J. exp. Biol. *116*, *343–355 (1985)*
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WHICH PARAMETERS CONTROL THE LEG MOVEMENT OF A WALKING INSECT?

I. VELOCITY CONTROL DURING THE STANCE PHASE

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Accepted 26 October 1984

SUMMARY

In treadwheel walking, the front and middle legs of the stick insect (*Carausius morosus*) propel the wheel, while the hind legs exert very little force and can even decelerate the wheel. This result is compared with observations on the function of the legs in different walking situations.

Several hypotheses assuming different types of position servo-mechanisms have been proposed in the literature on the control of leg movement during walking in insects. The experimental results support none of these hypotheses. Instead, they indicate that velocity rather than position is the variable controlled during the stance phase.

INTRODUCTION

A number of reflexes in the legs of standing arthropods are known to resist passive limb movements (for references see Mill, 1976). Their existence raises the following questions, to which this paper is addressed. Are such reflexes also active during intentional movements of the legs, and how are such feedback loops integrated into the whole system which controls leg movement?

Two resistance reflexes in the leg of the stick insect have been shown to function as negative feedback systems during active walking movement. These systems control (a) the angle between coxa and trochanter (Wendler, 1964; Schmitz, 1985) and (b) the angle of the femur-tibia joint (Cruse, 1981; Cruse & Pflüger, 1981; Graham & Bässler, 1981). These and other results (see Cruse & Saxler, 1980) led to the hypothesis that the movement of a walking leg is controlled by a 'follow-up position servo-system', the reference input of which changes continuously to represent the desired leg position during walking (Cruse, 1980). The actual position of the leg normally lags behind this value, causing an error signal which is assumed to direct the motor output.

An alternative hypothesis assumes that the reference input is not moved during the stance phase but rather remains fixed at a posterior extreme position during the whole stance phase (Cruse, 1983). This model will be referred to below as 'position servo with fixed reference input'.

Key words: Stick insect, walking, velocity servo-mechanism.

Yet other hypotheses are also feasible; three of them will be discussed here. First, it is possible that instead of position itself, higher-order derivatives of position, such as velocity or acceleration, are controlled. As a shorthand description, this will be termed 'velocity control'. Second, the possibility of 'open loop control' should be mentioned; this would mean that no feedback information at all is used for the control of the active leg movement. And third, Bässler, Foth & Breutel (1985) very recently suggested that position information is used but in a 'positive feedback' system rather than a negative one.

These hypotheses can be tested by the following experimental procedure. While a stick insect walks on a treadwheel, one leg is placed on a platform positioned beside the wheel (Wendler, 1964). When the platform is fixed to a force transducer, the force developed by the leg can be registered. This experiment was performed here in two ways. In the first, the leg was held stationary by fixing the platform at a given position relative to the insect's body (stationary situation); in the second, the leg was allowed to move as in a normal stance phase by moving the platform parallel to and at the same speed as the treadwheel (dynamic situation).

METHODS

Adult female stick insects (*Carausius morosus* Br.) walked on a styrofoam treadwheel (diameter 38·5 cm, breadth 9 mm, friction 0·8 mN measured at the outer margin of the treadwheel, moment of inertia 720 gcm^2), while tethered at the thorax (see Cruse & Saxler, 1980). The longitudinal axis of the body was horizontal. The coxae of the middle legs were arranged vertically over the axis of the wheel. The distance between wheel and body was fixed at 9 mm. One leg on the right side of the body was placed on a platform beside the treadwheel. This platform was attached to a force transducer in one of two conditions: in one case, the force transducer was almost rigid (platform displacement of 0·5 mm for 10 mN); in the other case, that of the 'soft' platform, the force transducer allowed considerable movement in the horizontal direction when loaded (displacement of 15 mm for 10 mN). The horizontal component of the force was measured parallel to the longitudinal axis of the body. Forces in the posterior direction were treated as positive. The platform, together with the force transducer, was mounted on a micromanipulator in order to adjust the position of the leg on the platform to the desired position. The force values were recorded on a pen recorder (Hellige Recomed 1305). The force developed by the standing leg of the walking stick insect oscillates considerably (Cruse & Saxler, 1980). As only the d.c. value of the force was of interest here, the individual d.c. values were calculated by means of a graphic-tablet (Apple) on the basis of walking periods lasting at least 6 s each.

