Coactivation of leg reflexes in the stick insect

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Abstract. Each leg of a standing stick insect acts as a height controller. The leg contains several joints. Most of these joints are known to be controlled by feedback loops which are the basis of resistance reflexes (review Bässler 1983). This leads to the question of whether the resistance reflex of the whole leg can be understood as a simple, vectorial sum of the individual reflexes provided by the different joints, or whether additional properties emerge by simultaneous stimulation of several joints. Force measurements were performed while passively moving the middle leg tarsus of a fixed stick insect (Carausius morosus) stepwise to different positions. From the dynamic and static forces the torques developed by each joint were calculated. They were compared with the torques developed when only a single joint was moved by the same amount. The comparison shows that for a large range of positions there are no differences between both situations. Differences occur in two cases. First, the muscle system controlling the coxa-trochanter joint seems to be more strongly excited when the entire leg is moved than when only the one joint is moved. This change increases the linearity of the whole system for small deviations from the zero position. Second, the torque developed by the extensor tibiae system for negative steps (corresponding to increased body height), and the levator of coxa and trochanter for positive steps, decreases rather than increases when the whole leg is moved to extreme positions. This contributes to a decrease in the slope of the force-height characteristic and thus to a more non-linear behaviour of the whole system for the extreme positions. It is well known that the amplification factors of resistance reflexes in the leg show a large variation (Bässler 1972a; Kittmann 1991). Our results indicate that any change of the amplification factor influences the reflexes in all leg joints in the same way.

Introduction

The individual joints of a stick insect leg are controlled by negative feedback loops (femur-tibia joint: Bässler 1965, coxa-trochanter joint: Wendler 1972; Schmitz 1985; 1986a, b, thoracic-coxal joint: Graham and Wendler 1981; Schmitz 1985; for a review see Bässler 1983). These controllers are sensitive to velocity and position and can, therefore, in technical terms be called P-D-controllers. These feedback loops cause the resistance reflexes observed when the leg joints are passively moved. In other experiments, where not just an individual joint, but the whole leg is passively moved, or where the height control of the whole animal is investigated, the whole leg acts like a feedback controller with P-D properties (Wendler 1964, Cruse Riemenschneider and Stammer 1989, Kemmerling and Varju 1981, 1982, and in the walking animal: Bässler 1977, Cruse 1976a). The question arises as to whether these properties of the whole leg are merely the sum of the properties of the individual joints of the leg, or whether the movement of the whole leg involves additional mechanisms. In order to answer this question, experiments were performed in which the resistance reflexes of the three leg joints were investigated separately and compared with those when the entire leg is moved. For comparison, the torques developed by the single joints in the latter cases have to be calculated from the total force measured at the leg tip.

Material and methods

Adult female stick insects Carausius morosus were used in these experiments. The experiments were performed at the University of Kaiserslautern and at the University of Bielefeld. In Kaiserslautern the animals were fixed dorsally to a holder by means of dental wax. The longitudinal axis of the body was horizontally oriented. The tarsi of the middle and hind legs were placed on balsa beams. One beam was fixed to a force transducer which could measure the force in either one or two
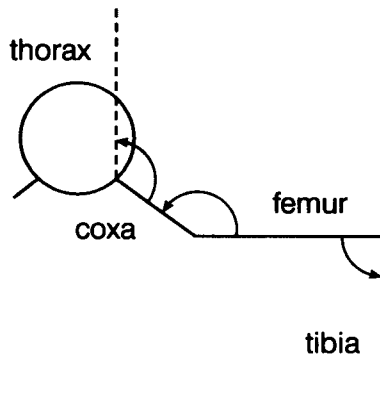
Fig. 1. Definition of the joint angles in the vertical plane. This is the plane of leg movement used in the experimental series two and three

perpendicular spatial directions. By means of micromanipulators the force transducer could be moved to different positions. In this way the leg was first moved to the "zero position". For the middle leg, the results of which are described here, the zero position is defined in the following way (see Fig. 1): the femur is held horizontally, i.e., perpendicular to the vertical body axis, and perpendicular to the long axis of the body. The tibia position is parallel to the vertical body axis. The angle between femur and tibia thus amounts to 90 deg. in the zero position. Starting from this position, the tarsus could be moved by hand using the micromanipulator to other positions. In the Kaiserslautern experiments, the tarsus was moved vertically upwards by either 3, 6, or 9 mm (positive steps) or downwards (negative steps) by -2, -4, or -6 mm. The movement was carried out with a velocity of about 10 mm/s. After this step the tarsus was held in the new position for 4 min. The tarsus was then moved back to the zero position. The forces produced during this step and the position of the force transducer were recorded on a pen recorder (Recomed, Hellige). The latter also served as a control for the velocity of the movement. For each step we evaluated the dynamic force value (the difference between the force exerted before the step and that exerted directly after the step movement was finished) and the static force (the difference between the force before the step and the force 4 min later, i.e., directly before the tarsus was moved back to the zero position). In this paper only the dynamic force values are used for further evaluation. After 4 min at the zero position the next step was performed.

