text{min}} = 1.05$ mm</td>
<td>$l_{F,\text{min}} = 1.50$ mm</td>
</tr>
<tr>
<td>Length of the fiber at $\gamma = 90^\circ$</td>
<td>$l_{E,0} = 1.41$ mm</td>
<td>$l_{F,0} = 2.11$ mm</td>
</tr>
<tr>
<td>Angle between tendon and muscle fiber at $\gamma = 90^\circ$</td>
<td>$\phi_{E,0} = 13.5^\circ$</td>
<td>$\phi_{F,0} = 12.6^\circ$</td>
</tr>
<tr>
<td>Distance between cuticle and tendon</td>
<td>$h_E = 0.34$ mm</td>
<td>$h_F = 0.42$ mm</td>
</tr>
<tr>
<td>Spring constants for the extension</td>
<td>$k_E = 2,700$ mN/mm$^2$</td>
<td>$k_F = 36.83$ mN/mm$^2$</td>
</tr>
<tr>
<td>Spring constants for the flexion</td>
<td>$k_F = 340$ mN/mm$^2$</td>
<td>$k_I = 197.47$ mN/mm$^2$</td>
</tr>
<tr>
<td>Viscosity of the muscle</td>
<td>$b_E = 12.5$ g/s</td>
<td>$b_I = 12.5$ g/s</td>
</tr>
<tr>
<td>Distance of tendon mounting and rotation point</td>
<td>$d = 0.28$ mm</td>
<td>$2d = 0.56$ mm</td>
</tr>
</tbody>
</table>

Geometrical parameters were measured by Guschlbauer et al. (2007) or were estimated from their measurements; the numerical values of the spring constants and the viscosity coefficient were obtained in simulations with a single, isolated femur-tibia joint. For further explanations, see RESULTS.
perform stepping movements but only ensured the stability of the body. A phase shift of a half of a stepping period was artificially imposed on the angular input signals to the active middle legs. Thus the legs were alternately in the swing and stance phase, respectively. It should be stressed here that this arrangement does not amount to a full dynamic simulation, since the forces (torques) due to body weight and inertia do not feed back into the equations for the angular movements. Thus only the angular movements produced by the internal forces (torques) under the control of the corresponding neuronal networks are simulated.

Turning generated by temporary switching to backward stepping. The simulated stick insect started walking forward. After a few steps, when the left middle leg switched to backward stepping, it seemed to rotate about an axis through the body. It thus changed its walking direction on the spot with a small or negligible radius. After a few additional steps, the left middle leg switched back to forward stepping, and the stick insect continued walking straight in a new direction. Figure 9A shows a sequence of screen shots during the simulation. The full video can be found in Supplemental Video S3. Figure 10 shows the complete trajectory of the movement. The first part (blue line) is forward walking, which is followed by the turning phase with the inner middle leg stepping backward (red curve). Finally, the black line emanating from the red one is again forward walking.

Turning generated by temporary switching to sideward stepping. Again the simulated stick insect started walking forward. After the same number of steps as in Turning generated by temporary switching to backward stepping, the left middle leg

Fig. 5. Angle (A) and angular velocity (B) of the tibia movement in the experiment. C and D: corresponding variables in the simulations.

Fig. 6. Time courses of the three joint angles α [thorax-coxa joint (ThC-joint); top], β [coxa-trochanter joint (CTr-joint); middle], and γ (FTi joint; bottom) in the model of a stick insect’s middle leg. Arrow at $t = 6,000$ ms: switch from forward to backward walking; arrow at $t = 9,250$ ms: switch from backward to forward walking. Enframed areas help compare the phases of the movement at the individual joints and correspond to the stance phase. Note that the transient periods at the switches are very short.
In this study, we have presented a neuromechanical model that mimics the neuronal and mechanical workings of a limb of the stick insect. The topology (connectivity), as well as the functional properties of its constituents, neurons and muscles, were obtained using relevant experimental data from the stick insect (Akay et al. 2004; Bässler 1983; Bässler and Büschges 1998; Borgmann et al. 2011; Büschges 1995, 2005; Büschges et al. 2008, 2011; Büschges and Gruhn 2008).

The model is an extension of that by Toth et al. (2012): we integrated the FE system into the existing model of the combined PR and LD systems. In terms of neuronal function, this meant that the FE system was connected to the existing model by a sensory pathway from the LD system, and, in addition, an intra-FE sensory pathway was also introduced to account for the effects of the IFO. Concerning the mechanical properties, the equation describing the motion of the tibia was added to the model, and the moment of inertia used in the equations of motion of the femur in the PR and LD systems was adjusted to take the presence of the tibia into account (cf. METHODS).