A technical problem complicates measurement of the force of the front or middle leg on the platform: in normal walking, the next posterior leg moves during its swing phase to the position of this leg on the platform (Cruse, 1979). To keep the next posterior leg from touching the platform, it was either placed on a platform of its own, or else its swing phase was blocked by a vertical stick held in front of the femur

(Dean & Wendler, 1982; Cruse & Epstein, 1982). The two situations can be considered to produce a continuous stance phase or continuous swing phase, respectively.

The forces measured on the standing leg of the walking animal (stationary situation) may not correspond to the forces developed during real walking. Therefore, the forces developed by the leg walking on the wheel were measured in the following way (dynamic situation). An animal was set walking on the wheel with all six legs. Then the platform with the stiff force transducer was moved by hand beside the outer rim of the treadwheel at about the same speed as the wheel. This movement was monitored by measuring the position of the force transducer. The starting position was about 5 cm in front of the animal. Occasionally a leg at the end of its swing phase grasped the platform instead of the rim of the wheel and the forces developed by the leg during the stance phase could be measured. For this experiment a light-weight double treadwheel of the sort described in detail by Graham (1981) was used. The other arrangements were as described above.

All position values are given relative to a coordinate parallel to the long axis of the body, with the origin in front of the tip of the head (Bässler, 1972) and positive values in the anterior direction. As the animals differed in length, all values were normalized to a mean body length of 72 mm (Cruse, 1976).

RESULTS

Force measurements on the standing leg

When a stick insect walks on a treadwheel with one leg standing on a fixed platform, this leg develops forces oscillating in time with the walking rhythm of the other legs. However, the d.c. value of the force varies when the position of the platform is changed parallel to the longitudinal axis of the insect's body (Fig. 1A). Mean values measured with the 'soft' platform show that the force value increases the more anterior the position of the leg (Fig. 2). The amplitude of the oscillations also increases with

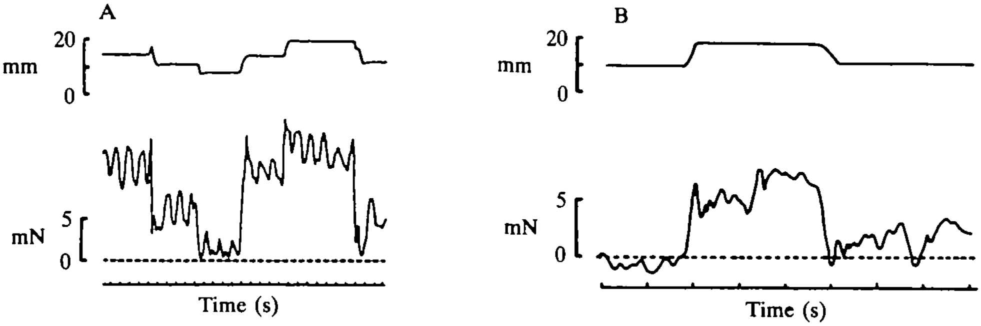

Fig. 1. D.c. force values depend upon leg position. (A) An example of an individual record of the force developed by a front leg standing on the platform while the other legs walk. Upper trace: relative position of platform – upward deflection shows movement in anterior direction; lower trace: force – positive forces act in posterior direction. This measurement was performed for demonstration only and was not evaluated, as the sections are too short for this purpose. (B) As (A) but with the receptor apodeme of the femoral chordotonal organ cut. Note that time scale is different.

increasing d.c. value, although this is not shown here. Using the stiff force transducer produced qualitatively the same results, with one difference. On the stiff platform the leg starts the swing phase from much more anterior positions than is the case with the soft platform (see also Cruse & Epstein, 1982). For this reason, force measurements with the stiff platform could only be obtained for a limited range of positions; these data are not shown here. (The results with the stiff platform showed that the force values increase still further for more forward leg positions. Since the latter were not measured with the soft platform, they are not shown in Fig. 2.) With the soft platform, the leg generally remains on the platform even at positions far beyond the normal range of movement. The only limit to these positions seemed to be due to the geometrical properties of the legs.

