A neuro-mechanical model for the neuronal basis of curve walking in the stick insect

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October 24, 2012

Abstract

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, 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, 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 neuro-mechanical 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 neuro-mechanical 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.

1 Introduction

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 in order 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; Zill et al. 2009; Zill et al. 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 neuro-muscular level by recording EMG activity, intracellular and extracellular electrical activity of motoneurons (MNs) (Büschges, 1995; Büschges et al., 2004; Ritzmann and Büschges, 2007; Büschges et al., 2008; Rosenbaum et al., 2010). However, 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 neuro-mechanical 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 insects 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 paper, 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) 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 be-
tween the neuro-muscular 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.

2 Methods

2.1 Experiments

2.1.1 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 12/12h 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 Corp., Tokyo, Japan) on it.
2.1.2 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 (3x5x100mm, W x H x 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 approximately 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.

In order 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 in order 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 (fCO) and its tendon, the retractor unguis I muscle and its tendon, the nervus cruris, and the F2 nerve were removed.

2.1.3 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. In order 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 1401k II, CED, Cambridge, UK), digitalized using Spike2 (Vers.5.05, CED, Cambridge, UK), 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-033C, Allied Vision Technologies, Stadtroda, Germany) at 100 fps 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 Farbmühle, 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 (12V AC/DC, Conrad Electronic, Germany). 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 $\gamma$ and the corresponding angular velocity is displayed in Fig. 5A-B.

### 2.1.4 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 $\sim 35\%$ of the entire femur length) and in the medial part of the femur (at $\sim 50\%$ 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: Godlewska (2012)). Length measurements were carried out at the following FTi-joint angles: $0 \pm 3^\circ$ (tibia maximally extended), $90 \pm 3^\circ$ (tibia perpendicular to the longitudinal axis of the femur) and $150 \pm 3^\circ$ (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, USA) solution or methylene blue (Merck KGaA, 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
OriginPro.8.5.0 (OriginLab Corporation, Northampton, MA, USA) 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.

2.2 The model

The protractor-retractor (PR) and levator-depressor (LD) neuro-mechanical 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 flexor-extensor (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 neuro-mechanical 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 the next subsection. Then, detailed consideration of the FE neuro-mechanical system will follow.
2.2.1 Modified moment of inertia in the protractor-retractor and levator-depressor mechanical systems

The preceding arguments enabled us to treat the 3 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 $\gamma$

$$\hat{I}_{FT}(\gamma) = I_F + I_T + m_T l_F^2 + m_T l_T l_F \cos \gamma$$

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

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

$$I_{FT} = I_F + I_T + m_T l_F^2 + m_T l_T l_F \frac{\sin \gamma_{\text{max}} - \sin \gamma_{\text{min}}}{\gamma_{\text{max}} - \gamma_{\text{min}}}$$

Its numerical value together with those of the masses and lengths, all being our own measurements, is given in Table 2.
2.2.2 The flexor-extensor system integrated in the full model

Fig. 1 shows the three neuro-mechanical 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 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 reasoning 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 $g_{app5}$ and $g_{app6}$ 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 neuro-muscular 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 intra-joint coupling mediated through position signals from the femoral chordotonal organ (fCO). All neurons in the network were modeled according to the Hodgkin-Huxley formalism (Hodgkin and Huxley,
The CPG neurons and the INs are non-spiking, while the MNs are spiking neurons (cf. Daun et al., 2009; Daun-Gruhn and Toth, 2011).

2.2.3 Equation of the mechanical motion of the flexor-extensor system

Fig. 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 the figure. 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 $CE$ and $TE$, and $CF$ and $TF$, 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 $EG = h$. The fiber is fixed to the tendon at point C, and to the cuticle at point G. In this position, it has length $l_0$, and its angle with the tendon is $\phi_0$. If the muscle contracts (with a force $F_m$), point C of the muscle fiber at the tendon will be shifted to point D, due to the force $F_p$ parallel to the tendon. The angle between tendon and fiber at D is $\phi$. The angle $\gamma$ 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° and 150°, 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 $h_E = 0.34$ 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

$$I_T \ddot{\gamma} = F_{pF} \cdot 2d \sin \gamma - F_{pE} \cdot d \sin \gamma + M_v$$

with the moment of inertia $I_T$, the parallel forces $F_{pF}$ and $F_{pE}$ 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:

$$M_v = 2dF_{vF} + dF_{vE}$$

$$= -2db_v v_F - db_v v_E$$

$$= -4d^2 b_v \dot{\gamma} - d^2 b_v \ddot{\gamma}$$

$$= -5d^2 b_v \ddot{\gamma}$$

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

$$\ddot{\gamma} = \frac{d}{I_T} [(2F_{pF} - F_{pE}) \sin \gamma - 5b_v d^2 \ddot{\gamma}]$$