The results obtained in Kaiserslautern are shown in Fig. 6 and indicated by open circles. All other experiments were performed in Bielefeld. They differed in that the animal was fixed to a hard rubber foam (Veneret) holder, and all the legs except the left middle leg were fixed to the holder. The long axis of the body was oriented vertically, i.e. parallel to the direction of gravity. The step amplitudes were $+/-1$, $+/-3$, and $+/-5$ mm in these experiments. The tarsus was fixed to the force transducer by means of sticky wax. Control

experiments showed no significant differences when the tarsus was not fixed by the wax but grasped the balsa beam actively.

In order to measure the forces produced when a single joint is moved individually, the force transducer was mounted on a device such that it could be moved around a circle. The center of the circle was oriented below the axis of rotation of the joint to be investigated. As the thoracic-coxal joint is a ball and socket joint, its movement was split into two perpendicular directions, the movement in the vertical plane (in body coordinates) with the axis of rotation parallel to the long axis of the body (dorsal-ventral movement), and the movement in the horizontal plane (rostral-caudal movement). In the latter case the axis of rotation was parallel to the dorso-ventral body axis. When measuring the reflex of the femur-tibia joint, the femur was fixed to the holder and the tibia was fixed to the force transducer. When measuring the coxa-trochanter joint, the thoracic-coxal joint had to be fixed to the body by means of dental wax to avoid additional movement of this joint. Then the femur was fixed to the force transducer. As the coxa is too short to fix it to a force transducer, the thoracic-coxal joint had to be moved by attaching the force transducer to the femur. To measure the reflex reaction in the vertical plane, the coxa-trochanter joint, which operates in the same plane, was fixed by means of dental wax, and the force transducer was attached to the femur.

A reaction to movements in the horizontal plane of the thoracic-coxal joint was only obtained by moving the whole leg. In this experiment (first series mentioned below), the long axis of the body was also oriented horizontally, and the force transducer was mounted such that it could be moved in a horizontal circle. The centre of this circle was arranged exactly below the thoracic-coxal joint. The tarsus was placed on the force transducer.

The spatial positions of the leg parts in the different positions were measured by means of a binocular. The angles were first measured relative to a body-fixed coordinate system; later, the joint angles were calculated from these data. The variation in the angle values shown in Figs. 2 and 5 is due to two causes; first, to errors occurring when reading the angle values by means of the binocular and, second, to interindividual changes of the angle values because of different limb lengths of the individual animals.

Results

Three series of experiments were performed. In the first series the tarsus of the middle leg was moved, starting from the zero position, forward and backward along a circle around the vertical axis of rotation of the thoracic-coxal joint. In this experiment, the thoracic-coxal joint is mainly moved around its vertical axis of rotation. However, movements occur also around the horizontal axis of rotation in this joint. Figure 2 shows the torques produced in this joint as a function of the
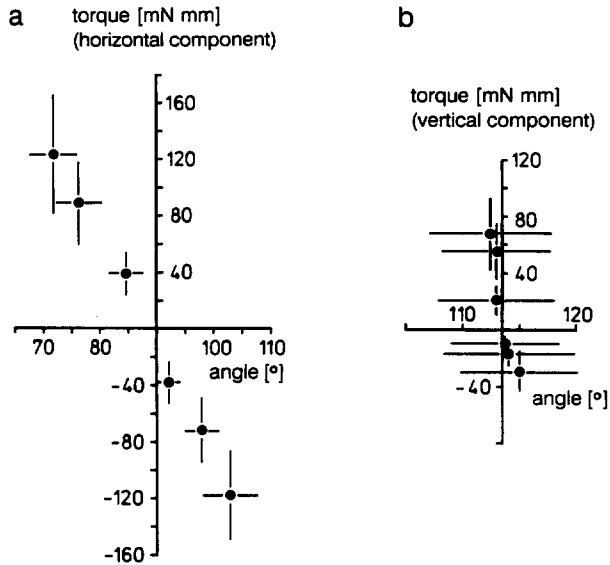
Fig. 2a, b. Torques developed in the thoracic-coxal joint of the middle leg when the tarsus is moved in a circle in a horizontal plane (mean +/−S.D.). **a** ordinate: torque around the vertical axis of rotation, *abscissa*: angle between longitudinal body axis and the projection of the long axis of the coxa in the horizontal plane. Forward movement of the tarsus increases the value of this angle. **b** *ordinate*: torque around the axis parallel to the longitudinal body axis. Abscissa: angle between vertical body axis and the long axis of the coxa. Downward movement of the coxa increases this angle (see Fig. 1). Note that the scale of the *abscissa* of **b** is twice that of **a**