To test whether position feedback plays a role, this experiment should be repeated after ablation of the possible position-measuring sense organs. Unfortunately, the existence of numerous internal sense organs in the proximal joints makes such an experiment very difficult. However in the front leg, movement during the stance phase occurs mainly in the femur-tibia joint, whose position is measured almost exclusively by the femoral chordotonal organ (for review see Bässler, 1983). Therefore, the experiment was repeated using insects in whose front legs the receptor apodeme of the chordotonal organ had been severed. To avoid influences from sense organs in other joints, the platform with the tarsus was held so that to a large extent, only the femur-tibia joint was moved during the experiment. The force values decreased after the operation. However, experiments with three animals directly

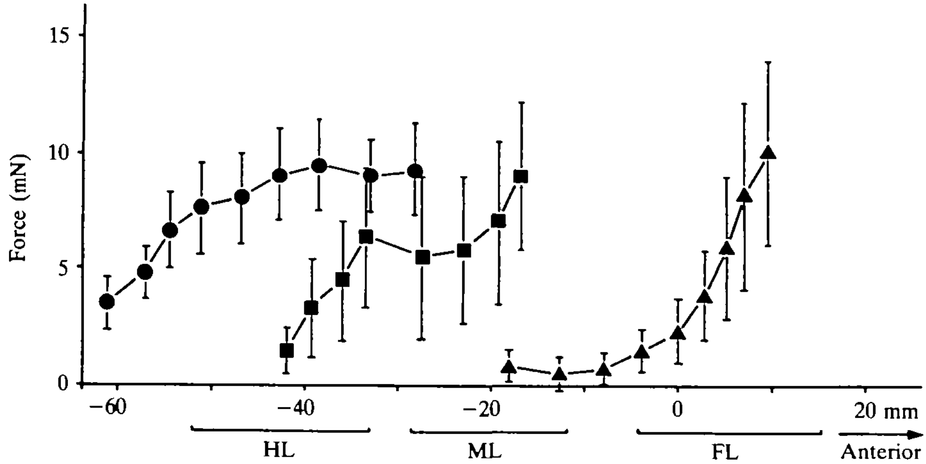

Fig. 2. Mean values and standard deviations of force *versus* position of the platform. Abscissa: position coordinate parallel to the longitudinal axis of the body. Origin is tip of the head. Positive values are anterior. Below the abscissa the ranges of normal movement during walking are given for front leg (FL, triangles), middle leg (ML, squares) and hind leg (HL, circles). Forces in posterior direction are positive. FL: 153 measurements from five animals; ML: 114 measurements from five animals; HL: 161 measurements from six animals. Each measurement produced a d.c. value from a walking period of at least 6 s duration during a continuous walk.

following the operation elicited force responses qualitatively the same as those of intact animals (Fig. 1B). The measurements of the d.c. forces after flexion and extension of the femur-tibia joint showed that the stiffness of the muscles is increased by about a factor of ten when changing from the standing to the walking state. This is true of both intact animals and those whose chordotonal receptor apodeme had been cut.

As has been shown by Bässler (1977), Dean & Wendler (1982) and Cruse & Epstein (1982), the position of a leg at the endpoint of the stance phase depends upon whether the next posterior leg is in stance or swing phase. Two of the position feedback hypotheses (follow-up servo, position servo with fixed reference input) were formulated to imply that influences from the posterior leg affect the reference input value of the feedback system. On the basis of both hypotheses, one would predict that on the fixed platform the force value for any given leg position would be higher if the posterior leg were in swing phase than if it were in stance phase. To test this prediction, the middle leg was held in either continuous swing phase or continuous stance phase (see Methods) and the forces developed by the front leg were measured;