Our model satisfactorily reproduces the neuronal and mechanical processes: forward, backward, sideward stepping of the middle leg together with the accompanying neuronal activities, as observed in the experiments. In particular, it enables us to study curve walking generated by two different mechanisms, which are also observed in the behaving animal: turning by backward stepping, and turning by sideward stepping of the inner middle leg. These two modes of turning can easily be emulated in the model: either by switching the inner middle leg to backward stepping or by setting a stationary retraction position (angle $\alpha$) of the femur using the same control network (cf. Fig. 7). The additional adjustment of the oscillatory properties of the CPG in the FE system in the case of turning with the help of sideward stepping (cf. Neuronal and Mechanical Properties of the Single, Isolated FE System) does not substantially alter this fact. Thus the whole process of switching to curve walking or switching back from it to forward walking requires only changing the same few (maximally 4) control variables. Although this switching network has quite appealing properties, it is, at least partly, hypothetical. We constructed it to provide a possible mechanism for switching between the different stepping modes. An important aspect of our hypothesis is that the CPG is not involved in the switching processes. At present, there is no direct experimental evidence to support the existence of the half-center-like network of the SF and SB neurons and of the presynaptic inhibition. Indirect evidence could nevertheless be gathered, at least in principle, by looking for presynaptic inhibition on neurons in the vicinity of the segmental MNs in the pro-, meso-, or metathoracic ganglia. Another possibility would be to stimulate brain areas that are conjectured to send descending command signals to the segmental CPGs with hyperpolarizing current pulse trains and observe whether any of the legs performs sideward stepping or similar movements during the stimulation.

To test our hypothesis on the mechanism of switching between forward and backward stepping, it would suffice to induce backward stepping in the stick insect while simultaneously recording the EMG activity of the protractor and retractor muscles. It should, at the same time, be checked by using intra- or extracellular recording whether the activity of the neuron E4, which is known to be part of the segmental CPG, is affected by the switch.

Here, we have also to discuss the fact that we used lumped afferent signals in the model. As it is well known (Büschges 2005), position, touch, and load signals all make contributions to the intrasegmental coupling of the individual CPGs in the middle leg of the stick insect. We, however, lumped them to a single afferent signal represented by the levator angle $\beta$ the threshold values of which trigger the sensory signals to the PR and FE systems, respectively. This admittedly gross simplification in the model can, in our opinion, be justified by three points: 1) the afferent signals of different modality eventually converge on premotor or pre-CPG neurons acting in their entirety; 2) the partial impact (weighting) of the individual sensory signals is not known in detail, hence, taking their integrated effect in form of a single signal offers a way to circumvent the weighting problem; and finally 3) the locomo-

![Proposed neural switching mechanism between forward and backward stepping](image-url)
tion task: walking on a plane surface to be mimicked by the model is so simple that it does not require the differential effects of the individual sensory signals. The fact that the threshold values of the levator angle $\beta$ have been chosen to be different for the PR and FE system expresses the differing effects these sensory afferent signals, represented by $\beta$, exert on the two neuromuscular systems. The differentiated use of the aforementioned sensory signals in a model is, no doubt, desirable and will be considered in future work as new, relevant experimental results emerge.

The equations of the mechanical motion contain only internal (muscle) forces. Hence, they describe the movement of a single middle leg without ground contact. For a complete description of normal locomotion, however, external forces such as body weight and ground reaction force would have to be taken into account. In this study, we have put emphasis on the neuronal control of the middle leg movement and hence did not build a full dynamical system of leg movement on the ground. Nevertheless, the simulations related to curve walking still clearly indicate the effectiveness of the neuronal control in producing the required stepping patterns.

It is a shortcoming of the model that the stationary retraction angle $\alpha$ cannot currently be set at any arbitrary value within the range of $\alpha$. Moreover, this stationary retraction angle strongly depends on the activity phase of the PR system. Thus the angle $\alpha = 102^\circ$ can only be obtained at a definite phase of the protraction-retraction period. It seems very likely that additional neuronal or muscular mechanisms that enable the system to attain any stationary angle position must be at work in the stick insect. Specialized contraction properties of the muscles, for example, may underlie such mechanisms. Indeed, Bässler et al. (1996) found such properties in the extensor tibiae muscle of stick insects.