Fig. 3. Slope of the resulting force vector (see Fig. 4a) with respect to a *horizontal line* in a body fixed coordinate system for the six leg positions (mean +/−S.D.). The direction of the vector is neglected. *Open circles*: theoretical values which should have been obtained when no influences occurred from other joints (see text). **b** slope of the resulting force vector (mean of all six leg positions) shown separately for the 19 animals investigated

change of the joint angles. These represent the mean values from 17 animals. In these experiments the coxa-trochanter joint moves less than 2 deg. and the femur-tibia joint less than 5 deg. The results show that the torques produced around the vertical axis of rotation, i.e., those resisting the forward-backward movement of the joint (Fig. 2a), are of the same order of magnitude as those developed by the coxa-trochanter joint and the femur-tibia joint (see Fig. 5b, c). The torques developed by the thoracic-coxal joint around the horizontal axis, i.e., those resisting up-and-down movement (Fig. 2b), are much stronger. This shows that the thoracic-coxal joint is quite stiff for this direction. This result agrees with findings shown in Fig. 5a (the mean start angle is different in both series of measurements).

In a second series the tarsus was moved up and down along a line parallel to the vertical body axis. In this situation, the thoracic-coxal joint is only moved around its horizontal axis of rotation, not around its vertical axis. Thus the axes of rotation of all three joints, of the femur-tibia and the coxa-trochanter joint, and the horizontal axis of the thoracic-coxal joint, are perpendicular to the plane of movement (Fig. 1). This is supported by the fact that the torque around the vertical axis, measured in a control experiment using a differently oriented force transducer, was smaller than 15 mNmm and thus was negligible. The torques developed at the tibia-tarsus joint are less than 10 mNmm and will not be considered here.
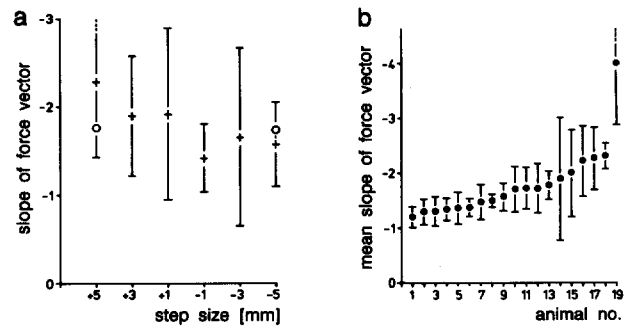
In 19 animals the two force components in the vertical plane (see Fig. 4a, b) were measured for each step. Figure 3a shows the direction of the force vectors (slope of the resulting force vector in the body-fixed coordinate system) varying systematically from positive to negative steps. Figure 3b shows the mean slope of
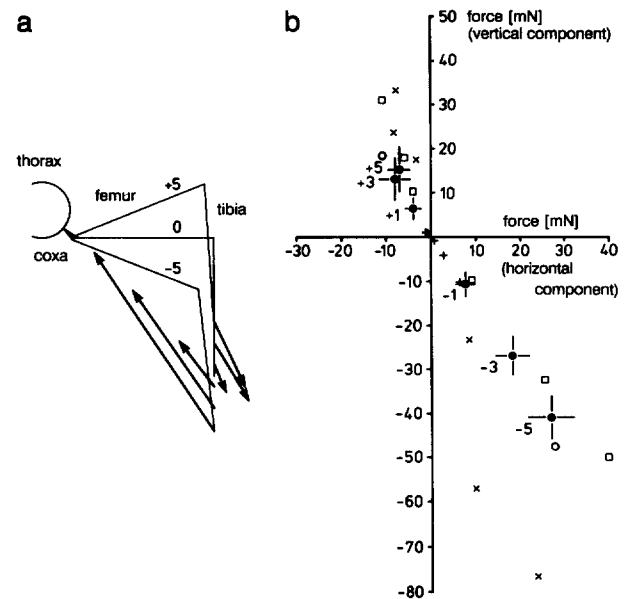