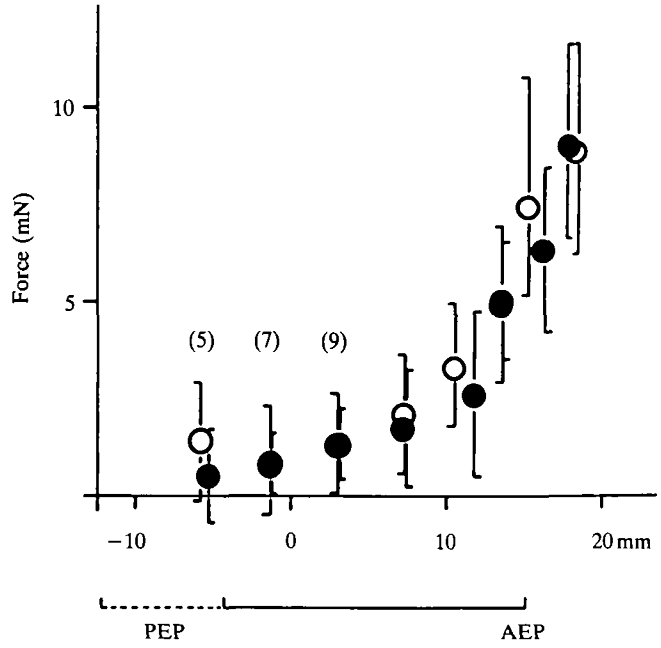

Fig. 3. D.c. force values *versus* position of front leg. Mean values and standard deviations from a total of 13 124 measurements. Ten animals were tested with the ipsilateral middle leg either on a fixed platform (●) or with blocked swing phase (○). Coordinates as in Fig. 2. For lower position values not all 10 animals remained on the force transducer in both experiments. Thus fewer animals were evaluated; the number tested is shown in brackets. Below the abscissa the range of normal leg movement is shown by the solid line. The range is extended as shown by the dashed line when the swing phase of the ipsilateral middle leg is blocked. AEP, anterior extreme position; PEP, posterior extreme position.

10 animals were used and both methods were applied with each. Mean values are shown in Fig. 3. The paired *t*-test showed no significant difference ($P \gg 10\%$) between the forces for each position measured. This means that the results are not consistent with the prediction of either hypothesis.

Force measurements on the walking leg

The dependence of forces upon position when measured on the standing leg of the walking animal may differ from the forces which are developed during real walking. To compare the forces developed by a leg standing on a fixed platform with those developed when walking on the wheel, the forces of freely walking front, middle and hind legs were measured by moving the platform with the force transducer parallel to the treadwheel. Fig. 4 gives sample results of individual steps plus the averaged results for all three legs. Front and middle legs normally produce forces which accelerate the wheel. Hind legs showed extremely variable results. Generally the force amplitude was very small; forces with negative values were frequent. As the individual measurement (Fig. 4) demonstrates, the sign of the force value could also change several times within one stance phase. For this reason, the shape of the averaged curve of the hind leg does not describe a 'typical' time course of the force.

A modification of this experiment permitted investigation of the influence of feedback mechanisms during the stance phase of a freely walking leg: this time the

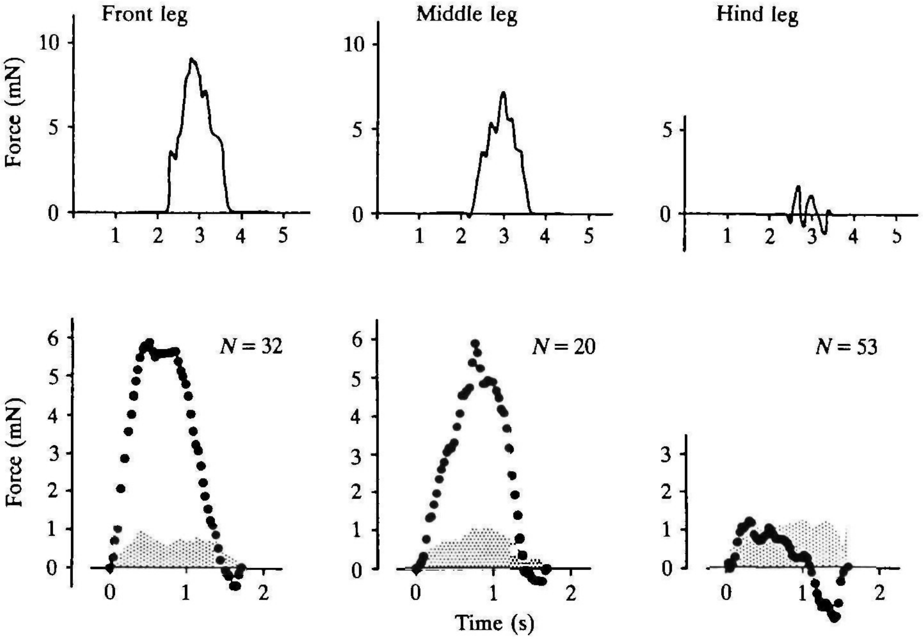

Fig. 4. Forces measured during a step with the force transducer being moved parallel to the treadwheel. Upper row: individual measurements; lower row: averaged results of front, middle and hind legs from five animals. The magnitude of the standard deviations is represented by the dotted area above the abscissa. Forces in posterior direction are positive.