**Comparison of the Model with Existing Ones**

Existing models of the stick insect walking system, which are based on behavioral data, have implemented turning by a
control module that reduces and increases the retraction amplitude in legs at the inner and outer side of the curve, respectively (Cruse et al. 1998; Dürr et al. 2004). A quantification of curve walking performance of this controller for different path curvatures and walking speeds has shown that the controller does well for curves with small but deviates from observations on real stick insects on curves with large curvature (Kindermann 2002). This is because the control mechanism only changes the retraction amplitude, but not the retraction and protraction phase. That is, no change from forward to backward stepping of the inner middle leg during turning is possible, even though this kind of direction change has been reported to exist in stick insect locomotion (Gruhn et al. 2009).

Another type of neuromechanical models that mimic the control of stick insect leg muscles was designed by Ekeberg et al. (2004). By means of this model, the authors could demonstrate that a leg controller in which identified sensory-motor pathways are implemented is able to generate coordinated forward stepping movements of the middle leg of a six-legged insect. Sideward stepping was produced by artificially fixing the ThC joint. For the purpose of their studies, they found it more helpful to make use of artificial bistable control systems, rather than of the biologically more relevant CPGs. Moreover, they did not aim at explaining or analyzing adaptive changes in the locomotor activity, such as change of direction of movement, hence they did not deal with problems of switching between forward, backward, or sideward stepping.

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Yet another group of models is based on phase oscillators. This includes models of salamander (Ijspeert et al. 2007) and cockroach locomotion (Holmes et al. 2006). Such models have been successfully used to test certain properties of neuromuscular systems with predetermined neuronal activity patterns, but it is usually not easy to interpret the model parameters in physiological terms. Harischandra et al. (2010), using their model of this type, have compared different tuning strategies during ground level stepping of a simulated salamander: only bending of the trunk, side-stepping of the front legs, or a combination of both were dealt with. It has turned out that the best turning strategy depends on the actual gait of the animal. However, this musculo-mechanical model of the salamander is not able to perform backward steps for turning, even though it has been observed that salamanders, too, can spontaneously exhibit short episodes of backward stepping during walking on land (Cabelguen et al. 2010).

We have elected an approach different to the aforementioned model types. The main constraint imposed upon our model is to preserve direct correspondence between model parameters and biological quantities. The merits of this approach are discussed in great detail in Daun-Gruhn and Büschges (2011). Here we should only like to emphasize the following aspect of our model. The CPGs in it can act both as intrinsic oscillators and nonoscillating units driven by sensory input signals. However, a nonoscillatory CPG can be transformed into an autonomously oscillating one by changing a single input signal to the CPG. The transformation in the other direction (from autonomously oscillating to nonoscillating CPG) can similarly be achieved. Thus the CPGs in our model suit well to behave adaptively, which is a very important property of functional units in living systems.

Having been able to implement the switch between forward, backward, and sideward stepping in the model, we can now mimic a large variety of direction changes depending on the extent of using backward or sideward stepping of the inner middle leg. To the best of our knowledge, our model is the first to produce this behavior. Moreover the changes between the stepping modes are, in essence, brought about by changing solely one or two control variables in the same control network.

Relevance of the Model to Physiology and to Other Fields

Despite its shortcomings, our model has some physiological relevance in that it proposes a unified neuromuscular system of the three leg joints and makes detailed suggestions as to how this system can carry out coordinated movements in a number of natural conditions, i.e., during forward walking, backward walking, and turning. The model also shows how the changes between the walking modes might be brought about in its biological counterpart, the stick insect. The simplicity of the mechanisms by which these changes can be carried out is, in our opinion, a particular merit of the model.

Because of these very same properties, our model might also have a bearing on the field of neuromotorics. First, it is built of nearly identical units: the neuromechanical systems of the three joints. Second, putting it in the language of this field, it uses low-dimensional control signals ($g_{3rb}$, $g_{3fb}$, $g_{app5}$, and $g_{app6}$) to bring about substantial changes in the system behavior. The low dimensionality of the space of control variables is always a desirable property of control systems, such as robots.

In summary, our model might thus become useful in two ways: 1) it may contribute to a better understanding of the biological mechanisms of locomotion in the stick insect, and perhaps in other insects; and 2) it may help construct biologically inspired robots that are more effective in performing locomotor tasks.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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