Fig. 4a, b. Mean values of the dynamic force values obtained when the tarsus is moved in vertical direction. **a** The leg in zero position (0) and when moved by 5 mm up (+5) or down (−5). Resulting dynamic forces in a body fixed coordinate system for all six tarsus positions investigated (+1, +3, +5, −1, −3, −5). For scale see **b**. **b** Horizontal and vertical force component after normalization (closed circles). The number indicates the step size in mm. Force components directed to the body and upwards are positive. *Abscissa*: horizontal force component, *ordinate*: vertical force component. The absolute results of three extreme individuals are indicated by separate symbols. Those of the animal with the smallest force values (no. 1, Fig. 3b) are marked by (+); two symbols (□, ×) are used for the two individuals with the highest force values. One of these (×) stands for the untypical animal no. 19 (Fig. 3b). The meaning of the open circles is explained in the Discussion

the absolute direction of the force vectors of each animal. The 19 animals are ordered on the abscissa according to their mean slope. (Later experiments, where the same animals were measured on eight consecutive days, showed that the variation of the mean values shown in Fig. 3b is not due to variation between individuals, as similar variations are found for different experimental sessions with the same animal.)

As is known from earlier investigations (Bässler 1972a; Kittmann 1991), the amplification factor of the femur-tibia joint reflex depends on the inner state of the animal and can vary by a large amount (Bässler found the forces to vary by a factor between 1 and 20). Variation in the amplification factor was also observed in our experiments when measuring the forces by moving the whole leg. Since, with one exception (animal no. 19, Fig. 3b), the force vectors of all animals show about the same slope (which means that changes in the amplification factor influence all reflex systems in about the same way), a normalization of the values of the different animals was performed as follows. The forces produced in the negative steps showed a nearly linear increase with step size, in contrast to the forces of positive steps. Therefore, as a measure for the different amplification factors, the mean value of both components of the three negative step forces was calculated for each animal. These values varied between 4.2 mN and 33 mN (i.e., by a ratio of about 1 : 8). These values were used to normalize all force values of this animal to the common mean. After normalization the force-step characteristics of all animals fall within a small range (Fig. 4b). To show the effect of this normalization, the figure also contains the data of three extreme individuals.

For 11 of these 19 animals the change of the leg geometry during the steps was measured. From the data for each step a mean leg position and a mean value giving the angle changes for each step was calculated. On the basis of the mean forces of these 11 animals, the torques which were developed by the individual joints for each step, were determined by means of a graphical construction (see Cruse 1976b). The results are given in Fig. 5 for all three joints. The slope in the force angle characteristic is much higher for the thoracic-coxal joint compared to that of the other joints.

In a third series of experiments the torques were measured when the joints were moved individually ("single joint movement"). This was done for the femur-tibia joint with 11, for the coxa-trochanter joint with 6, and for the thoracic-coxal joint with 5 animals. The latter 5 and 6 animals are the same as the 11 animals used in the investigation of the femur-tibia joint. This was done to enable us to compare different joints of the same animal, and thus to minimize the changes of the amplification factors. However, it turned out that due to the unavoidable manipulations of the animal when changing the experimental device, the amplification factors varied considerably. Thus, the values of each animal had to be normalized individually. This was done as described above (Fig. 4a), for the forces measured during movement of the entire leg but now using the torque values. As torques and forces are directly related, the amplification factor is the same whether it is calculated on the basis of the torque or the force. Thus, the normalization influences the data in the same way as above. To this end, the normalization factor was again taken from the three torque values obtained when we increased the angle values (corre-
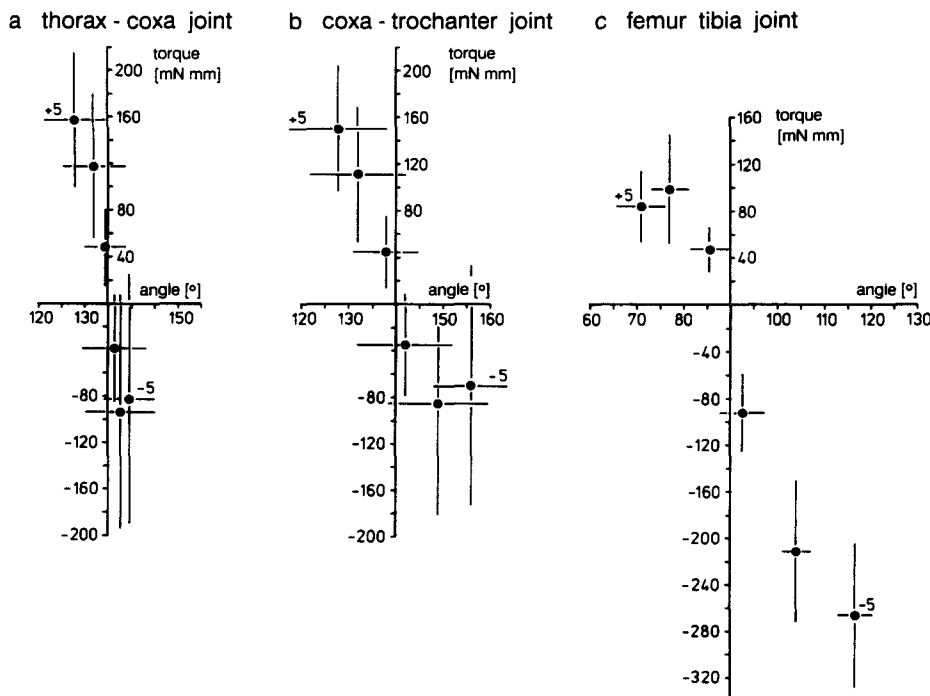