movement of the platform was not continuous but was interrupted in one of two ways. Movement was (a) stopped for a short time or (b) its speed was increased for a short time. The change of the platform speed will be referred to below as the stimulus. This experiment was performed with front legs for 63 steps for case (a) and 20 steps for case (b). The results (Fig. 5) were averaged using the beginning and end of the stimuli as reference points. The ordinate used in Fig. 5 is only a relative one, as the absolute force values at the trigger point differed from step to step. This variation was increased even further by the fact that the beginning of a stimulus was varied as much as possible during the stance phase (however, it was only possible to start the stimulus for the last two-thirds of the stance phase). The results shown in Fig. 5A demonstrate that the force values increase for about 0·3 s after the platform has stopped, but then start to decrease before the platform begins to move again. This result was also found in individual steps when the absolute force value before the stop was negative, i.e. when the leg tried to push the platform in the anterior direction. The increase in platform speed (Fig. 5B) resulted in a decrease of the force value.

DISCUSSION

Measurements of the forces developed by the legs of insects walking on a treadwheel (Fig. 4) show that front and middle legs normally accelerate the wheel, whereas hind

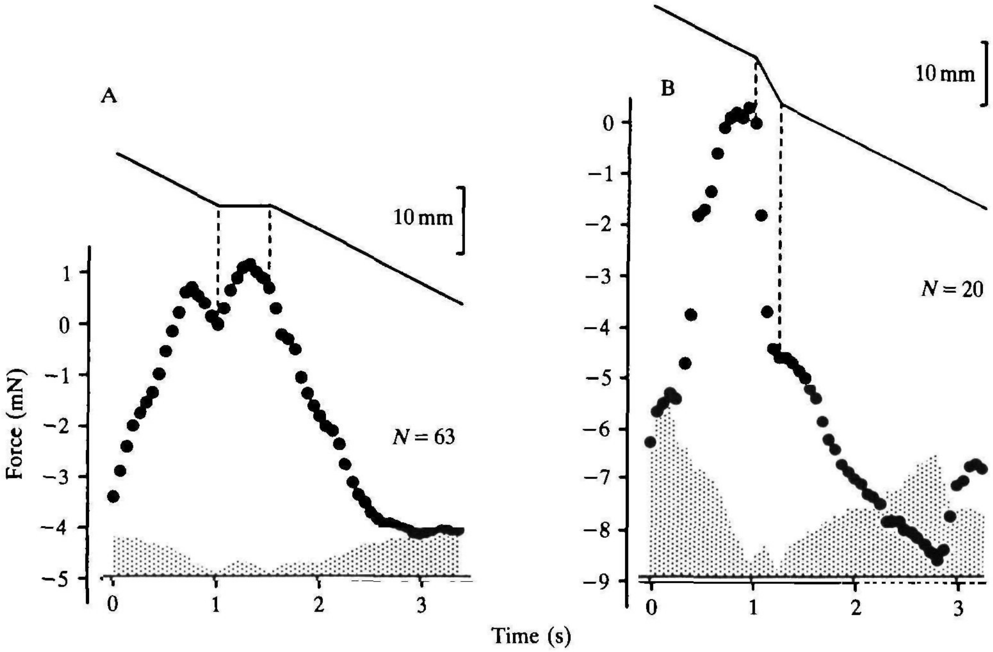

Fig. 5. Forces measured during a step of the front leg whereby the leg movement was changed by briefly decreasing (A) or increasing (B) the speed of the platform. Averaged results from 5 (A) and 4 (B) animals. The upper trace shows schematically the movement of the platform. Ordinate: changes of force relative to force value when the stimulus began. For further explanation see Fig. 4.

legs develop only small forces. These results can be compared with those of earlier force measurements from stick insects walking in different situations (Cruse, 1976). Front and middle legs behaved differently on the wheel than when walking on a horizontal path or plane. In the latter two situations both legs produce small and sometimes even decelerating forces, whereas on the wheel they typically accelerate. However, the behaviour of both legs on the treadwheel resembles that of animals walking vertically upward: in both situations the legs try to propel the body.

The hind legs were found to develop small and sometimes negative forces on the treadwheel. This bears out the qualitative observation that it is easier to persuade stick insects to walk on the wheel when both hind legs are placed on platforms and thus are unable to stop the movement of the wheel. It is also consistent with the report of Bässler *et al.* (1985) that when hind legs are allowed to walk on a wheel without front and middle legs, they tend to walk backwards. In contrast to the insect's performance on the walking wheel, the hind leg produces strong accelerating forces in all three free-walking situations, i.e.when walking vertically upward, walking on a horizontal plane, or on a horizontal path. During the stance phase of the hind leg in horizontal walking, the torque developed by promotor muscles was found to be stronger than that of the remotor muscles, although the forces measured at the tarsus were found to accelerate the body. Although at first sight these results seem contradictory, the mechanism described apparently helps free-walking animals to support the weight of the body; the net effect of the hind leg is nevertheless to propel the body (Cruse, 1976). For an animal supported by the holder over the wheel, this organization of the motor output of the hind legs should lead to the observed small or even decelerating force values. Thus, the difference found between free-walking animals and those walking on a wheel may be explained by the fact that in the experiments on the wheel, the body of the animal is supported by a holder.

Graham (1983) studied the velocity profile produced by stick insects walking on a treadwheel and concluded that front and hind legs together produce about the same force as the middle leg. This is consistent with the force measurements of individual legs shown here. However, Graham's method did not allow him to measure the relative contribution of the front and hind legs because they moved simultaneously. The force measurements reveal that, as Graham supposed, the largest part of the force is produced by the front leg. Graham further concluded that either the front or the hind leg must exert a strong decelerating force. The force measurements presented here show that to a large extent this force is produced by the hind leg.

The force measurements were performed to clarify how the movement of the leg is controlled during the stance phase. Five hypotheses concerning this problem were mentioned in the Introduction, postulating respectively open loop control, position servo with fixed reference input, follow-up position servo, velocity control and positive feedback. Fig. 6 illustrates for some of these hypotheses which results should be expected in the experiments performed here. In the upper row of this figure, the values of the reference input and the actual output are plotted against time. For the experiments with the fixed platform (stationary situation), the abscissa can also be interpreted as a position axis. The lower row shows the corresponding error signal (i.e. the difference between the reference input value and actual output value). As the error signal is assumed to direct the motor output, the experimental results have to be compared with these figures.

If we assume the existence of a 'position servo with fixed reference input' (Fig. 6A), then during the stance phase the reference input corresponds to a posterior position. Therefore the error signal and thus the motor output should increase the further anterior the positon of the leg. The results with the leg on the fixed platform (Figs 1A, 2) confirm this prediction. In the dynamic situation (i.e. when the platform with the leg is moved), the force is also expected to be about proportional to position; however, the low pass filter properties of the system (mainly the muscles) must be taken into account as well. The results shown in Fig. 4 are also compatible with this prediction. The increase of the force while the platform is stopped (Fig. 5A), however, would not be expected in such a system.

With respect to the 'open loop control' hypothesis, qualitatively the same results are to be expected in the intact animal as are predicted by the position servo with fixed reference value. Under the open loop control, the excitation of the muscles is