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

$$F_{pF} = F_{mF} \cos \phi_F$$

$$F_{pE} = F_{mE} \cos \phi_E$$
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); Guschlbauer (2009), the muscle forces are quadratic functions of the muscle length:

$$F_{mF} = k_F(l_F - l_{Fmin})^2$$  \hspace{1cm} (9)

$$F_{mE} = k_E(l_E - l_{Emin})^2$$  \hspace{1cm} (10)

$l_{Fmin}$ and $l_{Emin}$ 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

$$l_F(\gamma) = \sqrt{l_{F0}^2 + s^2_F(\gamma) - 2l_{F0}s_F(\gamma) \cos \phi_{F0}}$$  \hspace{1cm} and  \hspace{1cm} (11)

$$l_E(\gamma) = \sqrt{l_{E0}^2 + s^2_E(\gamma) - 2l_{E0}s_E(\gamma) \cos \phi_{E0}}$$  \hspace{1cm} (12)

with $\cos \phi_{F0} = \sqrt{1 - (h_F/l_{F0})^2}$ and $\cos \phi_{E0} = \sqrt{1 - (h_E/l_{E0})^2}$ and the shifts $s_F(\gamma) = -2d \sin \gamma$ and $s_E(\gamma) = d \sin \gamma$. $l_{F0}$ 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 $\dot{\gamma}$ and $\ddot{\gamma}$ vanish at the switch points, and we get the following relation for the spring constants from eqn 6:

$$a = \frac{k_F}{k_E} = \frac{1}{2} \frac{(l_E - l_{Emin})^2 \cos \phi_E}{(l_F - l_{Fmin})^2 \cos \phi_F}$$  \hspace{1cm} (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. In order to determine the absolute values of the spring constants, we have, however, to resort to computer simulations.

2.3 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.

3 Results

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

3.1 Neuronal and mechanical properties of the single, isolated flexor-extensor 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 ($l_{E\text{min}}$, $l_{F\text{min}}$, $l_{E0}$, $l_{F0}$, and $\phi_{E0}$, $\phi_{F0}$), 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 $b_v$ 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 2.

Our experimental results show high variability in the values of the extreme leg positions, hence in the angular range for $\gamma$ ($\gamma_{extF} \in [100^\circ, 130^\circ]$ and $\gamma_{extE} \in [40^\circ, 60^\circ]$). The choice of $\gamma_{max} = 110^\circ$ and $\gamma_{min} = 45^\circ$ was made in order 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, $\gamma = \gamma_{max} = 110^\circ$, $a = a_F = 0.5808$.

Fig. 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 the bottom trace 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 approximately 1:1. In the model, this is achieved by setting $g_{app5} = 0.2095$ nS and $g_{app6} = 0.1000$ 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
panel 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. 5A-B. We adjusted our model to the experimental data by setting the conductances of the input currents to the CPG to $g_{app5} = 0.1895 \text{ nS}$ and $g_{app6} = 0.1200 \text{ nS}$. With this choice, the simulations (Fig. 5C and D) satisfactorily reproduced the experimental data of sideward stepping in the stick insect (Fig. 5A and B). Note that the values of all other parameters of the FE network were left unchanged.

### 3.2 Neuro-mechanical 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 neuro-mechanical behavior of its biological counterpart. Here, we integrate this model into that of the previously existing neuro-mechanical 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). In order 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 (c.f. Fig. 1). It can be interpreted as sensory input from the fCO, which measures angular change of the femur (Büsches, 2005). If the angle in the FTi-joint exceeds a certain value, which is $\gamma_{thF E} = 90^\circ$, 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.

### 3.2.1 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. Fig. 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 upper 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 the Supplementary Material, an animation illustrates these switches in the middle leg (Suppl. 1).

3.2.2 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 $\alpha_0 = 102^\circ$. As mentioned earlier (cf. subsection 3.1), 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 subsection 3.1. 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 supplementary video (Suppl. 2) shows the switch from forward to sideward stepping of a single middle leg.

