A neuromechanical model explaining forward and backward stepping in the stick insect

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Submitted 9 December 2011; accepted in final form 5 March 2012

Tóth TI, Knops S, Daun-Gruhn S. A neuromechanical model explaining forward and backward stepping in the stick insect. J Neurophysiol 107: 3267–3280, 2012. First published March 7, 2012; doi:10.1152/jn.01124.2011.—The mechanism underlying the generation of stepping has been the object of intensive studies. Stepping involves the coordinated movement of different leg joints and is, in the case of insects, produced by antagonistic muscle pairs. In the stick insect, the coordinated actions of three such antagonistic muscle pairs produce leg movements and determine the stepping pattern of the limb. The activity of the muscles is controlled by the nervous system as a whole and more specifically by local neuronal networks for each muscle pair. While many basic properties of these control mechanisms have been uncovered, some important details of their interactions in various physiological conditions have so far remained unknown. In this study, we present a neuromechanical model of the coupled protractor-retractor and levator-depressor neuromuscular systems and use it to elucidate details of their coordinated actions during forward and backward walking. The switch from protraction to retraction is evoked at a critical angle of the femur during downward movement. This angle represents a sensory input that integrates load, motion, and ground contact. Using the model, we can make detailed suggestions as to how rhythmic stepping might be generated by the central pattern generators of the local neuronal networks, how this activity might be transmitted to the corresponding motoneurons, and how the latter might control the activity of the related muscles. The entirety of these processes yields the coordinated interaction between neuronal and mechanical parts of the system. Moreover, we put forward a mechanism by which motoneuron activity could be modified by a premotor network and suggest that this mechanism might serve as a basis for fast adaptive behavior, like switches between forward and backward stepping, which occur, for example, during curve walking, and especially sharp turning, of insects.

GENERATING INDIVIDUAL STEPS and producing coordinated joint movements is essential for the locomotion of legged animals. During stepping, the individual limbs have to produce a cyclic, two-phase stepping pattern. One of them is the stance phase during which the leg has ground contact and produces the propulsion of the body. The other is the swing phase during which the leg is lifted and moved to the new starting position. Even though this process may appear simple, the underlying neuronal control is quite sophisticated. Evidence shows that the different joints of a multisegmented leg are individually controlled and the motions of the separate legs must be coordinated. The question of what neuronal and muscular mechanisms take part in generating and shaping the two phase stepping pattern has been intensively studied for a long time, and a large body of work has been amassed, even if we restrict ourselves to one species, the stick insect (Carausius morosus; Büssler and Büschges 1998; Büschges et al. 2008, 2011; Dürr et al. 2004; Orlovsky et al. 1999; Ritzmann and Büschges 2007). The basic nature of the specific interactions between sense organs and central networks, necessary to produce leg movements in varying internal states or under environmental constraints, has been known for some time. Load signals, for instance, are known to play an important role in the coordination of central pattern generators (CPGs) of single leg joints (Akay et al. 2004; Büschges 1995; Büschges and Gruhn 2008; Daun-Gruhn 2011; Ekeberg et al. 2004; Zill et al. 2004, 2011) as well as in establishing coordinated walking patterns of all legs in an intact stepping animal (Büschges 1995; Zill et al. 2009).

Studies on locomotion approached the problem of coordination between leg joints in a number of different ways. Early ones were behavioral observations (e.g., Cruse 1990; Graham 1972; von Buddenbrock 1921; Wendler 1965, 1978). Later, when electrophysiological methods became practicable, EMG activity was recorded from the muscles, as well as extra- and intracellular electrical activity of the neurons involved in shaping the motor activity (e.g., Büschges 1995; Büschges et al. 2004; Büschges and Gruhn 2008; Ritzmann and Büschges 2007 for reviews). In addition to these physical observations, a growing amount of theoretical work has been published over the years (e.g., based on behavioral studies and/or artificial neural networks Cruse 1990; Cruse and Bartling 1995; Cruse et al. 1998, 2000; Schilling et al. 2007; Schumm and Cruse 2006). The knowledge gained in this field has been applied to robots that use biological principles of locomotion, which were deduced from the experimental and theoretical investigations (Dürr et al. 2004; Iliespeert et al. 2007; von Twickel et al. 2011).

Despite the great progress in this field, many details have remained in want of better understanding, hence further investigation. One such detail is how rhythmic electrical activity of the CPGs that drive the individual joints is transformed into mechanical movement of the corresponding limb joint. Another such detail is backward walking and the switch between the two directions of movement. Very little is known about the underlying neuronal mechanisms. In contrast, forward walking has been thoroughly studied in the single middle leg of the stick insect, and the mechanisms underlying the coordination of the sensory-motor systems of the three leg joints to produce regular stepping patterns have, in essence, been uncovered. One of the findings is that during walking, the leg motoneurons (MNs) in the stick insect are tonically depolarized, presumably by descending pathways from the brain and the anterior seg-
ments. In addition, they receive phasic inhibitory input from the CPG, and phasic excitatory, as well as inhibitory, inputs from leg sense organs (Büschges 1995, 1998; Büschges and Manira 1998; Büschges et al. 2004; Driesang and Büschges 1993; Ludwar et al. 2005). However, it is still unclear whether the same mechanisms are also active during backwards walking, and how the motor outputs are generated by the nervous system under such conditions. Earlier studies by Rosenbaum et al. (2010) on the muscle activity of the six main muscles in the middle leg of the stick insect during forward and backward walking on a slippery surface showed strongest alteration in MN activity of the thorax-coxa (ThC) joint: protractor and retractor nearly completely exchanged their timing and magnitude of activity, whereas those of the coxa-trochanter (CTr) and the femur-tibia (FT) joint remained virtually unchanged. In this study, we aim at answering the question as to which neural mechanisms may be involved in forward and backward stepping of a single middle leg and how the switch between them could be realized. To this end, we first introduce a neuromechanical model of each of the first two joints: the protractor-retractor (PR) and the levator-depressor (LD) system that takes into account their specific mechanical properties. Figure 1 displays this mechanical system in a schematic form. The scheme mirrors the properties of the middle-leg joints and shows the basic movement directions. It is this mechanical system that is controlled by designated neuronal networks of the stick insect nervous system. We have omitted the flexor-extensor muscle system from the present considerations, because the timing and magnitude of the activity of the flexor and extensor MNs remain the same irrespective of the walking direction, as Rosenbaum et al. (2010) have found. Including the flexor-extensor neuromuscular system into our model would not contribute to a better understanding of the mechanisms involved but make the model more complicated. Having introduced the neuromechanical models, as a first step, we shall describe the basic properties of the controlling neuronal network. We then turn to the question of how the coordinated activity of these two systems can generate forward stepping and what the nature of this coordination is. Finally, we propose a simple mechanism that can bring about the switch between forward and backward stepping in the model. We use experimental observations to underpin our hypothesis that a similar mechanism might also act in the stick insect’s, and possibly other insects’, nervous system when the animal has to show fast, adaptive behavior as during curve walking or a change in walking direction.

METHODS

In this section, we first present the full neuronal network model and explain the structure of its constituent parts separately. Then, the muscle model used will be introduced, followed by the presentation of the neuromuscular coupling. In the last part, the equations of the mechanical motion of the femur will be derived.

Neuronal Network

Figure 2 shows the topology of the coupled neuronal network of the LD (lower subnetwork) and PR systems (upper subnetwork).