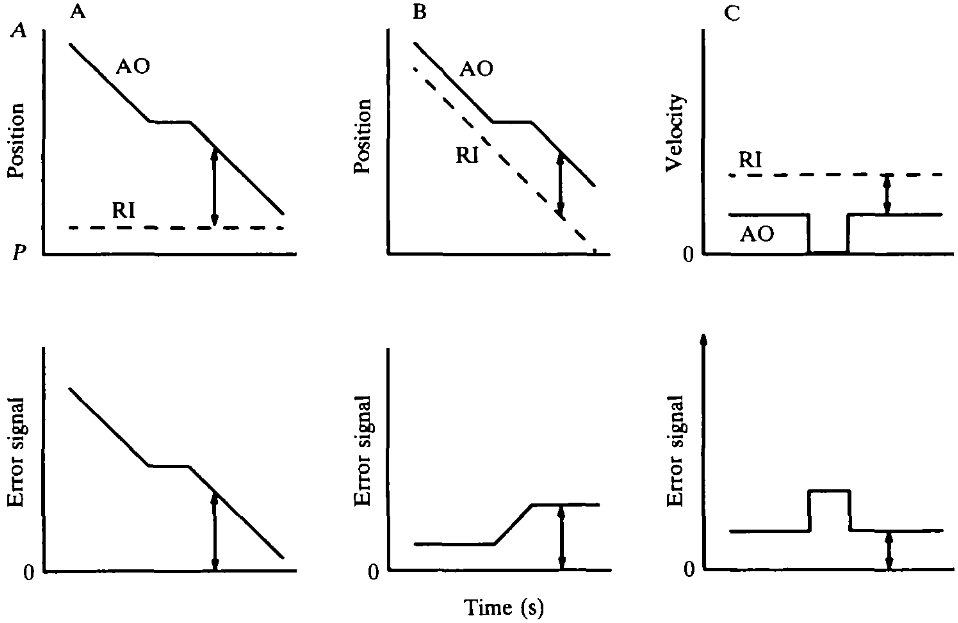

Fig. 6. Schematic diagram representing the control of leg movement during stance phase from an anterior (*A*) to a posterior (*P*) position for three different control mechanisms: (A) position servo with fixed reference input, (B) follow-up position servo and (C) velocity control. The upper figures show the reference input (RI, dashed line) and the actual output (AO, continuous line). The lower figures show the corresponding error signals (difference between reference input and actual output). For further explanation, see text.

independent of sensory feedback, in this case of leg position. This means that the muscles behave like elastic springs pulling the leg backwards during the stance phase. Therefore in this case as well, the force is expected to be proportional to leg position. However, there is one difference between open loop control and the position servo with fixed reference input: the former should produce the same results when position sense organs are severed whereas the latter should be strongly dependent on signals from such organs. As the force values were shown to be qualitatively the same after removal of the position sense organ (Fig. 1B), the results using the stationary leg are mainly caused by the elastic properties of the retracting muscles. The increased muscle stiffness caused by the greater excitation of the walking state makes it possible for the high force values to occur. A system of an open loop control also fits the findings of S. Epstein & D. Graham (in preparation), who moved the middle leg of a walking stick insect and found no increase of motor output to either the retractor or the depressor muscle during passive protraction of the leg. In contrast there was a small decrease in excitation, although in the experiment described here the force values increase. As for the position servo with fixed reference input, the increase of the force during the stop of the platform is not expected, but the assumption of an additional velocity control (see below) could be a sufficient explanation.

In the experiment with the stationary leg, a follow-up position servo would produce the same results as an open loop control system or a position servo with fixed reference input: when the leg stands on the platform for a time much longer than a normal step, its reference input can be considered to correspond to an extreme posterior position and therefore in this situation cannot be distinguished from the other two systems. However, in the dynamic situation, when the platform stops the error signal increases and therefore the motor output is expected to increase as well (Fig. 6B). Although the first increase of force upon stopping (Fig. 5A) supports the follow-up position servo hypothesis, the decrease of the force during the second part of the stimulus is not predicted by this hypothesis. Instead, the force should increase further or at least remain constant (if the hypothetical reference input has reached its final posterior value).

Positive feedback depending upon position signals should lead in the dynamic experiment to a decrease of motor output while the platform is stopped and to an increase as the platform speed increases. The results described in Fig. 5A are clearly not compatible with this hypothesis, nor do those shown in Fig. 5B support it. However, in the experiment with the increased platform speed the effect might be masked by the decrease of force produced by the elastic properties of the muscles.

Thus, the results do not support a positive feedback model, nor do they support either of the two versions of the position control feedback mechanism or an open loop control. However, as a clear response to the stimulus does occur, feedback activity must take place which does not depend upon position error signals. It was found earlier that the reflex of the femur-tibia joint, which is slowly phasic in the standing animal, decreases its time constant to a value below 100 ms when walking; therefore, it can be interpreted as a velocity transducer in this situation (Cruse, 1981; Cruse & Pflüger, 1981; Cruse & Schmitz, 1983). This suggests the existence of a velocity servo-system that controls leg movement during the stance phase. A schematic drawing of the expected properties of such a system is shown in Fig. 6C. The abscissa is time or position, which is equivalent to time during the movement in the stance phase. The ordinate in the upper drawing is velocity. When the platform stops, the actual velocity becomes zero. Thus the error signal (difference between desired velocity and actual velocity, lower drawing) increases, which in turn increases the motor output. The results shown in Fig. 5A are compatible with the existence of such a system, as the force increases with a time constant of the order of 0·1 s when the speed of the leg is decreased to zero. Velocity control is further supported by the finding that the force decreases strongly as the leg speed increases (Fig. 5B). However, much if not all of this decrease in force is probably due to the elastic properties of the excited muscles; therefore, a quantitative evaluation of the latter experiment is impossible. However, after the end of the stimulus a small positive force seems to be superimposed upon the further decrease of force, thereby slowing the rate of decrease of the force. This is to be expected on the basis of the velocity control hypothesis, as leg speed is decreased at the end of the stimulus, which should lead in turn to a short increase in muscle excitation. This has been clearly shown in a similar experiment performed by D. Graham (personal communication). He found that when the speed of the treadwheel is experimentally increased during the stance phase, the retractor muscles are inhibited and the protractor muscles are excited. While the leg moves at constant speed, the motor output (excitation of the muscles) is predicted to be constant (Fig. 6C). However, the force value clearly decreases (Fig. 5A). This is to be expected as a consequence of the elastic properties of the constantly excited muscles as described above for the open loop situation.

A pure velocity control system would not produce the small decrease of force near the end of the zero-speed stimulus (Fig. 5A). The latter result indicates that the control system may be enhanced by an additional acceleration-sensitive mechanism within the system. Such acceleration-sensitive units were recently found by Hofmann & Koch (1985) in the femoral chordotonal organ of the stick insect. The leg movement of the stick insect has also been shown to be velocity controlled during the swing phase (Dean, 1984). Velocity control systems have been found to affect the limb control of higher vertebrates as well (Dufresne, Soechting & Terzuolo, 1979).

However, one might argue that the increase of force is due to an additional reflex mediated by such load-sensitive organs as the campaniform sensilla. The deceleration of a leg at the beginning of the stimulus produces an increase of load which might by positive feedback result in an increase of force. However, the force produced by this deceleration is calculated to be smaller than 0·01 mN and is thus less than 0·2 % of the load on the leg before the stimulus begins. It seems improbable that this effect would increase the force by about 1 mN, as was found in the experiments. (It should be kept in mind that this possible positive feedback mechanism would have to be active before the stimulus occurred.)

In summary, rather than having a position control system, leg movement in stick insects seems to be controlled by a system similar to a velocity, and perhaps higher order derivative, servo-system. As a rough approximation, one can assume that the reference value changes during the step cycle in a square wave-like manner, thus producing a constant excitation of the muscles during the whole stance phase. Such a constant excitation has indeed been found in stick insects walking on a slippery surface, a situation in which the legs are not mechanically coupled (Epstein & Graham, 1983), as well as in free-walking cockroaches (Pearson & Iles, 1970).

In the hind leg, very small forces were found to be produced when the platform was moved parallel to the wheel. But why were considerable backwards-directed forces present in the experiment with the fixed platform (Fig. 2)? With the moving platform, the hypothetical velocity control system could be expected to produce a small motor output which might result in low retractor forces or even, because of the normal function of supporting the body, in low protractor forces. However, with the fixed platform, the velocity control system would increase the motor output, thus decreasing the protracting force and increasing the retracting forces.

It is known from earlier work that the posterior extreme position of a leg is shifted backwards when the swing movement of the next posterior leg is blocked (Dean & Wendler, 1982; Cruse & Epstein, 1982). Thus, signals from the next posterior leg can influence the system which controls the movement of a leg. The results shown in Fig. 3 indicate that these signals do not influence the motor output during the stance phase as was assumed earlier (Cruse, 1980). Instead, they seem to influence only the time or the position at which the leg is lifted.

I want to express my thanks to Dr D. Forsythe for correcting the English manuscript. Supported by DFG (Cr 58–4).

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