Fig. 5a–c. Mean values of the torques developed by the three leg joints between a thorax and coxa, b coxa and trochanter and c femur and tibia, when the joint is moved by a given angle (*abscissa*) from the zero position by moving the whole leg. Step size and direction is marked for the extreme cases (+5, −5). For definition of the angles see Fig. 1

sponding to negative steps). The results can be seen in Fig. 6a, b, c for the three joints. The normalization factors varied between 1 and 7.7 for the thoracic-coxal joint, between 1 and 3.7 for the coxa-trochanter joint, and between 1 and 68 for the femur-tibia joint. Finally the ordinates of these three mean characteristics were multiplied by a factor to fit the results shown in Fig. 5a, b, c. The characteristic of the coxa-trochanter joint (Fig. 6b, crosses) shows a very different slope for positive and negative steps. Therefore, for the normalization in this case only the values of the other branch, namely that of the positive steps, were used.

Discussion

The question to be answered by this investigation is whether the resistance reflex which can be measured for the movement of the entire leg can be interpreted as the simple (vectorial) sum of the resistance reflexes which are known to exist in the individual leg joints. This requires a comparison of the torques generated in both situations, i.e., a comparison of the results shown in Figs. 5 and 6.

A comparison of the absolute values is not possible because of the large variation in the amplification factors (Bässler 1972a). The fact that in spite of this variation the force values after normalization fall within a narrow range (Fig. 4b) show that, for the whole leg movement, a change in the amplification factor influences all force values, and thus all torque values, by the same amount. This indicates that the amplification fac-

tors of the individual joints do not vary independently from each other. Rather, these factors seem to change by the same amount for all leg joints. Our qualitative impression is that there is a general trend for the amplification factors to be higher and to vary less in the whole leg movements.

When comparing the normalized data, no obvious differences can be found for most of the values between the torques of the single joint movements and those obtained for the whole leg movements. Nevertheless, there are two qualitative differences. In the whole leg movements, the torques of the coxa-trochanter joint and thoracic-coxal joint seem to decrease when the highest angle values are reached (Fig. 5). By contrast, for the single joint movements the torques continue to increase for even higher angle values (Fig. 6a, b). For the femur-tibia joint a corresponding situation is found for the lower angle values (Fig. 6c). Because of the large S.D. this decrease of the torque at the extreme values is not significant. However, much the same results were obtained in an experiment which was performed several years ago with 16 animals in Kaiserslautern. The result of these experiments are also given in Fig. 6b, c (open circles). Although the decrease of torque values is not significant, the mean value is significantly smaller ($p < 1\%$) than the value expected if the torque had increased as observed in the single joint movements.