### 3.3 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 neuro-mechanical system of the three leg joints could produce the required intra-leg coordination, we carried out “pseudo-dynamical” 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. In order 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 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.
3.3.1 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. Fig. 9A shows a sequence of screen shots during the simulation. The full video can be found in the Supplementary Material (Suppl. 3). Fig. 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.

3.3.2 Turning generated by temporary switching to sideward stepping

Again the simulated stick insect started walking forward. After the same number of steps as in 3.3.1, the left middle leg switched to sideward stepping. The right middle leg continued stepping forward, but the left middle leg pulled the body to the inner side of the curve. This curve had a larger radius than the one in the former case. After the same number of steps as before, the left middle leg switched back to forward stepping, and the stick insect continued walking straight. Fig. 9B displays a sequence of screen shots of the simulation (see also supplementary file Suppl. 4). Comparing the trajectory of this turning movement with that of the preceding one, one can see the clear difference in the turning paths (red vs. green curve) resulting in different turning angles. The directions of the straight walking in the final
part of the trajectory (black lines) differ in the two cases quite remarkably. While the angle of turning is much larger in the former case, the walking distance is much longer in the latter one at the same number of steps in both cases.

4 Discussion

In this paper, we have presented a neuro-mechanical model which 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; Büschges and Gruhn, 2008; Büschges et al., 2011).

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 in order to account for the effects of the fCO. 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 in order 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. subsection 3.1) 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 in order 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 intra-segmental 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 $\beta$ whose threshold values 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 two points: i) the afferent signals of different modality eventually converge on pre-motor or pre-CPG neurons acting in their entirety; ii) 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 iii) the locomotion 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 neuro-muscular 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 paper, we have put emphasis on the neuronal
control of the middle leg movement, 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.

4.1 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 neuro-mechanical 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.

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 neuro-muscular 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 turning 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 non-oscillating units driven by sensory input signals. However, a non-oscillatory 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 non-oscillating 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.

4.2 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 neuro-muscular 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 neuro-robotics. First, it is built of nearly identical units: the neuro-mechanical systems of the three joints. Second, putting it in the language of this field, it uses low-dimensional control signals ($g_{sb}$, $g_{sf}$, $g_{app5}$, $g_{app6}$) 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: i) it may contribute to a better understanding of the biological mechanisms of locomotion in the stick insect, and perhaps in other insects; and ii) it may help construct biologically inspired robots that are more effective in performing locomotor tasks.

Acknowledgments

This work was supported by the DFG grant to S. Daun-Gruhn (DA1182/1-1) and to A. Büschges (Bü857/8-1 and Bü857/9-1).

We should like to thank A. Büschges and M. Blümel for valuable discussions on the manuscript.

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Smith R. http://www.ode.org


Supplementary Materials

Animations of the graphical results were implemented by using the software package ‘Open Dynamic Engine’ (ODE) (Smith, 2006). As input signals, the time courses of the angular movements $\alpha$, $\beta$ and $\gamma$, which were computed by the model, were fed into ODE. Thus ODE carried out only a visualization task, and was not used for a full dynamical simulation. The supplementary videos are slowed down by a factor of 2.5, i.e. a stepping cycle lasts about 1.25 s, in order to enable the viewer to study in more detail the coordination of the leg joints during stepping.

Supplementary video S1 shows a model stick insect attached to a horizontal slider (1.5 cm above the ground). Thus the (animated) insect is confined to forward or backward walking. It can neither fall onto the ground nor step sideways, nor rotate about the slider axis. There is friction between the tarsus and the ground. This enables propulsion of the body but it has no effect on the neuro-mechanical processes producing the angular movements of the leg. The sequence begins with forward walking (9 steps), continues with backward walking (7 steps), and finishes with forward walking (5 steps).

Supplementary video S2 shows a model stick insect attached to a vertical slider, i.e. it can only change height. The lower thorax height (z-coordinate) is 1.5 cm above the ground. There is no friction between the ground and the tarsus of the animated stick insect (virtual slippery surface). Mechanical motion takes place at the FTi- and the CTr-joint. The ThC-joint is fixed at
Supplementary video S3 shows a free walking model stick insect. The front and hind legs are fixed, and there is no friction between them and the ground. Friction is present, however, between the ground and the middle legs. They are coupled such as to have a phase shift of half of a period between them. The left middle leg walks forward 10 steps, then it switches to backward walking (12 steps) and finishes by walking forwards 10 steps. The right middle leg performs forward walking, only, all this time.