LD network. The core of the LD network is the CPG (Büschges 2005; Daun-Gruhn et al. 2012), which controls the activity of the levator and depressor MNs via the inhibitory interneurons (INs). This arrangement is corroborated by experiments that indicate that alternating motoneuronal activity is achieved by tonic depolarization of the MNs, $g_{app}$, in the model, and rhythmic inhibition of the MNs by the CPG (Büschges 1998, 2005; Gabriel 2005; Westmark et al. 2009). The CPG receives central inputs labeled by the conductances $g_{app}$ and $g_{app}$ of the driving current (Daun et al. 2009; Daun-Gruhn 2011). In addition, its function is affected by the input from the peripheral sense organs, called campaniform sensillae (CS), via the INs IN7 and INCS. The effect of the sensory input is of dual nature: it excites the “depressor” CPG neuron (C4) directly via INCS but inhibits the “levator” CPG neuron (C3) via an additional inhibitory IN IN7. This part of the network was constructed on the basis of experiments (Borgmann et al. 2012) and accompanying simulations (Daun-Gruhn et al. 2012). Thus it is supported by experimental and modeling results. It therefore constitutes a network that, in its basic properties, is likely to be close to that present in the stick insect. Note that the “levator” CPG neuron (C3) does not directly excite the levator MN but it inhibits the other CPG neuron (C4). This results in a disinhibition of the levator MN. Exactly the same mechanism applies to the “depressor” CPG neuron (C4) and the corresponding MN.

In certain experimental situations (e.g., partial amputation of the femur of the middle leg), permanent activity of the levator MNs and permanent silent state of the depressor MNs can be observed. However, load stimuli applied to the remaining CS can still excite the depressor MNs (Borgmann et al. 2012). It can therefore be assumed that in an animal with an intact middle leg a sufficiently high level of average tonic excitation is present that keeps the CPG autonomously oscillating.

The neuron models used are of Hodgkin-Huxley type (Hodgkin and Huxley 1952). In the stick insect, the CPG neurons and the INs are assumed to be nonspiking ones (Büschges 1995), but the MNs do fire sodium action potentials and show spike frequency adaptation (Schmidt et al. 2001). A detailed description of the properties and analysis of the behavior of these neuron models, together with the synaptic models, can be found in Daun et al. (2009) Daun-Gruhn (2011), and Daun-Gruhn and Toth (2011).

PR network. The upper part of the neuronal network in Fig. 2 is the neuronal part of the PR system. As it can easily be seen, its structure and constituent elements closely resemble those in the LD network: it is essentially the same system applied to a different antagonistic muscle pair. One difference is that the input of IN4 emanates from sensory signals that include, especially, load and position signals. Thus the angle $\beta$ represents their combination in the model. The other one is that the CPG of this network is normally outside, but near to, its oscillatory regime. It is activated and entrained by the sensory signals just mentioned and represented by $\beta$ (Daun et al. 2009; Daun-Gruhn 2011). The values of parameters of the same kind (e.g., $g_{app}$ values) may, of course, differ in the two subnetworks.

Fig. 1. Schematic illustration of the middle-leg joints and the basic movement directions as indicated in the figure. Shaded regions on or near the leg represent the different muscles. Note that the flexor-extensor muscle system is omitted from considerations in the present study (adapted with permission from M. Gruhn, unpublished observations).
Coupled LD and PR model. In the stick insect, a combination of sensory afferent signals (load, motion and ground contact) elicits the retraction movement, which forms the basis of forward walking (Büschges 2005). It is known (Cruse 1985a,b) that load and position sensory afferent signals (load, motion and ground contact) elicits the retraction movement, which forms the basis of forward walking.

Muscle Model

We used the same muscle model for all four muscles (cf. Fig. 2) but with different numerical values of the parameters. The model is a simplification of the one by Hill (1953). Figure 3 shows schematically Hill’s model (Fig. 3A) and the simplification we used (Fig. 3B). The main point is that we merged all active and passive elastic muscle properties into a single spring with nonlinear characteristics (Eq. 1) and variable elasticity modulus (spring constant). The remaining spring obeys the nonlinear elasticity law found by Guschlbauer (2009):

\[ F = k(l - l_{\text{min}})^2 \]  

where \( k \) is the variable elasticity modulus, and \( l_{\text{min}} \) called the “minimal” length, is the length of the muscle at which no force (stress) is present. The actual value of \( k \) is controlled by the activity of the MNs that innervate the muscle (see below).

Despite its simplicity, our muscle model is still capable of exhibiting both isometric and isotonic contraction: the former simply by keeping the muscle length \( l \) constant and varying \( k \), the latter by adjusting \( k \) such that \( F = F(l - l_{\text{min}})^2 \) when varying \( l \) (\( F \) being the constant force).

There exist, of course, far more elaborate muscle models, in particular, for the flexor-extensor muscles of the stick insect (e.g., Blümel 2011). For our present study, however, a much simpler model proved to be more suitable, since our main aim was to produce simulated angular movements at the different joints that resemble those seen in the stick insect. The details of intramuscular processes during the neuromuscular transmission of excitation could therefore be omitted. This made our muscle model fast enough to be included into an integrated neuromuscular model, but it remained still sufficiently accurate to produce simulated mechanical movements that proved to be good approximations to those in the stick insect.

Fig. 2. Coupled protractor-retractor (top) and levator-depressor (bottom) network. CPG: central pattern generator; MN, motoneuron, its type is indicated in parentheses; IN, interneuron; INCS, sensory interneuron receiving stimuli from the campaniform sensillae (CS); \( \odot \), inhibitory synapses; \( \bullet \), excitatory synapses (for technical reasons, the neurons are also consecutively numbered as C1, C2, \ldots). The \( g_{\text{app}1} \) to \( g_{\text{app}4} \) are the conductances of the central driving currents to the CPG neurons, and \( g_{\text{app}5}, g_{\text{app}6}, g_{\text{app}7} \) and \( g_{\text{app}8} \) are those of the driving currents to the interneurons IN1, IN2, and IN5, IN6, respectively, which inhibit the corresponding MNs but receive excitation from the CPG. All of these conductances are individually variable. Those of the central driving currents to the MNs, \( g_{\text{app}4}, g_{\text{app}7} \), are, however, uniform for all MNs in the system. Conductance \( g_{\text{app}5} \) determines the intensity of the excitation from the stimuli to the CS. Ramp symbol stands for the CS stimulation. Pro m., Ret m., Dep m., Lev m.: the muscles innervated by the corresponding MNs. Hexagon with the letter \( \beta \) in it expresses the fact that the coupling between the two subsystems is done through the angular extension position of the femur. For further details, see text.

Coupled LD and PR model. In the stick insect, a combination of sensory afferent signals (load, motion and ground contact) elicits the retraction movement, which forms the basis of forward walking (Büschges 2005). It is known (Cruse 1985a,b) that load and position signals play an important role in the swing-to-stance and stance-to-swing transition of the step cycle. In addition, Akay et al. (2004, 2007) showed that load signals from the legs alter the timing of ThC motoneuron activity by resetting and entraining the activity of the central rhythm generating network of the ThC joint.

In the model, the coupling is mediated by the position of the femur as expressed by the angle \( \beta \) (cf. small hexagon with \( \beta \) written in it in Fig. 2) measuring the elevation of the femur above the fully stretched state of the coxa-trochanter joint. When the femur is moving down, at a critical value of \( \beta \), the neuron IN4 receives an excitatory synaptic input from the LD system. The excitatory synaptic input activates the PR system by exciting the CPG neuron C1, which is activated during retraction, thus activating the retractor MN. Simultaneously, the “protractor” CPG neuron C2 is inhibited via IN3, to enhance the retraction. When the leg is lifted again (swing phase), the excitation of the PR system via the neuron IN4 rapidly decays.

Eq. 1

\[ F = k(l - l_{\text{min}})^2 \]  

**Fig. 3.** Hill’s muscle model (A) and simplified muscle model (B) used in our model. A: \( k_p \), modulus of the passive parallel elasticity; \( k_s \), modulus of the passive serial elasticity; \( b_v \), viscosity coefficient characterizing the viscosity of the muscle; ACU, active contraction unit responsible for the development of (isotonic or isometric) contraction force. Model in B is obtained by omitting the passive serial elasticity, and by merging ACU with the passive parallel elasticity. Thus in B, \( k_{ae} \) is the variable modulus of the active, nonlinear elasticity, \( b_v \), as in A.
Neuromuscular Coupling

We used the same model for the neuromuscular coupling at the different muscles, but, again, the parameter values may differ for the individual muscles.

Basic idea of the neuromuscular coupling. In the stick insect, MN action potentials evoke (strong) depolarization of the muscle via the motor end plates, which are synapses from the MNs to the muscle. This leads to the release of intracellular Ca"`, which in turn initiates the muscle contraction. The neuronal excitation is thus eventually transformed into muscle force via a chain of complex physiological and biophysical-biochemical processes.

In the present model, we did not construct separate models for the constituent elementary processes of the electromechanical coupling in the muscle. Had we done so, this would have increased the complexity and the size (the number of system variables and equations) of the model enormously and might have rendered it impracticable. Instead, we made simplifications and modeled the two main aspects of this system: the coupling between MN and muscle by using a synapse model and the dependence of the strength of the muscle contraction on the firing frequency of the MNs. These properties are merged into a single model to be introduced here.

The synapse model can be described by a linear, first order ordinary differential equation of the following form:

\[ \dot{u} = a(t) (1 - u) - bu \]  

(2)

where \( u \) is the activation variable of the postsynaptic ligand-gated channel (\( \dot{u} \) being its time derivative) and \( a(t) \) and \( b \) are coefficients. While \( b = const. > 0 \), \( a(t) \) is only positive (equals \( a_0 \)) during an incoming (presynaptic) action potential, i.e., \( a(t) = a_0[H(t - t_0) - H(t - t_0 + \Delta t_{syn})] \), \( H(t) \) being the Heaviside step function: \( H(t) = 1 \), if \( t > 0 \), and \( H(t) = 0 \) otherwise, where \( t_0 \) is the onset of the action potential and \( \Delta t_{syn} \) is its duration. The basic idea behind the mathematical formalism is that opening the postsynaptic ion channels can only take place during an action potential. The value of \( a_0 \) determines the efficacy of the transmitter release. Such models have been used successfully and widely for some time (Destexhe and Mainen 1994; Antal et al. 1996; Emri et al. 2000; Toth et al. 2007). A great advantage of this model is that the solution to Eq. 2 can be written down explicitly:

\[ u(t) = u_e - [u_e - u(t_0)] \exp[-(a_0 + b)(t - t_0)] \]  

if \( t_0 \leq t < t_1 \)

\[ u(t) = u(t_1) \exp[-b(t - t_1)] \]  

if \( t_1 > t \geq t_1 \)  

(3)

(4)

In Eqs. 3 and 4, \( t_1 = t_0 + \Delta t_{syn} \), \( t_0 \) is the arrival time of the next action potential, and \( u_e \) is the stationary, or final, value of \( u(t) \). In this solution, \( 0 < u(t) < 1 \) but the above formulas for \( u(t) \) remain valid for functions \( u(t) \geq 1 \), which are then solutions to a differential equation similar to Eq. 2.

Now, the electromechanical coupling is done very simply: the activation variable \( u \) is set to be equal to the elasticity modulus \( k \) of the muscle in Eqs. 3 and 4. Of course, \( k \) is not restricted to the interval (0, 1) but can assume values that are appropriate in the mechanical system (see below). The rate constants \( b \) were chosen small (\( b = 0.01 \text{ ms}^{-1} \)) for all muscle types, representing a slow decay, while the values of \( a_0 \) varied between 0.2 ms\(^{-1} \) (protractor muscle) and 15 ms\(^{-1} \) (levator muscle) expressing the various needs for fast dynamics. For the remaining two types, \( a_0 = 5.0 \text{ ms}^{-1} \) (depressor and retractor muscles).

Implementation of the neuromuscular coupling in the model. This part of the model is rather technical. We therefore put the detailed description of the implementation into the APPENDIX.

Description of the Mechanical Movements

The mechanical movement of the femur is described by means of appropriate angles that characterize its anterior-posterior and vertical position. The former is thus described by the angle \( \alpha \) measured from the longitudinal axis of the insect’s body towards the posterior direction. The angle \( \alpha \) can change between 28° (anterior extreme position) and 128° (posterior extreme position; Schumm and Cruse 2006). The angle of elevation of the femur from the fully stretched state of the coxa-trochanter joint is called \( \beta \), and it can take values between 30°, lowest position during ground contact of the leg (stance phase), and 60°, highest position during swing phase (Schumm and Cruse 2006). The trigger signal from the LD to the PR system is generated shortly before ground contact of the leg, i.e., at \( \beta = 38° \).

The mechanical movement of the femur in the forward-backward as well as in the up-down direction can be described by appropriate equations of motion of the mechanics taking into account the specific geometric arrangement of the muscles. This will be done separately in the next two paragraphs. The effect of the gravitation will be ignored throughout the considerations to follow, since the mass of the femur is very small; hence, the torque due to the gravitational force is negligible compared to the torques generated by the elastic and viscous muscle forces (Hooper et al. 2009).

Equation of the forward-backward mechanical motion of the femur. Figure 4, A and B, shows the gross anatomy of the LD and PR systems, respectively. To be precise, the forward-backward movements are those of the coxa-femur complex, since they originate at the thorax-coxa joint (Fig. 4B). However, the mass and size of the coxa are much smaller than those of the femur (Blümel 2011); hence, they can be neglected when considering the equation of motion of this mechanical system. The simplified geometric arrangements used in our model are displayed in Fig. 4, C (LD) and D (PR). In Fig. 4D, the black thick line represents the thorax, the empty rod the femur, and the thick point on the thorax line the rotation axis at the thorax-coxa joint, which is perpendicular to the plane of the figure. The thick arrows stand for the muscles and the muscle forces: \( F_P \) for the protractor and \( F_R \) for the retractor force. The corresponding muscle lengths are \( l_P \) and \( l_R \), respectively. The angles \( \phi_P \) and \( \phi_R \) are the angles between the muscle fibres and the femur. We assume for the sake of simplicity that the protractor and retractor muscle join the femur at the same point in a distance of \( d \) as measured from the axis of rotation (Fig. 4D). The other ends of the muscles end in the same distance \( r \) from the rotation axis, an additional simplifying assumption (Fig. 4D).

The above geometric arrangement is clearly a simplification of the arrangement of the protractor and retractor muscles in the stick insect but retains the most important feature of the latter: a rod (the femur) being rotated about an axis by a pair of springs (muscles), one on either side of the rod, is preserved in the kinematic model (cf. Fig. 4D). We are thus able to compute the mechanical torques that bring about the forward-backward angular movement of the femur and provide the equation of motion for this mechanical system. It reads:

\[ I \ddot{\alpha} = F_P d \sin \phi_R - F_R d \sin \phi_P - F_{v,d} \]  

(5)

where \( I \) is the inertial momentum of the femur (and muscles), but it does not include that of the tibia. The \( \alpha \) is the angular acceleration (2nd time derivative of the angular movement \( \alpha \)), and \( F_P \) and \( F_R \) are the protractor and retractor elastic muscle force, respectively, obeying Eq. 1, i.e.:

\[ F_P = k_P (l_P - l_{min})^2 \]  

(6)

\[ F_R = k_R (l_R - l_{min})^2 \]  

(7)

\( F_v \) is the force due to viscosity of the muscles. The viscosity force is assumed to be linearly proportional to the actual velocity \( v = \dot{\alpha} \) (\( \alpha \) being the angular velocity), i.e., \( F_v = b v = b \dot{\alpha} d \dot{\alpha} \), being the viscosity coefficient for the PR system. The other quantities have been introduced in Fig. 4D. Now, using the sine theorem for triangles, we obtain:
equation of the up-down mechanical motion for this joint. This as functions of \( \alpha \) and \( \beta \) elongates along the perimeter of the half-circle of radius \( b_r \) axis at \( d \) position). When the femur moves up, or down, i.e., rotates about the coxa-trochanter joint is in fully stretched state (a nonphysiological situation) when both muscles are assumed to have the same length: the distance between the points \( A \) and \( B \), \( d = AB \). Femur is at right hand side. It hinges about the axis through the point \( B \), orthogonal to the plane of the figure. \( C \): femur is tilted upward by an angle \( \beta \). Note the shortening of the levator and the elongating of the depressor muscle. For calculating the actual lengths in this case see Eq. 9–10. \( D \): simplified geometrical arrangement when looking at it from above. Posterior-anterior direction is the one from up to down, the same as in \( B \). Thick black line represents the thorax, the unfilled rod the femur, the trochanter being very short has been neglected. Angle \( \alpha \) characterizing the position of the femur is counted from anterior to posterior (as indicated). \( F_L \) and \( F_D \) are the forces in the retractor and protractor muscle, respectively. Corresponding muscle lengths are \( l_L \) and \( l_P \). The meaning of the other quantities are clearly indicated in the figure and are explained in more detail in the text.

\[
I\alpha = rd \sin \alpha \left( \frac{F_R}{l_R} - \frac{F_P}{l_P} \right) - b_r d^2 \alpha
\]  
(8)

To use Eq. 8, we need to compute the actual muscle lengths \( l_L \) and \( l_P \) as functions of \( \alpha \). By the cosine theorem for triangles, we have:

\[
l_L^2 = r^2 + d^2 - 2rd \cos \alpha
\]  
(9)

\[
l_P^2 = r^2 + d^2 - 2rd \cos \alpha
\]  
(10)

which give us the desired functions. Introducing the constants \( c_4 = rd/l \) and \( c_5 = b_r d^2/l \), the final form of the equation of forward-backward mechanical motion is obtained as

\[
\alpha = c_4 \sin \alpha \left( \frac{F_R}{l_R} - \frac{F_P}{l_P} \right) - c_5 \alpha
\]  
(11)

**Equation of the up-down mechanical motion of the femur.** The geometry is much simpler for the LD muscle system and the femur than for the PR system (Fig. 4C). Here, the basic idea is that both the levator and the depressor muscle are of the same length \( d \) when the coxa-trochanter joint is in fully stretched state (a nonphysiological position). When the femur moves up, or down, i.e., rotates about the axis at \( B \), perpendicular to the plane of the figure, one of the muscles elongates along the perimeter of the half-circle of radius \( r \) with center at \( B \), the other shortens by the same amount. Thus the actual lengths of the levator and depressor muscles are given as

\[
l_L = d - r \beta
\]  
(12)

\[
l_D = d - r \beta
\]  
(13)

These equations define the actual lengths of the above muscles as functions of the rotation angle \( \beta \). This will be needed in solving the equation of the up-down mechanical motion for this joint. This equation has a simpler form than that for the PR system. It reads

\[
\dot{\bar{\beta}} = r(F_L - F_D - F_v)
\]  
(14)

where \( I \) is again the inertial momentum of the femur (and muscles), \( \bar{\beta} \) is the angular acceleration, \( F_L \) and \( F_D \) are the levator and depressor elastic muscle forces, respectively, obeying Eq. 1, i.e.:

\[
F_L = k_L (l_L - l_{Lmin})^2
\]  
(15)

\[
F_D = k_D (l_D - l_{Dmin})^2
\]  
(16)

\( F_v \) is the viscosity force having the form \( F_v = b_v y = b_r r \bar{\beta} \). Again \( b_v \) is the viscosity coefficient for the LD system. The final form of the equation of mechanical motion of the LD system then reads

\[
\dot{\bar{\beta}} = c_6 (F_L - F_D) - c_7 \dot{\bar{\beta}}
\]  
(17)

with \( c_6 = r/l \) and \( c_7 = b_r r^2/l \). The equations of mechanical motion both for the forward-backward and the up-down movements of the femur are obtained separately. The two systems (LD and PR) are, however, mechanically coupled. Fortunately this passive mechanical coupling is very weak compared with the size of the elastic forces measured in the experiments. Indeed, Hooper et al. (2009) have recently shown that the torques due to passive mechanical coupling can be neglected in small animals in general and in the stick insect and cockroach locomotor system in particular. This sufficiently justifies the separate treatment of the two mechanical systems.

One should also bear in mind that the elasticity moduli (\( k_L \), etc.) appearing in the above equations are variable; their value is controlled by the activity of the corresponding MN. The elasticity moduli of one muscle system (LD or PR) are, however, not independent of each other. There exists a set of important criteria presented in the next paragraph that constrain the values of the elasticity moduli that they can assume. The LD and PR elasticity moduli constraints are derived
in the exact same manner. Below is the derivation and illustration of the LD system.

An Important Constraint for the Values of the Elasticity Moduli of the Muscles

When the movement of the femur changes direction, this is due to a change of the contraction forces in the levator and the depressor muscles. The point of the switch in direction is normally determined by the periodic activity of the CPG that ultimately controls the contraction of these muscles. Thus the switch usually takes place at the end of the de- and hyperpolarization phases of the CPG activity that correspond to the end of the swing or the stance phase of the stepping leg. The question is what kinematic conditions should apply to the movement of the femur at the switch points. We assumed that the switch takes places at the stationary points of the movement. This assumption has quite recently received experimental support from measurements of the angular movement and velocity in the flexor-extensor system (M. Gruhn, personal communication). From this assumption, two conditions can be derived. First, the angle velocity \( \beta = 0 \) at the switch point; otherwise there would be no switch of direction of the movement at this point. Second, the acceleration of the femur should vanish at the switch point. Trying to force the switch before \( \beta \) reaches zero would cost extra (mechanical) work. Hence we have the second condition: \( \beta = 0 \). The end position of the femur, hence the corresponding angle \( \beta_e \), at the switch points has been determined through experimentation (i.e., \( \beta_e \approx 30^\circ \text{ and } \beta_e \approx 60^\circ \); Schumm and Cruse 2006). If the time instant of the switch is denoted by \( T_{sw} \), we have:

\[
\beta(T_{sw}) = \beta_e, \quad \dot{\beta}(T_{sw}) = 0, \quad \text{and} \quad \ddot{\beta}(T_{sw}) = 0 \quad (18)
\]

Having defined the switch conditions in terms of the stationary states of the mechanical movement of the femur, we use them to determine the stationary values of the elasticity moduli \( k_L \) and \( k_R \) at these states. They, in turn, are used as the stationary values (\( k_w = a_w \)) in Eq. 3, which yields the actual value of \( k = k(t) \). As a first step to determine the stationary values of the elasticity moduli at \( \beta = \beta_e \), we can compute their quotient as follows. We substitute the values in Eq. 18 into Eq. 17 and use Eqs. 15 and 16 to obtain the following condition for the elasticity moduli of the muscles at \( \beta = \beta_e \):

\[
a = \frac{k_R}{k_L} = \frac{d - r\beta_e - l_{min}}{d + r\beta_e - l_{min}} \quad (19)
\]

On the right-hand side, all quantities have known values; thus the quotient \( a \) of \( k_p \) and \( k_L \) is uniquely determined. Note that the value of \( a \) is different in the two switch points (from up to down, and from down to up, respectively).

Even though these are important constraints on the stationary values of elasticity moduli, they do not determine their absolute values. We determined the absolute values of these parameters and the viscosity coefficient \( b_v \), through computer simulation. The results of the simulations will be presented in the first paragraph of RESULTS.

Implementation of the Model

The simulation program of the model was written in C using the CVODE software package for numerical quadrature of the differential equations (Cohen and Hindmarsh 1996). The differential equation system to be solved consisted of 44 equations for the neuronal network and two equations each for the mechanical movements. The computation was carried out within real time; that is, a simulation run for a typical 14-s long period was completed within 10.7 s of computational time.

RESULTS

Simulations to Determine the Values of the Elasticity Moduli and the Viscosity Coefficients

In these simulations with both the LD and the PR system, we solved the relevant equation of motion (Eqs. 11 or 17) numerically choosing various values for both the elasticity moduli and \( b_v \), but under the constraint arising from the stationary condition (Eq. 18). We then checked whether the stationary conditions in Eq. 18 for the actual angle (\( \alpha \) or \( \beta \)) were fulfilled at the predetermined switch time \( T_{sw} \). If so, we accepted the parameter values that yielded the satisfactory result.

PR system. To carry out simulations with the PR mechanical system, we needed the numerical values of the geometric parameters \( d \) and \( r \). We estimated them from the anatomical figures of Bässler (1983) (cf. Fig. 4B; \( r = 2.5 \text{ mm}, d = 2 \text{ mm} \)). The inertial momentum of the femur was calculated from the data by Bümmel (2011): \( I = 0.73 \text{ g-mm}^2 \). Accordingly, we obtained \( c_4 = 6.85 \text{ l/g} \). We set \( l_{pmin} = 1.0 \text{ mm} \) and \( l_{rmin} = 1.5 \text{ mm} \). The value of the constant \( c_5 \) could not be determined at this stage, since it depends on the viscosity coefficient \( b_v \), the value of which was unknown at this stage.

The measured range of movements for the angle \( \alpha \) was \( 28^\circ \text{ and } 128^\circ \) (Schumm and Cruse 2006). Moreover, this range has to be swept from \( \alpha = 28^\circ \) to \( \alpha = 128^\circ \) during the stance phase of the stepping, which lasts, during tetrapod gait, \( 3T_{pe}/4 \approx 375 \text{ ms} \) \( (T_{per} = 500 \text{ ms} \text{ being the full period of the stepping sequences}; \text{ Graham, 1972; Büschges 2005; Daun-Gruhn 2011}) \). Applying the stationary conditions of Eq. 18 to the PR system at \( T_{sw} = 3T_{pe}/4 \) and \( \alpha_e = 128^\circ \) \([\text{starting at angle } \alpha(0) = 28^\circ]\) by Eq. 11, we have:

\[
a_1 = \frac{k_R}{k_p} \frac{l_R(\alpha_e)}{l_R(\alpha_e) - l_{pmin}^2} \quad (20)
\]

Using Eqs. 9 and 10 for computing the values of \( l_R \) and \( l_p \), respectively, we obtained \( a_1 = k_R/k_p = 17.160 \). Choosing \( k_p = 25 \text{ mN/mm}^2 \), hence \( k_R = 429 \text{ mN/mm}^2 \), \( b_v = 25.5 \text{ mN/mm/s} \) \([c_5 = 139.73 \text{ mN/(g-mm)}]\) on the basis of the simulations, the results shown in Fig. 5A emerged. The time course of the corresponding angular velocity \( \alpha(t) \) is displayed in Fig. 5B. It is clear that the conditions in Eq. 18 are fulfilled for \( \alpha \) with good numerical accuracy (<1% relative error) at \( t = T_{sw} - 3T_{pe}/4 \).

Now, when starting from the position \( \alpha(0) = 128^\circ \) and moving to the end position \( \alpha_e = 28^\circ \), analogous results were obtained at \( t = T_{sw} - T_{per}/4 \):

\[
a_2 = \frac{k_R}{k_p} \frac{l_R(\alpha_e)}{l_R(\alpha_e) - l_{pmin}^2} \quad (21)
\]

Equation 21 yielded \( a_2 = k_R/k_p = 0.0160 \). For the absolute values of \( k_R \) and \( k_p \), we obtained \( k_R = 16 \text{ mN/mm}^2 \) and \( k_p = 1,000.0 \text{ mN/mm}^2 \) in the simulations. The numerical value of \( b_v \) remained unchanged \([b_v = 25.5 \text{ mN/(mm/s)}]\). The corresponding results are displayed in Fig. 5, C and D. Again, it can be seen that conditions Eq. 18 are fulfilled with good numerical accuracy (<1% relative error) at \( t = T_{sw} = 125 \text{ ms} \). The relation \( a_2 < a_1 \) can be attributed to the requirement that the end state must be attained much faster (within \( T_{pe}/4 \)) in the swing phase than in the stance phase (\( 3T_{pe}/4 \)).
LD system. Again, the geometric data \( r \) and \( d \) (cf. Fig. 4A) needed in the simulations were obtained as estimates from the anatomical figures in Bässler (1983). Thus \( d = 3.5 \) mm, \( r = 1.0 \) mm. We set \( l_{\text{Lmin}} = 2 \) mm, and \( l_{\text{Dmin}} = 3 \) mm. Using \( I = 0.73 \text{ g·mm}^2 \) (Blümel 2011) again, we have \( c_y = r/I = 1.3699 \) \text{1/gmm in Eq. 17 but } \( c_y = b, r^2/I \) had to be determined from the simulations. In the experiments, it was found that the LD angle \( \beta \) varied between 30° and 60° (Schumm and Cruse 2006). When simulations were performed under the constraint of the stationary conditions Eq. 18, the absolute values of the elasticity moduli \( k_L \) and \( k_D \), as well as that of the viscosity coefficient \( b_y \) could be determined for both angles above at the switch times of \( T_{sw} = 3T_{\text{per}}/8 \) (\( \beta_y = 60° \)) and \( T_{sw} = 5T_{\text{per}}/8 \) (\( \beta_y = 30° \)) (Büschges 2005; Daun-Gruhn 2011). They read, for \( \beta_y = 60° \), \( k_L = 1808.1 \text{ mN/mm}^2 \) and \( k_D = 160 \text{ mN/mm}^2 \), and or \( \beta_y = 30° \), \( k_L = 879.21 \text{ mN/mm}^2 \) and \( k_D = 800 \text{ mN/mm}^2 \). The viscosity coefficient \( b_y \) was 84 \text{ mN/(mm/s)} in both cases. A check of the simulation results obtained with these parameter values confirmed that the stationary conditions were fulfilled with good numerical accuracy (<1% relative error) (not illustrated).

To convince ourselves that the findings of Hooper et al. (2009) apply to our case, we carried out simulations with the mechanically coupled LD and PR mechanical system (results not shown). We found that the pure mechanical coupling between the two mechanical systems indeed had only a small effect on their behavior; hence, the separate treatment of the two mechanical systems is justified and supported by the findings of Hooper et al. (2009).

Simulations with the Coupled Neuromuscular Model

We used the coupled neuromuscular model for simulations to uncover the time course of the important system variables during locomotion. Figure 6 shows the behavior of the coupled PR and LD system during normal forward locomotion (control conditions). In the activity of the PR CPG, the relative length of the retractor phase within one period of locomotion (i.e., one step) is longer than that of the protractor phase (Fig. 6A) (Graham 1972; Ekeberg et al. 2004; Büschges 2005; Daun-Gruhn 2011; Rosenbaum et al. 2010). This is preserved in the MN activities and faithfully reflected in the periodic angular movement \( \alpha \). The activity of the LD CPG shows an \( \sim 3:5 \) proportion between the levator and depressor phases (Büschges 2005; Daun-Gruhn 2011), which again is expressed both in the MN activities and the angular movement \( \beta \) (Fig. 6B). For an easier understanding of the explanations to follow, we have inserted a box across the rows of Fig. 6 to mark one “electrical retractor phase” during the movement of the leg. This roughly corresponds to the stance phase of the stepping. The trigger signal from the LD system to the PR system (cf. Fig. 2) is evoked at \( \beta = 38° \) at the left edge of the box. This angle is somewhat greater than that at full ground contact (\( \beta = 30° \)) because it represents a combination of sensory afferent signals (load, motion, and ground contact) (Büschges 2005). We set the same critical angle (\( \beta = 38° \)) for the lift-off. Now, when the trigger signal is evoked in the LD system, it excites the retractor CPG neuron (C1) of the PR system (Fig. 2) via the pathway IN4 to C1 and inhibits the other CPG neuron (C2) via the pathway IN4-IN3-C2. The CPG neuron C1, in turn, directly excites the retractor MN, which starts firing (Fig. 6A). The firing of the retractor MN activates the corresponding muscles and the mechanical retraction movement sets in. By this time, the downward movement of the leg will have been completed, and full ground contact established. Towards the end of the retraction phase, the leg is again lifted, and at \( \beta = 38° \), the excitatory signal to the PR system is switched off terminating the retractor MN activity. The femur still moves backward for a very short time while the leg is already in the air, a behavior that is also observed in the animal. This is the

Fig. 5. Transient sweep of the femur from the starting position \( \alpha = 28° \) to the end position \( \alpha = 128° \) (A and B) and back (C and D). A: time course of the angle \( \alpha \) when the femur is moving from \( \alpha = 28° \) to \( \alpha = 128° \). B: the corresponding time course of the angular velocity \( \dot{\alpha} \), C: time course of the angle \( \alpha \) when the femur is moving from \( \alpha = 128° \) to \( \alpha = 28° \); D: the corresponding time course of the angular velocity \( \dot{\alpha} \). Note that the stationary conditions formulated in Eq. 18 are satisfied at \( t \approx 375 \text{ ms} \) and \( t \approx 125 \text{ ms} \), respectively.
time from the right edge of the box to the closest peak of the angle $\alpha$ in Fig. 6A, top.

The model also enabled us to uncover the time course of other important model variables, such as the elasticity forces muscles develop during locomotion. As an illustration, we show the time course of the forces in the levator and the depressor muscle during normal stepping (Fig. 7A). In Fig. 7A, the angular movement $\beta$ is displayed at the top for the sake of comparison with the forces (middle) of the depressor (red) and levator (blue) muscles. In Fig. 7A, bottom, the time course of the corresponding variable elasticity moduli ($k_D$: red and $k_L$: blue) are shown. It can be seen that the stance phase (downward movement of the femur) is initiated by a sharp peak of the force in the depressor muscle. Similarly, the swing phase (upward movement) is elicited by a large pulse of force in the levator muscle. These sudden increases in the muscle forces are essentially due to the sudden increases of the corresponding elasticity modulus (Fig. 7A, middle and bottom) and the large rate constants $a_0 + b$ during an action potential (cf. Eq. 3). Unfortunately these transient forces, which appear to be quite strong, cannot be measured in experiments with the experimental techniques available but the forces in the almost stationary state that follows the force peaks have recently been measured. The almost stationary values shown in Fig. 7A are in the same range as the measured values (C. Guschlbauer, personal communication).

In Fig. 7B, we show the relationship between the corresponding neuronal (voltage) signals and the mechanical variables: angle ($\beta$), forces in the depressor (red) and levator (blue) muscle, and the corresponding elasticity moduli ($k_D$ and $k_L$; bottom) driven by the action potentials of the depressor and levator MNs. Arrow from the angular trace to those of the muscle forces points to the large transient depressor muscle force that brings about the rapid start of mechanical downward movement. The same is true in relation of the levator force and the upward movement of the femur. For further details, see text.
ables of the model. Again, it can be clearly seen that the CPG neurons trigger the activity in the MNs, which, in turn, cause the muscle to contract quickly via the neuromuscular coupling mechanism of the model. The sharp peaks of the contraction forces are due to the high firing frequency of the MNs at the beginning of their firing regime.

For the PR system, similar relations between the mechanical and neuronal variables exist (not illustrated).

**Modeling Switches Between Forward and Backward Movements**

With a slight modification, the present model (Fig. 2) can also emulate backward movement of the leg and switching between forward and backward walking. The basic idea is that the output activity of the CPG of the PR system is redirected via additional connections from the CPG neurons to the inhibitory interneurons IN1 and IN2 (Fig. 2). Thus, while IN1 receives the excitatory synaptic input from C1 and IN2 from C2 during forward walking, these connections are exchanged during backward walking. That is, C1 excites IN2 and C2 IN1 in the latter case. Note, that no change occurs in the activity of the CPG. The protractor and the retractor muscle, however, exchange their working regimes due to the redirection of the CPG output when a switch from forward to backward walking takes place. The activity of the LD muscles with regard to the stance and swing phase remains, however, the same. Thus C1 and MN1(P), and C2 and MN2(R) are coactive during backward walking. This is in full agreement with the experimental observation that, during backward walking, the protractor muscles contract during the stance phase and the retractor muscles do so during the swing phase of the stepping. (Rosenbaum et al. 2010). This experimental fact is illustrated in Fig. 8. It should be emphasized that the other muscles do not change their working regimes with respect to the stance and swing phases.

As far as the modification of the network is concerned, Fig. 9 shows a possible physiological implementation of the modified PR network complete with command signals to switch between forward and backward walking. The command signals are of central origin, in agreement with most recent experimental findings concerning stick insect locomotion (P. Rosenbaum and A. Büschges, personal communication). They control presynaptic inhibition on the synaptic paths connecting the CPG neurons C1 and C2 to both inhibitory interneurons IN1 and IN2. During forward walking the central command activates SF, which inhibits the excitatory pathways from C1 to IN2 and C2 to IN1. Because SF also inhibits neuron SB, the presynaptic inhibition of the excitatory pathways from C1 to IN1 and C2 to IN2 is also stopped. The input to the PR system through the sensory pathway (IN3 and IN4 in Fig. 2) remains the same in both conditions, because the working regime of the coxatrochanter joint does not change. In the model, the network of central commands for the forward-backward movement has the same structure as the CPG: a pair of mutually inhibitory neurons.

Figure 10 illustrates how a switch from forward to backward walking takes place in the stick insect (Fig. 10A) and in the model (Fig. 10B). The experiments showed that during forward walking, the retractor muscle was active during the ground contact of the tarsus (stance phase; Fig. 10A, left box), while

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**Fig. 8. Activity of the leg muscles during forward and backward walking.**

**A:** EMG recordings from the protractor and the retractor muscles during forward and backward walking as indicated. Vertical grey bands emphasize the periods of discharges of the protractor and retractor muscles during forward and backward walking, respectively.

**B:** Schematic illustration of the activities of the leg muscles, their names are indicated, during forward and backward walking. Grey shaded area is the swing phase starting at lift-off (LO) and ending at touch-down (TD). Remaining white area is the stance phase. Both are labeled in the panels of B. Note that the protractor and the retractor muscle exchange their working regimes when a switch from forward to backward walking takes place but the activity of the other muscles with regard to the stance and swing phase remains the same [adapted from Rosenbaum et al. (2010) with permission].
the INs IN1 and IN2, we can now understand why this is happening. Just before the switch, CPG neuron C1 (blue) can still evoke a short discharge (of one action potential) in the protractor MN (red), since IN1 (blue) is at rest. Because, at the same time, IN2 (red) is activated by C1, the retractor MN (blue) is inhibited. However, when the switch occurs, C1 starts activating IN1; hence, the protractor MN is inhibited. However, IN2 remains active after the switch because of the early switch-off of the excitatory input from the CPG neuron C1. It continues to remain in this state, since meanwhile the switch has taken place, and, now, the CPG neuron C2 activates it (a tiny peak in the voltage trace of IN2). [A detailed analysis of this type of neuron models can be found in Daun et al. (2009).]

As a result, the retractor MN remains silent for exactly one period, whereas the protractor MN starts firing already for the first time after the switch (cf. box in Fig. 11). It should be pointed out that the patterns of the angular movement $\alpha$ presented in these examples are not during backward walking the retractor muscle activity occurred when the tarsus was in the air (Fig. 10A, box right box). Our model is in agreement with the experimental data: the activity of the retractor MN coincided with the stance phase when simulating forward walking (Fig. 10B, left), and it coincided with the swing phase, when simulating backward walking (Fig. 10B, right).

In the stick insect, the switch to backward walking coincided with a short EMG activity of the retractor muscle (Fig. 10A, middle box, EMG trace) during the stance phase, followed by an EMG activity of full length in the swing phase. In the model, too, a similar process takes place at switch: a short activity of the retractor MN drives the angular movement $\alpha$ during the stance phase, and a full length MN burst occurs during the swing phase still moving $\alpha$ towards the posterior extreme position of 128°. However, in Fig. 10B, the activity of the protractor MN is also displayed (Fig. 10B, 3rd trace in red). It shows that the protractor MN remains silent during the transient period. This is a prediction of the model that needs to be tested in experiments.

It is, of course, possible to simulate the switch in the opposite direction: from backward to forward walking. Figure 11 shows the results of these simulations. In this case, the roles of the MNs are exchanged. A short activity, in fact, a single action potential, of the protractor MN can be seen just before the switch to forward walking takes place during the stance phase. This is followed by a full burst of the same MN, which completes the transition to forward walking. The retractor MN remains silent during this transient period. If we make use of the activity of the INs IN1 and IN2, we can now understand why this is not
DISCUSSION

In this study, we have presented a neuromechanical model that integrates neuronal activity and mechanical movement of an extremity, based on data from the stick insect. It consists of two neuromuscular systems: the LD and the PR system, which are synaptically coupled. More precisely, the LD system excites the PR system shortly before the start of the stance phase of a step via an excitatory synaptic pathway. The output units of the neuronal network are the four MNs, which control the activity of the muscles they innervate. This control works through the neuromuscular coupling, which is part of the model and described above. The muscle forces controlled by the MN activity generate the mechanical movement of the femur characterized by the time functions of the angles $\alpha$ (PR system) and $\beta$ (LD system). By means of this model, we could study how changes in the neuronal activity affect the mechanical movement of the femur. We successfully simulated the coordination of the muscle activities during stance and swing phases under different behavioral conditions. In particular, the model is capable of doing this coordination both during forward and backward stepping according to the actual requirements of the movement. Currently, ours is the only model that can produce both forward and backward stepping and switching between them, and this provides a possible explanation as to the underlying physiological mechanisms.

However, the femur-tibia joint, together with the tibia and the flexor-extensor muscle system, is missing in our model and so is the sensory information that is conveyed from the sense organs of this joint, most notably from the femoral chondral organ, to the LD system, and helps drive it. This omission is nevertheless admissible because 1) this information from the flexor-extensor system is the same irrespective of the walking direction; 2) the missing sensory information (drive) is compensated for in the model by using an autonomously oscillating CPG in the LD system; and 3) the mechanical movement of the tibia remains unchanged whether the animal walks forward or backward (Rosenbaum et al. 2010).

Also the effect of gravitation was neglected in the mechanical models. Consequently, the limb in the model does not carry the load of body, and therefore the leg cannot sense mechanical loading and unloading from other legs. Since we, in the present study, are concerned with the movement of one leg, only, the lack of these effects does not put any serious limitations on the physiological relevance of our model.

Interpreting the Simulation Results

Walking, expressed by the time courses of the two angles $\alpha$ and $\beta$, showed the appropriate stance and swing phases that had been observed in an intact stepping middle leg of the stick insect. This fact is especially lucidly demonstrated as an animation in the Supplementary Materials (available online at the J Neurophysiol website). The successful simulations are due to two main factors: 1) the proper workings of the neuromuscular coupling in all four muscle types, including the appropriate choice of the stationary values of the elasticity moduli ($k_p$, etc., cf. Fig. 5), and 2) a physiologically reasonable way of coupling between the neuronal networks of the LD and PR systems. The latter determines the phase relations between the two subsystems, the former the proper timing and time course of the muscle contraction. Together they ensure that the correct phase relations arise between the forward-backward and the up-down movement of the femur (cf. Fig. 10).

The simulations have also revealed how mechanical signals (angles and forces), and neuronal signals are synchronized within the whole system (cf. Figs. 6–7, 10–11). Our model predicts accordingly that each phase of the locomotion (stance or swing) is initiated by a fast and large transient force (cf. Fig. 7). At present, there are still some technical hurdles to overcome, measuring such forces in the stick insect. However, as soon as such measurements become practical, and will be carried out, this will also become an important test for the correctness of our model.
It is an important achievement of our model that it is able to explain the rapid switch from forward to backward walking and vice versa. The model is in very good agreement with the experimental results so far. The switch in the stick insect takes place almost promptly, with no long transitional period (cf. Fig. 10A), which is well reflected in the corresponding simulations (Figs. 10B and 11). Moreover, in the model, the switching in either direction is brought about by just a single central (synaptic) command signal to the PR system (to SF or SB in Fig. 9) with no change in the activity of any of the CPGs. Here, our model makes an important prediction, too, concerning the activity of the PR MNs during the switch. The activity pattern of the retractor MN can partly be verified from the experimental records during switching from forward to backward walking but the behavior of the protractor MN in the experiment remains unknown. Specific experiments aimed at investigating this point will be needed to verify or reject the model’s predictions.

We should especially like to emphasize that we did not implement the switching from forward to backward walking in the model by modifying the CPG activity, which means that we did not reset the activity of the oscillator driving the MNs and ultimately the muscles of the ThC joint. A change of the MN activity through a change of the oscillatory state of the CPG would have produced a transient time exceeding by far the stepping period (~0.5 s). Such a long transient time between changes of the direction of the movement was not observed in the experiments. During curve walking of the stick insect, for instance, several step-to-step switches from forward to backward stepping of the middle leg, and back, can occur within a short period of time (Gruhn et al. 2011). By redistributing the CPG output to the MNs via the layer of INs, IN1 and IN2 in the model, instead of changing the CPG activity itself, we achieved almost instantaneous changes of the direction of the movement in the model. The modulation of the MN activity via the INs IN1 and IN2 allows thus fast changing motor patterns during complex stepping patterns that may last a few cycles, only. Recent data by P. Rosenbaum (personal communication) on forward/backward motor patterns in a stepping middle leg with deafferented and deafferented ThC joint suggest that the “choice” of direction is centrally determined. To test our hypothesis concerning the switching mechanism between forward and backward stepping, experiments should be performed in which the protractor and retractor MN activity as well as that of interneuron E4 are simultaneously recorded during forward and backward stepping of the middle leg. Since E4 is known to be part of the CPG related to the ThC joint, its activity would determine whether our hypothesis could be accepted.

Comparison with Other Models

Besides theoretical models on the coordination of multiple legs, which are based on behavioral data (Cruse 1990; Graham 1977; Wendler 1968), there exists a large number of models that are also based on neuronal networks controlling the mechanical movement of the extremities (e.g., Cruse et al. 1998, 2000; Dürr et al. 2004; Schilling et al. 2007; von Twickel et al. 2011). The network models these studies employ consist of artificial neurons related only vaguely to their biological counterparts in the nervous system of insects (e.g., Cruse et al. 1998, 2000; Schilling et al. 2007; von Twickel et al. 2011). However, they are well suited to the questions these authors investigate, for example, description and reproduction of the behavior observed in the animal (e.g., Cruse et al. 1998, 2000; Schilling et al. 2007). Other studies aim at deriving various network topologies with putative biological relevance to produce stable locomotion (von Twickel et al. 2011).

In a different type of models, Ekeberg et al. (2004) designed a neuromechanical one for the control of the stick insect leg muscles, as well as a basic controller architecture for single- and single-leg movement during stepping for the cat hind leg (Ekeberg and Pearson 2005). On the basis of those models, they could verify 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. For the purpose of their studies, it was therefore appropriate for them to make use of artificial bistable control systems and not of biologically more relevant CPGs. Moreover, it was not the authors’ intention to explain adaptive changes in the locomotor activity, e.g., during backwards stepping, by means of their models.

In a third group of models, neuronal ensembles, such as CPGs, are modeled as coupled phase oscillators, for example, in the case of the locomotion of the salamander: Ijspeert et al. (2007), or of the cockroach: Holmes et al. (2006). In such models, a direct correspondence between these elements and biological neuronal networks is somewhat problematic, since the parameters of those models, e.g., the ones of the phase oscillators and the couplings, are in no direct relationship to experimentally measurable physiological quantities.

Our approach is somewhat different in that we adhere to a closer biological correspondence of our model. We therefore use neuron models that are based on biophysical properties of real neurons, such as voltage-gated ion channels and synapses in the spirit of Hodgkin and Huxley (1952). Consequently, we have spiking MNs (Schmidt et al. 2001) and nonspiking INs (Büschges 1995, 2005) in the neuronal network model, mirroring the findings of the experiments. The network topology of our model reflects the experimental findings from stick insects (Borgmann et al. 2012; Büschges 1998, 2005). The neuromuscular coupling is also based on neurophysiological principles, even though this part of the model is admittedly a grossly simplified version of the reality. Thus our network model is closer to its biological counterpart than the aforementioned ones. As far as the mechanical components of the model are concerned, they are strong simplifications of the anatomy in the stick insect but they produce agreement with the findings by Hooper et al. (2009), which state that the torques due to passive mechanical coupling can be neglected in small animals, in particular, in the stick insect locomotor system. This has enabled us to mechanically decouple the two mechanical systems, LD and PR, and yet, to obtain satisfactory results for the mechanical movements.

Our model uses both an autonomously oscillating CPG (LD system) and a CPG, which is itself not in the oscillatory regime but can be, and is driven by external signals to exhibit oscillatory behavior (PR system). This model thus occupies a midway position in the chain of existing models that starts with models using autonomous oscillators only (e.g., Ijspeert et al. 2007) and ends with those using solely nonoscillating reflex chains (e.g., Cruse et al. 1998). However, our model is unique.
in that it is currently the only one which is capable of simulating forward and backward stepping and the switch between them.

All the advantages of our model notwithstanding, it is evidently clear that this model is still incomplete. One reason for this is that the sensory signals controlling the PR system are lumped together. An individual treatment of these signals of different modality (load, motion, ground contact) needs to be included into the model at a later stage. Another shortcoming that should also be remedied is that the extensor-flexor neuromuscular system that moves the tibia at the femur-tibia joint is missing. Even so, some important properties of the leg joint coordination during locomotion can be studied by means of this model. The results may thus have a real bearing on our understanding of the functional mechanisms of locomotion in the stick insect itself, and possibly in other insect species, too.

APPENDIX: IMPLEMENTATION OF THE NEUROMUSCULAR COUPLING IN THE MODEL

Once the stationary values of the spring constants have been determined, they can be used to calculate their actual values during contraction. In model of the neuromuscular coupling, the actual contraction is determined by the last action potential from either of the two antagonistic MNs. Thus, if, for example, the last action potential was evoked in the depressor MN, then the stationary values of \( k_D, k_L \) become those that correspond to the angle in the lowest position of the femur. A change of the stationary values of the elasticity moduli takes only place, if the last two action potentials were of different origin. In this example, a change of the stationary values of \( k_D, k_L \) occurs, only, if the action potential preceding the last one from the depressor MN was fired by the levator MN. The spring constant \( k(t) = u(t) \) still obeys the Eqs. 3–4, but the final value \( k_\text{f} \) has changed. Figure A1 illustrates the temporal relations when two subsequent action potentials are of different origin, hence a change of the final values of \( k_D, k_L \) occurs. We note that discrete time is used due to the numerical procedure. The distance between the two consecutive output times is \( t \) (output step size). In the case illustrated, the latest action potential has been evoked in the depressor MN, Since it falls, between two latest output times \( t - \Delta t \) and \( t \) of the computational procedure, it will be recognized as a new one. Because the preceding action potentials from the two antagonistic MNs are kept track of, it can be determined that the actual and the preceding action potential are of different origin, hence the final values of the above parameters will be changed accordingly to the MN type that fired last, in this case the depressor MN. Before this change takes place, the values of the above parameters are computed at time \( t_{\text{old}} \) which is the “base” time \( t_0 \) value in Eq. 3) for the new set of final values of \( k_D, k_L \).

Fig. A1. Illustration of the temporal relations when two subsequent action potentials are of different origin. \( t_{\text{old}} \) onset of an action potential of the levator MN; \( t_{\text{old}} \) onset of an action potential of the depressor MN; \( t \) actual output time of the computational procedure; \( t - \Delta t \), preceding output time of the computational procedure.

ACKNOWLEDGMENTS

We thank Drs. A. Büschges, M. Gruhn, and J. Schmidt for valuable discussions of the manuscript.

GRANTS

This work was funded by the Deutsche Forschungsgemeinschaft Grant DA1182/1-1. We thank the Department of Animal Physiology for start-up support of the Emmy Noether Group.

DISCLOSURES

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

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A behavioural analysis of the temporal organisation of walking

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