One could argue that the decrease of the torques for the extreme values in Fig. 5 may simply be due to the fact that, when moving the whole leg, the velocity of the angular movement is not the same as that of the tarsus,
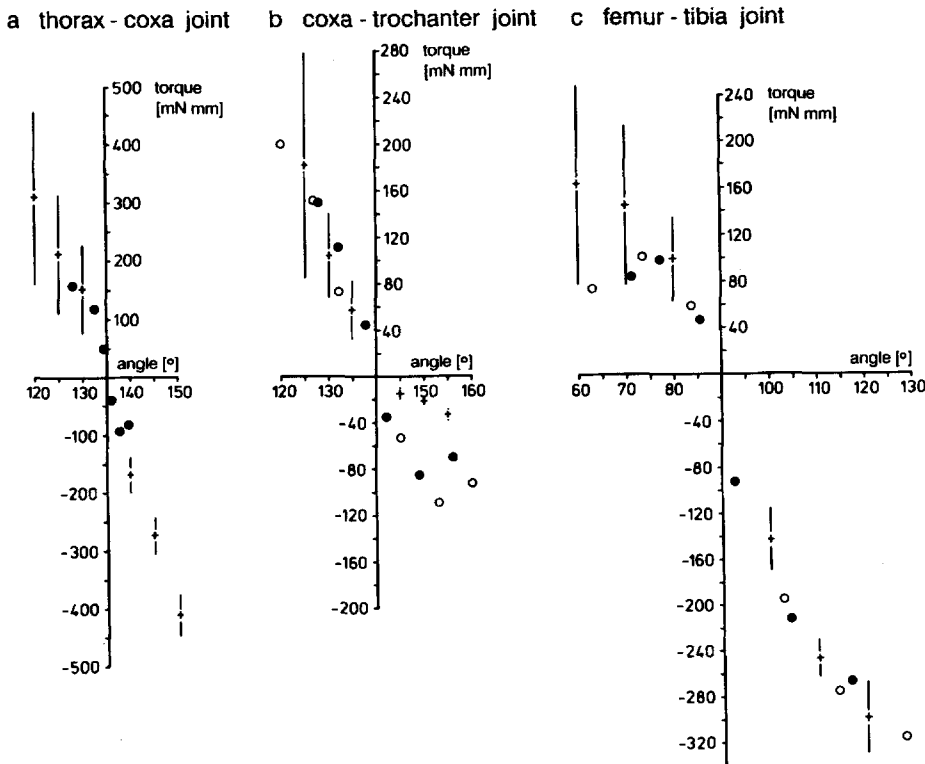

a thorax - coxa joint   b coxa - trochanter joint   c femur - tibia joint

Fig. 6a–c. Torques developed by the three joints, when the joints between thorax and coxa a, between coxa and trochanter b and between femur and tibia c are moved separately (crosses, mean +/−S.D.). These values are compared with the torque values shown in Fig. 5 (*closed circles*) and another series performed by a similar measurement (*open circles*) in which the whole leg is moved. Note that the ordinate of a has a different scale than that of b, c and of Fig. 5a, b, c

but depends upon the range of the movement. As the dynamic part of the reaction depends on the stimulus velocity (Bässler 1972b), this might influence the resulting force. However, similar results are also found for the static forces, i.e., those forces measured four minutes after the leg was moved (not shown here). Thus, at least the latter results cannot be explained by possible, small differences in angular velocity.

Another, even more obvious difference between both measurements can be observed for the torques of the coxa-trochanter joint. When moving this joint individually, the slope of the characteristic differs considerably for positive and negative steps. This difference amounts to a factor of about 5 (Fig. 6b). This agrees qualitatively with the results of Schmitz (1988a, b) who found a factor of 3.6. The latter value was obtained for the angles between 145 and 165 deg. and Schmitz found that this difference increased for smaller angle values. When the whole leg is moved, no significant difference is found for positive and negative steps in the linear part of the reaction (Fig. 5b). This is also true for the experiment with horizontally oriented animals (Fig. 6b, circles). In another investigation, Schmitz (1985, Fig. 3c) measured the force development of the coxa-trochanter joint while moving the whole leg. In this experiment the coxa-trochanter joint was moved stepwise in both directions, and the force value was again about the same in both cases.

When the joints were moved individually, the limb was fixed to the force transducer. One could argue that the differences found in the reflex responses are due to the fixation of the limb and thus to a different stimulation of leg sense organs, in particular the campaniform sensillae. However, the qualitative results for the coxa-trochanter joint were the same in the following, additional experiment (2 animals). Here, as in the experiments where the entire leg is moved, the tarsus, rather than the femur, was fixed to the force transducer and was moved in a circle around the coxa-trochanter joint so that the angle of the femur-tibia joint was held constant.