Supplementary video S4 shows an animation similar to that in S3 with the difference that the middle leg switches to sideward walking.

Figure legends

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. $g_{app1}$, $g_{app2}$, $g_{app3}$, $g_{app4}$, $g_{app5}$, $g_{app6}$: central excitatory inputs to the CPG neurons; $g_{d1}$, $g_{d2}$, $g_{d5}$, $g_{d6}$, $g_{d9}$, $g_{d10}$: 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, flexor muscles in the model innervated by the corresponding MNs. β-hexagon in the LD system: combined sensory signal originating in the LD system and conveyed to the PR and FE system; γ-hexagon in the FE system: inhibitory signal from the femoral chordotonal organ counteracting the excitatory signal from the LD system.

Fig. 2 A: Front view of the trochanter-femur and the tibia with the flexor
and extensor muscles (modified from Bässler, 1983). B: geometric arrangement of the flexor and extensor muscles that move the tibia. The extensor tendon $T_E$ is fixed to the tibia at point A, and the flexor tendon $T_F$ at point B. The extensor muscle fibers (thick oblique lines), arranged in parallel, mechanically connect $T_E$ with the cuticle of the extensor $C_E$. Similarly, the flexor fibers do so between $T_F$ and the flexor cuticle $C_F$. The tibia rotates, with angle $\gamma$, about the axis at point $O$. This axis is perpendicular to the plane of the figure. C: Geometrical arrangement of a single muscle fiber between tendon and cuticle, and muscle forces. The fiber is fixed to the cuticle at point $G$. $l_0$: length of the muscle fiber when its other end is at position $C$ (reference length); $l$: its length at point $D$ (generic length); $h$: distance between tendon and cuticle; $\phi_0$ and $\phi$: angles corresponding to the positions at $C$ and $D$, respectively. $F_m$: muscle force in the fiber at point $D$ (length $l$); $F_p$: parallel component of $F_m$ moving the tendon.

**Fig. 3** Boxplots of the distance $h$ between tendon and cuticular edge vs. the angle at the FTi-joint for the medial and the proximal regions of the muscles for three different flexion angles ($0^\circ$, $90^\circ$ and $150^\circ$). A: extensor tibiae muscle, B: flexor tibiae muscle. In each box; data were obtained from the same 6 animals, Upper edge: 75 percentile; bottom edge: 25 percentile; line: median; small black square: mean value.

**Fig. 4** Simulation results obtained with the model of a single, isolated FTi-joint. Time course of the angle $\gamma$ describing the mechanical movement of the tibia (top panel); the simulated angular velocity $\gamma_{vel}$ (second panel); corresponding extensor motoneuron activity (blue, third panel); flexor motoneuron activity (red, fourth panel); and CPG activity (bottom panel).

**Fig. 5** A: angle and B: angular velocity of the tibia movement in the experiment; C and D: the corresponding variables in the simulations.
Fig. 6 Time courses of the three joint angles $\alpha$ (ThC joint, upper panel), $\beta$ (CTr joint, middle panel) and $\gamma$ (FTi joint, bottom panel) in the model of a stick insect’s middle leg. Arrow at $t = 6000$ ms: switch from forward to backward walking; arrow at $t = 9250$ ms: switch from backward to forward walking. The 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.

Fig. 7 Proposed neural switching mechanism between forward and backward stepping. The upper part of the protractor-retractor system is shown (cf. Fig. 1) complete with a small, CPG-like control network consisting of the mutually inhibitory neurons SF and SB that brings about the switch between the directions of movement. Small filled circles on excitatory synapses are presynaptic inhibitions. They control the connections between the CPG and the premotor interneurons IN1 and IN2. Note that the CPG neurons are here connected to both premotor interneurons: ”parallel” and ”cross” connections. If the neuron SF is active, the ”cross” connections between the CPG and the premotor interneurons are presynaptically inhibited, and the ”parallel” ones are active. Neuron SB is also inhibited, and the presynaptic inhibition to the ”parallel” connection is therefore inactive. Hence, normal forward stepping takes place. If SB is active, the ”parallel” connections will be blocked and backward stepping will emerge. From Toth et al. (2012) with permission.

Fig. 8 Mechanical movement and neuronal activity in the PR system before and after fixing the retraction position of the femur, i.e. the angle $\alpha$. The command to keep $\alpha$ constant arrives at $t = 4690$ ms. The stationary retraction angle is $\alpha = 102^\circ$. The time functions shown are as indicated at the individual panels. For more explanation on the neural control mechanism
that sets the stationary value of the angle $\alpha$, see text.