The shape of the torque angle characteristics measured for the individual joints (Fig. 6) cannot easily be quantitatively compared with other results from the literature. Although several investigations exist, a somewhat different method was used in each case. Schmitz (1986a, b) used the same method to investigate the coxa-trochanter joint, but measured only the reaction to $+/-10$ deg. stimuli in different angle ranges. As mentioned above, as far as a comparison is possible, his results agree with ours. Wendler (1972) also investigated the coxa-trochanter joint, but presented only electrophysiological recordings from the depressor muscle nerve during sinusoidal stimulation. The femur-tibia joint has been thoroughly investigated, however, force measurements of steps of different sizes are only published for negative steps, i.e., stimuli exciting the flexor force (Storrer and Cruse 1977). Although the method was different – the leg joint was held fixed and the joint movement was simulated by stimulating the appropriate receptor, the chordotonal organ – the results agree with our findings. Bässler (1965) used the same stimulation, but measured the amplitude of the

freely moving tibia. He also found a monotonic increase in the reaction and a smaller response of the extensor tibiae muscle compared to the flexor system. No data are known from the literature concerning the vertical movement of the thoracic-coxal joint. Movements of this joint in the horizontal plane around a vertical axis of rotation have been done by Schmitz (1985). The joint was moved by 15 deg. in the anterior direction and back to the 90 deg. starting position. The amplitude of the force change was the same in both directions which agrees with our results, as can be seen from the characteristic shown in Fig. 2, which has a symmetrical form. Electrophysiological investigations also exist (Graham and Wendler 1981; Graham 1985), using sinusoidal stimulation, but permit no comparison with our force measurements.

Although, the comparison between Figs. 5 and 6 permits the following interpretation: basically, the levator trochanteris system seems to be more strongly excited when the whole leg is moved. With this exception the results show that within a given range – from step -3 to step $+3$ – the behaviour of the whole leg shows no difference to that expected if the joint reflexes worked independently from each other. However, when the leg reaches the extreme positions of step $+5$ or -5, the reflex amplitudes of the femur-tibia joint or of the two joints between coxa and trochanter, and between thorax and coxa, respectively, are diminished compared to the reflex when these joints are moved separately. Thus, when the whole leg is moved, i.e., in the more biological situation, some muscles decrease their force output when moved to the extremes. These muscles are the extensor tibiae for the femur tibia joint, and the levator trochanteris for the coxa-trochanter joint. If this had not been the case, the direction of the force vectors would have depended less on the step size and direction than shown in Fig. 3a. The force directions which would have appeared if the muscles had increased their force as when being moved individually, are shown as open circles for step $+5$ and -5 in Fig. 3a. The corresponding changes in the force vectors are indicated in Fig. 4b by open circles. This shows that the amplitude of the force vector is smaller when the whole leg is moved. It should be mentioned that a change of reflex sign, which was reported in an earlier abstract (Dautenhahn and Cruse 1990), could not be supported by the more detailed experiments described here.

The joint torques may be biologically less important than the force output, in particular the component acting parallel to the vertical body axis. This is the component that provides support for the body when the animal stands on a horizontal plane. Although the torques may decrease at the extreme positions measured, this force value is increased monotonically with step size (Fig. 4a, ordinate, see also Wendler 1964; Cruse et al. 1989). This is also the case for several other starting positions of middle and hind legs with only minor quantitative differences. The results of these experiments are not shown in detail here. They were obtained in experiments with the animals oriented horizontally, and with the following starting positions for

the middle leg: two starting positions differed from the zero position used here because the tarsus was moved horizontally either 5 mm away from, or 5 mm to, the body. Two other starting positions were obtained by moving the tarsus from the latter position, or from the zero position in a circle around the vertical axis through the coxa by 30 deg. in the anterior direction. These experiments show furthermore that the result of Fig. 5 is not dependent on whether the long axis of the body is oriented vertically, i.e., parallel to the direction of gravity, or horizontally. Thus, concerning the vertical force component, a change of the amplification factor in the levator system increases the linearity of the system in the whole leg movement, whereas a decrease of the torques at the extreme positions changes the linear behaviour such that the characteristics show a kind of saturation effect at extreme values.

The results show that eliciting a reflex in one joint can also influence the reaction in another. Such distributed reflexes were described earlier on the basis of electrophysiological investigations. For crustaceans, Clarac (1977) and Ayers and Davis (1977, 1978) describe reflexes which excite muscles extrinsic to the passively moved joint. An interesting example was described by Delcomyn (1971) for the cockroach. He extended the femur-tibia joint and thereby elicited an excitation of the flexor muscle which was not measured as such. Instead, he recorded from the extensor muscle in the coxa which corresponds to the Depressor trochanteris in the stick insect. Extending only the tibia also excited the depressor. In our experiments with negative steps the Flexor tibiae is excited together with the Levator trochanteris because here the coxa-trochanter joint is not fixed, but also extended. On the basis of the reflex found in the cockroach one would expect that the excitation of the Levator might be smaller than when the coxa-trochanter is moved alone. However, the exact opposite was found (Fig. 6b). One possible interpretation is that the reflex found in the cockroach does not exist in the stick insect. The other interpretation is that, in both cases, the joint reflexes operate together in order to move the tip of the leg, the tarsus, in a direction opposite to the imposed movement. This would be a consistent explanation for both experiments.

References

Ayers JL, Davis WJ (1977) Neuronal control of locomotion in the lobster, Homarus americanus. II. Types of walking leg reflexes. J Comp Physiol 115:29–46

Ayers JL, Davis WJ (1978) Neuronal control of locomotion in the lobster, Homarus americanus. III. Dynamic organization of walking leg reflexes. J Comp Physiol 123:289–298

Bässler U (1965) Proprioreceptoren am Subcoxal-und Femur-Tibia-Gelenk der Stabheuschrecke und ihre Rolle bei der Wahrnehmung der Schwerkraftrichtung. Kybernetik 2:168–193

Bässler U (1972a) Der Regelkreis des Kniesehnenreflexes bei der Stabheuschrecke Carausius morosus: Reaktionen auf passive Bewegungen der Tibia. Kybernetik 12:8–20

Bässler U (1972b) Der "Kniesehnenreflex" bei Carausius morosus: Übergangsfunktion und Frequenzgang. Kybernetik 11:32–50

Bässler U (1977) Sensory control of leg movement in the stick insect Carausius morosus. Biol Cybern 25:61–72

Bässler U (1983) Neural basis of elementary behavior in stick insects. Springer, Berlin Heidelberg New York

Clarac F (1977) Motor coordination in crustacean limbs. In: Hoyle G (ed) Identified neurons and behavior of arthropods. Plenum Press, New York pp 167–186

Cruse H (1976a) The control of the body position in the stick insect (Carausius morosus), when walking over uneven surfaces. Biol Cybern 24:25–33

Cruse H (1976b) On the function of the legs in the free walking stick insect Carausius morosus. J Comp Physiol 112:235–262

Cruse H, Riemenschneider D, Stammer W (1989) Control of body position of a stick insect standing on uneven surfaces. Biol Cybern 61:71–77

Dautenhahn K, Cruse H (1990) Resistance reflexes in the leg of an insect: is the whole more than the sum of its parts? In: Elsner N, Roth G (eds) Brain – perception – cognition. Proceed. of the 18th Göttingen Neurobiology conference, 55, Thieme, Stuttgart New York

Delcomyn F (1971) Computer aided analysis of a locomotor leg reflex in the cockroach. Z Vergl Physiol 74:427–445

Graham D (1985) Influence of coxa-thorax joint receptors on retractor motor-output during walking in Carausius morosus. J Exp Biol 114:131–139

Graham D, Wendler G (1981) The reflex behaviour and innervation of the tergocoxal retractor muscles of the stick insect Carausius morosus. J Comp Physiol 143:81–91

Kemmerling S, Varju D (1981) Regulation of the body-substrate-distance in the stick insect: responses to sinusoidal stimulation. Biol Cybern 39:129–137

Kemmerling S, Varju D (1982) Regulation of the body-substrate-distance in the stick insect: step responses and modelling the control system. Biol Cybern 44:59–66

Kittman R (1991) Gain control in the femur-tibia feedback system of the stick insect. J Exp Biol, 157:503–522

Schmitz J (1985) Control of the leg joints in the stick insects: differences in the reflex properties between the standing and the walking states. In: Gewecke M, Wendler G (eds) Insect locomotion. Parey, Berlin Hamburg 1985 pp 27–32

Schmitz J (1986a) The depressor trochanteris motoneurones and their role in the coxo-trochanteral feedback loop in the stick insect Carausius morosus. Biol Cybern 55:25–34

Schmitz J (1986b) Properties of the feedback system controlling the coxa-trochanter joint in the stick insect Carausius morosus. Biol Cybern 55:35–42

Storrer J, Cruse H (1977) Systemanalytische Untersuchungen eines aufgeschnittenen Regelkreises am Bein der Stabheuschrecke Carausius morosus. Kraftmessungen an den Antagonisten Flexor und Extensor Tibiae. Biol Cybern 25:131–142

Wendler G (1964) Laufen und Stehen der Stabheuschrecke: Sinnesborsten in den Beingelenken als Glieder von Regelkreisen. Z Vergl Physiol 48:198–250

Wendler G (1972) Körperhaltung bei der Stabheuschrecke: ihre Beziehung zur Schwereorientierung und Mechanismen ihrer Regelung. Verh Dtsch Zool Ges 65:214–219