Fig. 9 Curve walking of the simulated stick insect in two different modes. A: curve walking with backward stepping; B: curve walking with sideward stepping. Only the middle legs are driven actively by angle vectors $\{\alpha(t), \beta(t), \gamma(t)\}$ on either side of the simulated insect. The two signal vectors are set to have a phase difference of half of a stepping period. The other four legs are passive, and kept in fixed positions; they stabilize the trunk during movement. In the first two panels from top to bottom, forward walking is performed. In the 3rd slide from the top, backward (A) or sideward (B) stepping ensues. This continues in the subsequent two panels, producing the change of direction of the movement. Finally, in the bottom panel, forward walking resumes.

Fig 10: Trajectory of the simulated stick insect walking in the plane. The trajectory describes the movement of the center of the body. Blue line: forward walking (identical for both turning modes); red line: backward stepping of the inner middle leg during turning; green line: sideward stepping of the inner middle leg during turning; black lines: forward walking after turning. The trajectories now differ as a result of the different turning modes used. It is easily seen that turning with backward stepping produces a much sharper turn than that with sideward stepping.
Table 1: Parameters in the muscles used in the simulation. The 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 FTi-joint. For further explanations, see Results.

<table>
<thead>
<tr>
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<th>Extensor</th>
<th>Flexor</th>
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<tbody>
<tr>
<td>Minimal length of the fiber</td>
<td>$l_{E,\text{min}} = 1.05 \text{ mm}$</td>
<td>$l_{F,\text{min}} = 1.50 \text{ mm}$</td>
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<tr>
<td>Length of the fiber at $\gamma = 90^\circ$</td>
<td>$l_{E,0} = 1.41 \text{ mm}$</td>
<td>$l_{F,0} = 2.11 \text{ mm}$</td>
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<tr>
<td>Angle between tendon and muscle fiber at $\gamma = 90^\circ$</td>
<td>$\phi_{E0} = 13.5^\circ$</td>
<td>$\phi_{F0} = 12.6^\circ$</td>
</tr>
<tr>
<td>Distance between cuticle and tendon</td>
<td>$h_E = 0.34 \text{ mm}$</td>
<td>$h_F = 0.42 \text{ mm}$</td>
</tr>
<tr>
<td>Spring constants for the extension</td>
<td>$k_E = 2700 \frac{\text{mN}}{\text{mm}^2}$</td>
<td>$k_F = 36.83 \frac{\text{mN}}{\text{mm}^2}$</td>
</tr>
<tr>
<td>Spring constants for the flexion</td>
<td>$k_E = 340 \frac{\text{mN}}{\text{mm}^2}$</td>
<td>$k_F = 197.47 \frac{\text{mN}}{\text{mm}^2}$</td>
</tr>
<tr>
<td>Viscosity of the muscle</td>
<td>$b_v = 12.5 \frac{\text{g}}{\text{s}}$</td>
<td>$b_v = 12.5 \frac{\text{g}}{\text{s}}$</td>
</tr>
<tr>
<td>Distance of tendon mounting and rotation point</td>
<td>$d = 0.28 \text{ mm}$</td>
<td>$2d = 0.56 \text{ mm}$</td>
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Table 2: Parameters of the tibia segment used for the simulation. The parameter values in this table are our own measurements and calculations. For further explanations, see Methods.

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<tr>
<td>Minimal angle</td>
<td>$\gamma_{\text{min}} = 45^\circ$</td>
</tr>
<tr>
<td>Maximal angle</td>
<td>$\gamma_{\text{max}} = 110^\circ$</td>
</tr>
<tr>
<td>Femur mass</td>
<td>0.006 g</td>
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<tr>
<td>Femur length</td>
<td>12 mm</td>
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<tr>
<td>Tibia mass</td>
<td>0.002 g</td>
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<td>Tibia length</td>
<td>12 mm</td>
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<tr>
<td>Momentum of inertia of the tibia</td>
<td>0.096 gmm$^2$</td>
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<tr>
<td>Corrected value of the momentum of inertia</td>
<td>0.288 gmm$^2$</td>
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PR control network

LD control network

FE control network
Figure 2:
Figure 3:
Figure 4:

Figure 5:
Figure 6:

Figure 7:
Figure 8:
Figure 9:
Figure 10: