

## Stick Insects Walking Along Inclined Surfaces<sup>1</sup>

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**SYNOPSIS.** In the experiments stick insects walk on an inclined substrate such that the legs of one side of the body point uphill and the legs of the other side point downhill. In this situation the vertical axis of the body is rotated against the inclination of the substrate as if to compensate for the effect of substrate inclination. A very small effect has been found when the experiment was performed with animals standing on a tilted platform which shows that the effect depends on the behavioral context. When, however, animals first walked along the inclined surface and then, before measurement, stopped walking spontaneously, a rotation of the body has been observed similar to that in walking animals. In a second experiment it was tested whether the observed body rotation is caused by the change of direction of gravity vector or by the fact that on an inclined surface gravity necessarily has a component pulling the body sideways. Experiments with animals standing on horizontal ground and additional weights applied pulling the body to the side showed similar body rotations supporting the latter idea. In a simulation study it could be shown that the combined activity of proportional feedback controllers in the leg joints is sufficient to explain the observed behavior. This is however only possible if the gain factors of coxa-trochanter joint controller and of femur-tibia joint controller show a ratio in the order of 1 : 0.05 to 1 : 1.8. In order to describe the behavior of animals standing on a tilted platform, a ratio of 1 : 1.7 is necessary. In walking animals, this body rotation requires to change the trajectories of stance and swing movements. The latter have been studied in more detail. During swing, the femur-tibia joint is more extended in the uphill legs. Conversely, the coxa-trochanter joint appears to be more elevated in the downhill legs which compensates the smaller lift in the femur-tibia joint. The results are discussed in the context of different hypotheses.

### INTRODUCTION

The neural system that controls behavior has to deal with two aspects. On the one hand a given behavior, for example foraging or courtship, has to be performed in a stable way, *e.g.*, on the basis of some form of neuronal pattern generator. On the other hand, the control system has to be able to adapt the actual behavior to a variety of possible disturbances or unpredictable irregularities in the environment. This in particular is true for walking over irregular substrate. For insects a number of investigations have dealt with particular aspects of this problem. Walking over obstacles (Cruse, 1976a; Pearson and Franklin, 1984), uphill and downhill walking either in free walking animals (Bässler, 1962, 1965, 1967; Cruse, 1976b; Duch and Pflüger, 1995; Full and Tullis, 1990a, b; Pelletier and Caissie, 2001; Spirito and Mushrush, 1979; Wendler, 1969, 1972) or simulated on a treadmill augmented with positive or negative friction (Dean, 1991) has been investigated in some detail. For some of these cases there exist also modeling studies (Cruse *et al.*, 1998; Schmitz *et al.*, 2002). However, systematic studies of animals (insects, crustaceans) walking along an inclined surface are rare (Frantsevich *et al.*, 1993; Horn, 1982; Horn and Lang, 1978). The latter focus on control of head position and the explicit or implicit interest of these studies is whether the compensation of head position found in these experiments serves for stabi-

lization of visual input. As in this paper the focus is on control of leg movement, we concentrate on body position instead of head position, because the system that controls the movement of leg joints in a standing or a walking animal necessarily determines body position, too.

Specifically, in this paper we ask the question whether a similar compensation is found with respect to the dorso-ventral axis of the body position (Fig. 1, z-axis). To this end, we investigate the behavior of stick insects walking along an inclined surface in such a way that the long axis of the body is perpendicular to the direction of gravity, in other words, that the animal walks along a horizontal line. This means that in this situation the legs of one side of the body are positioned uphill and the other legs are positioned downhill. In the fly studies mentioned it has been found that the compensation depends on the behavioral context. A compensation effect on head position has only been found in tethered walking, but not in standing animals (Horn Lang, 1978) nor in flying animals (Hengstenberg, 1988; van Hateren and Schilstra, 1999). Therefore we investigate body rotation in animals walking along inclined surfaces and compare this with animals walking on a horizontal plane (experiment Ia). We further investigate animals that first stand on a horizontal surface which is tilted, while the animal is standing (experiment Ib). As a difference has been found in both experiments, we also investigate animals that walk along an inclined surface and then stop spontaneously and therefore stand on the inclined surface (experiment Ic). A comparison between the results of these three experiments will show whether the

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compensation depends only on the actual behavioral context, standing or walking, or whether it depends on the preceding behavioral situation.

These experiments indeed showed a compensation effect, *i.e.*, a rotation of the body around its long axis which leads to the question as to how direction of gravity is recorded? This information might be achieved by means of some specific sense organs as is known for example for dragon flies (Mittelstaedt, 1950) or crickets (Nicklaus, 1968) or by statocysts as found in many non insect species. Another possibility is that there are no specific sensory structures to detect direction of gravity, but that the effect of gravity on the body indirectly influences leg position, *i.e.*, joint angles. These changes in angular position might then affect the orientation of the vertical axis of the body. To distinguish between both possibilities, in experiment II the body axis was measured when the animal was standing on a horizontal plane and the body was pulled sideways.

As a rotation of the vertical body axis was also found in this experiment, in a simulation study it was tested whether the observed behavior could result from the effect of simple position controllers that stabilize leg joint position against external disturbances. A combined effect of two proportional position controllers, one for each leg joint, could qualitatively describe the observed effects. However, different gain factors had to be assumed for the different experimental situations.

Rotation of body axis can only result from corresponding changes in leg joint position. The simulation study proposed a hypothesis that can explain the situation when the legs have contact with the substrate. During swing movement, in walking animals, legs have to be lifted off the ground. Therefore, in a final experiment (experiment III) it is tested whether the rotation of body axis influences the leg movement during swing, *i.e.*, whether there is a difference between swing trajectory of uphill and downhill legs. This experiment decides between two hypotheses proposed earlier: One hypothesis (Cruse *et al.*, 1998) predicts that there is no difference between both legs. The other predicts that different trajectories should be found (Cruse, 2002). Results show that the amplitude of leg lifting is about the same for uphill and downhill legs, which, at first sight, seems to support the first hypothesis. However, a closer inspection shows that different leg joints contribute in different ways to swing trajectory in uphill and downhill legs, which can be better explained by the second hypothesis.

#### MATERIALS AND METHODS

Adult female stick insects *Carausius morosus* were used throughout. In the first experiment (I) the vertical axis of the body of standing or walking animals is measured. For this purpose a paper flag, made from a small piece of white cardboard is glued to the dorsum of the mesothorax in about vertical direction (length 35 mm). The animal stands or walks on a flat plane covered with black cardboard and is filmed with a vid-

eo camera in front view (camera Sony AF ccd, recorder Panasonic AG-7355, 50 frames/sec). The walking plane together with the camera could be tilted around the long axis of the body. Inclination angles of  $\lambda = 0^\circ, 15^\circ, 35^\circ, 45^\circ,$  and  $60^\circ$  are used. The paper flag itself does not change its form in these situations. For the measurement, the walking plane is rotated such that the animal is heading to the camera. Because in walking animals the direction of the vertical body axis shows a more or less regular oscillation, the angle values are always recorded for a complete step (beginning and ending when the left front leg touches ground after swing phase). Step frequency is between 0.5 Hz and 2 Hz which corresponds to the normal walking range of *Carausius*. Therefore, mean values of 25 to 100 frames have been calculated. This value has been used to determine the deviation of the vertical body axis from vertical axis relative to the substrate, angle  $\delta$  (see Fig. 2a).

In a second experiment (II), the change of the vertical body axis of the animals is investigated when the animals are standing on the horizontal path (inclination angle  $\lambda = 0^\circ$ ), but the body is pulled to the side with a thread fixed to the metathorax near the center of gravity of the body (Fig. 3a, inset). The thread which is fixed to a weight via a pulley (distance 50 mm), pulls the body into the y-direction, *i.e.*, horizontally. The thread forms a loop around the body such that the orientation of the body is only minimally influenced by the thread. In the experiment, the animal first walks on the path until it stops walking spontaneously. The angle of the paper flag is measured. Then the weight is applied which takes about 10 to 15 sec, and the angle is measured again after another 5 sec. Three different weights have been applied in random order. The orientation of the vertical axis of the body is measured via video camera and screen using a paper flag as in the first experiment.

A simple 2D simulation is carried out to test whether the observed rotation of the vertical axis of the body could be explained under the assumption that the leg joints are subject to proportional position controllers. To investigate this question, a simplified 2D insect consisting of a body and two contralateral legs was simulated which represent both middle legs, for example. For the simulation of the body kinematics a MMC type recurrent network has been used (Steinkühler and Cruse, 1998). This network permits the kinematic simulation of an arbitrary complex kinematic chain. In our case the chain consists of five segments (Fig. 4) one representing the body, the other four representing tibia and femur of two legs, respectively (lengths: tibia 10 mm, femur 6 mm, body 3 mm). The end of the tibia is assumed to be fixed to the substrate with passive hinge joints. The temporal dynamics of the MMC network are described by a damping factor. In this simulation a factor of 5 has been used. This value is not critical here as we only look at the static behavior. This is a sensible approximation for the experiments using standing animals (experiments Ib, c,

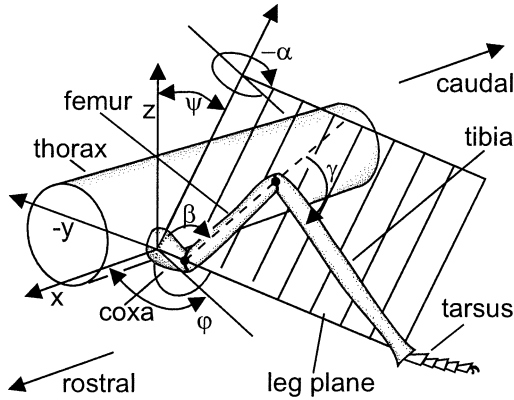


FIG. 1. Schematic model of a stick insect leg showing the arrangement of the joints, their axes of rotation and the leg based coordinate system.

II). For the walking animals (experiment Ia) a dynamic simulation would provide more reliable results. However, a 3D dynamic simulation of an insect consisting of 19 body segments is quite complex. Therefore, as a first step we focus on the approximation based on a 2D kinematic simulation.

In this simplified version, each leg contains two joints, a coxa-trochanter joint and a femur-tibia joint. Each of these two joints is subject to a proportional negative feedback controller, that controls position, *i.e.*, joint angles. In the simulation, the gain of both controllers were varied and the behavior of the body (lateral shift, change of body height, rotation of vertical body axis) was observed when i) the angle of gravity vector was changed as in the first experiment and when ii) an additional weight was applied pulling the body to the side as in the second experiment. Reference inputs were always kept at constant values.

In the final experiment (III), the trajectories of swing movements are recorded when the animals walk along an inclined surface. The animals walk free along a wooden path covered with black cardboard (breadth 32 mm). In this case, the tarsi of all legs usually grasp

around the margin of the path. To measure trajectories, the animal was videotaped from above and, via a mirror, from the side in order to allow a 3D reconstruction of leg positions. The whole device could be turned around the long axis of the walking path. Substrate inclination was  $\lambda = 0^\circ$  or  $60^\circ$ . Left legs and right legs were measured from separate walks. To obtain leg trajectories and joint angles, single frame analysis has been applied and orientation of body long axis, the spatial position of coxa, the femur-tibia joint and the end of the tibia (tibia-tarsal joint) was recorded in both top view and side view. Application of inverse kinematics (Cruse and Bartling, 1995) allows to determine the joint angles. The geometrical arrangement of leg segments and angle definitions are given in Figure 1. The x-axis determines the longitudinal axis of the body (positive values rostral), the y-axis determines the transversal axis (positive values to the left side, values for the right side are negated in Table 1), the z-axis determines the vertical body axis (positive values up). The origin of this coordinate system is in the base of the coxa of each leg (thoracic-coxal joint, Fig. 1).

RESULTS

*Experiment I: Vertical body axis of animals walking along inclined surfaces*

The angles of the vertical axis of the body were measured when the animal stood or walked on an inclined surface. To compensate unavoidable deviations of the paper flag from exact vertical, for each animal the changes of the angles were measured relative to its angle obtained for the control situation (inclination  $\lambda = 0^\circ$ ). Therefore, for the inclination of  $\lambda = 0^\circ$  the mean deviation from vertical is  $\delta = 0^\circ$  by definition. In the first experiment (Ia) only continuously walking animals (6 animals and five different substrate inclinations) were used. The angular deviations  $\delta$  for the different substrate inclination angles  $\lambda$  investigated are given in Figure 2 by closed circles (mean  $\pm$  SD). When, however, the animals walked on the horizontal substrate ( $\lambda = 0^\circ$ ) until they stopped spontaneously

TABLE 1. Extreme positions of swing trajectories.\*

	Front leg			Middle leg			Hind leg		
	AEP	SEP	PEP	AEP	SEP	PEP	AEP	SEP	PEP
control, $0^\circ$									
X	$19.3 \pm 3.8$	$11.3 \pm 4.7$	$-1.4 \pm 3.8$	$10.8 \pm 2.5$	$2.5 \pm 4.1$	$-11.2 \pm 2.6$	$-0.6 \pm 2.2$	$-12. \pm 4.4$	$-20.3 \pm 2.3$
Y	$10.4 \pm 4.5$	$24.1 \pm 3.4$	$11.2 \pm 3.8$	$13.3 \pm 2.6$	$20.2 \pm 1.6$	$12.3 \pm 2.3$	$13.2 \pm 1.4$	$18.7 \pm 2.6$	$10.3 \pm 3.3$
Z	$-14.6 \pm 3.3$	$-1.9 \pm 7.$	$-10.5 \pm 2.7$	$-9.3 \pm 2.6$	$-2. \pm 5.7$	$-6.7 \pm 2.1$	$-5.4 \pm 2.3$	$-0.8 \pm 3.2$	$-3.5 \pm 1.9$
uphill, $60^\circ$									
X	$21.7 \pm 2.4$	$7.2 \pm 5.8$	$-4.1 \pm 2.6$	$12.2 \pm 2.3$	$2.9 \pm 3.6$	$-10.7 \pm 2.9$	$1.2 \pm 2.6$	$-11.4 \pm 4.1$	$-20.7 \pm 1.8$
Y	$14.7 \pm 4.4$	$24.3 \pm 2.8$	$14.1 \pm 2.7$	$14.4 \pm 2.9$	$20.4 \pm 2.4$	$14. \pm 2.5$	$15.2 \pm 1.6$	$19.5 \pm 3.4$	$11. \pm 2.4$
Z	$-6.3 \pm 2.7$	$3.2 \pm 5.8$	$-4.2 \pm 2.5$	$-3.8 \pm 2.7$	$5.2 \pm 5.8$	$-2.8 \pm 5.9$	$-1.5 \pm 2.1$	$6.5 \pm 4.2$	$-0.4 \pm 1.6$
downhill, $60^\circ$									
X	$22. \pm 3.9$	$15.8 \pm 4.8$	$3.5 \pm 4.4$	$12.3 \pm 4.$	$2.7 \pm 4.1$	$-10.3 \pm 3.6$	$-0.8 \pm 2.6$	$-14.1 \pm 5.5$	$-19.3 \pm 2.9$
Y	$9.6 \pm 4.$	$20.7 \pm 4.6$	$9.2 \pm 4.4$	$11. \pm 2.7$	$19.2 \pm 2.4$	$8. \pm 2.6$	$10. \pm 2.$	$15.2 \pm 3.3$	$7. \pm 3.1$
Z	$-15.3 \pm 4.4$	$-5.3 \pm 4.8$	$-12.5 \pm 2.2$	$-12.5 \pm 1.2$	$-6.2 \pm 2.8$	$-9.9 \pm 1.9$	$-9.7 \pm 1.8$	$-5.1 \pm 3.1$	$-8.8 \pm 2.5$

\* Five animals, data from 10 steps for each animal and each leg. Mean  $\pm$  SD. Coordinates x, y, z as shown in Figure 1, but y values for right legs being negated.

and then the substrate was tilted, the body rotation was negligible or small ( $\lambda = 45^\circ$ :  $\delta = 0.03^\circ \pm 1.0$ ;  $\lambda = 60^\circ$ :  $\delta = 0.4^\circ \pm 2.3$  (experiment Ib, *t*-test, not significant,  $n = 60$ , 6 animals, data not shown graphically). In a parallel measurement, the body movement in  $y$ - $z$  coordinates was investigated. The results show that there is nearly no movement ( $\lambda = 45^\circ$ :  $\Delta y$  (positive values uphill)  $0.3 \pm 0.5$  mm,  $\Delta z$  (positive values up)  $-0.25 \pm 0.5$  mm;  $\lambda = 60^\circ$ :  $\Delta y$  (positive values uphill)  $0.25 \pm 0.6$  mm,  $\Delta z$  (positive values up)  $-0.5 \pm 0.8$  mm,  $n = 17$  animals).

In experiment Ic, the animal walked along the inclined surface until it stopped walking spontaneously. The angle of the vertical body axis was measured when the animal was standing. As shown in Figure 2 (triangles), angle  $\delta$  was  $7.8^\circ (\pm 3.3)$  for  $\lambda = 45^\circ$  and  $6.4^\circ (\pm 2.3)$  for  $\lambda = 60^\circ$  inclination ( $n = 60$ , the same 6 animals). There is no significant difference (*t*-test) between standing (experiment Ic) and walking animals (experiment Ia).

#### Experiment II: Application of forces in horizontal direction

The experiments described above have shown that changing the direction of gravity influences the vertical axis of the body. This leads to the question whether the observed body rotation is caused by the measured change of direction of gravity vector or by the fact that, on an inclined surface, gravity necessarily has a component pulling the body sideways. As described in the methods section, the body of an animal standing on a horizontal path is pulled to the side ( $y$ -direction) via a thread fixed to a weight (Fig. 3a, inset). Three different weights were used (0.5 g, 1.1 g and 1.7 g). The vertical axis of the body was measured using the paper flag glued to the mesothorax as above. The results are shown in Figure 3. Ten animals and 10 measurements for each animal and each weight were used. Average body mass of the animals was 0.84 g (SD  $\pm 0.17$ ). Figure 3a shows the lateral shift of the body (measured at the dorsal margin of mesothorax, basis of the flag) for control, 0.5 g, 1.1 g, and 1.7 g, when the weight pulls the body to the side. It can be seen that even for the largest weight of 1.7 g, the body is moved downward by only a very small amount (1.7 g produce a decrease of the mean in vertical direction by 0.31 mm, *i.e.*, about 3.5% of body height). The movement to the side (direction of  $y$ -axis) is negligible for the smallest weight, but about proportional to the weight value for the larger weights. Maximum deviation is about 2 mm. Figure 3b shows the change of the vertical body axis. Qualitatively this shows the same behavior as when the inclination of the surface is increased. The largest weight corresponds to about twice the average body weight of the animals. Therefore, the direction of the force vector acting on the body approximately corresponds to that of  $\lambda = 60^\circ$  inclination. A weight of 0.84 g would correspond to an inclination of  $\lambda = 45^\circ$ . However, the situations are still different because the absolute value of the force

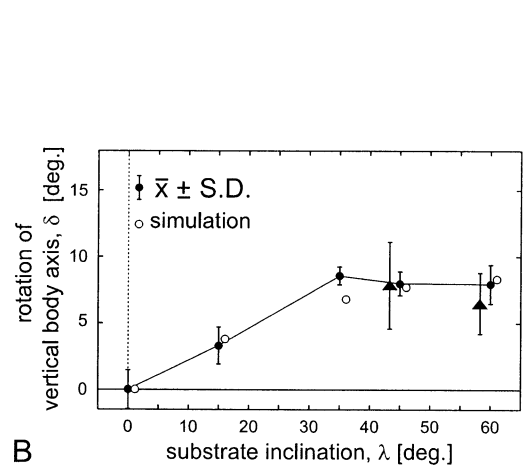
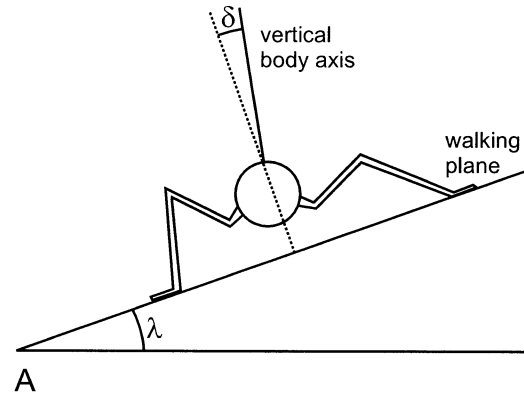


FIG. 2. Deviation of vertical body axis from the axis perpendicular to substrate (angle  $\delta$ ) for different angles of substrate inclination  $\lambda$ . a) Schematic illustration of substrate inclination  $\lambda$  and body rotation  $\delta$ . b) Mean values and SD. 6 animals, 10 steps for each substrate inclination and animal. Open symbols show simulation results. Triangles show results from standing animals that first walked along an inclined surface and then stopped walking spontaneously (experiment Ic).

is higher than in the first experiments (Fig. 2), where the animals have only to carry their own body weight. Therefore, both data sets cannot be compared quantitatively. Nevertheless, results of Figure 3b clearly show that body rotation is also found when direction of gravity is not changed.

#### Simulation

As has been explained in the Methods section, a simple 2D kinematic insect is simulated. The 2D insect contains two legs that are fixed to the substrate (Fig. 4). Each leg has two active joints, representing the  $\beta$  joint and the  $\gamma$  joint. In the simulation, the position of these joints are controlled by proportional negative feedback controllers. As right and left leg are considered to be symmetric, both  $\beta$  joint controllers have the same gain as had both  $\gamma$  joint controllers. The reference inputs to these position controllers are kept constant. In the simulation, the two gain values of these controllers have been varied systematically. The resulting position of the body has been observed when i) the angle of gravity vector was changed as in the



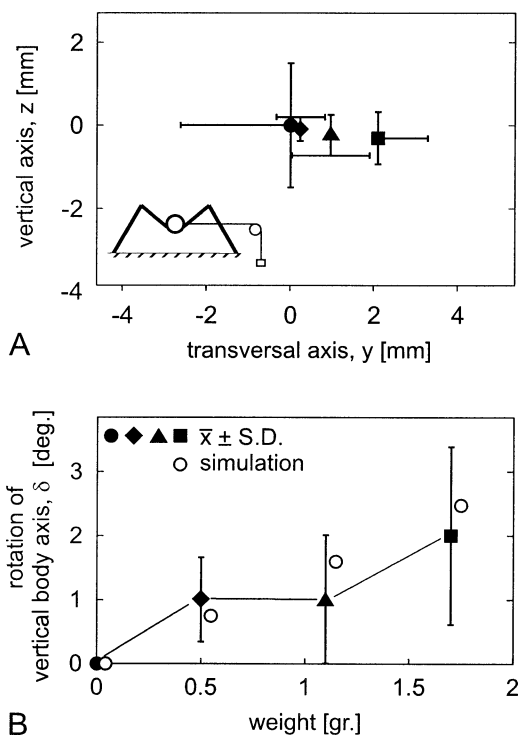


FIG. 3. Body position and rotation of vertical body axis when the body is pulled to the side by different weights (0 g, circle, 0.5 g, diamond, 1.1 g, triangle, and 1.7 g, square). a) Movement of the body in y-z plane (front view, see Fig. 1). The weight is pulling the body to the right (see inset). The origin marks the body position of the unloaded animal (closed circle). b) Rotation of vertical body axis. 10 animals, 30 measurements for each animal and weight. Mean values  $\pm$  SD. Open symbols show simulation results.

first experiment (Fig. 2 and related text) and when ii) an additional weight was applied pulling the body to the side as in the second experiment (Fig. 3 and related text).

It is obvious before any simulation that there are lower limits for the gain factors: If the gain values are too small, the body position cannot be stabilized against the influence of gravity. As known from control theory there are also upper limits: If the gain factors are too high, the system may show oscillations. The simulation has shown that the upper limit of the possible gain factors decreases further, if stability is not only required for horizontal body positions ( $\lambda = 0^\circ$ ), but also for inclined substrates. In the simulation, we systematically varied the gain values for each joint within the range given by these limits. For particular configurations, namely sprawled leg positions (angle between tibia and ground about  $45^\circ$ ) the results have shown that the gain of the femur-tibia joint must not exceed that of the coxa-trochanter joint, because otherwise the body could not be stabilized against gravity. Therefore only a comparatively small range of gain factors was at all able to stabilize body position. The remaining two-dimensional array of possible gain factors could be subdivided in two regions, a section which shows an increase of body-ground distance with

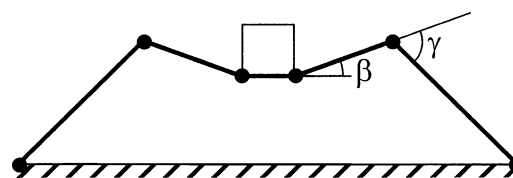


FIG. 4. Schema showing the simulated 2D insect.

increasing substrate inclination or increased weight pulling the body to the side, and the remaining section showing the opposite behavior. As the results of experiment Ib and experiment II (Fig. 3a) have shown that body height was quite constant, only a small “band” of possible gain factors remained that corresponds to the boundary between both sections. Within this band, the gain of the coxa-trochanter joint and that of the femur-tibia joint showed approximately the same ratio. For a gain of 1 for the coxa-trochanter joint controller (the absolute values depend on the details of the simulation and are of no particular interest here) the appropriate gain for the femur-tibia joint was in the range between about 0.05 and 1.8. Using these values we attempted to predict the body rotation found in the two different experiments, changing substrate inclination (exp. Ia) and adding weights in horizontal direction (exp. II). Application of a factor of 1 for the coxa-trochanter joint and a factor of 0.08 for the femur-tibia controller provides a sufficient approximation for experiments Ia and Ic (Fig. 2b, open circles). The body is shifted to the side by about 1 mm for an inclination of  $\lambda = 60^\circ$  and body height remains constant (not shown). However, these gain factors produced overly large rotations for experiment II (a weight of 1.7 g produced a  $\delta$  angle of  $18^\circ$  instead of  $2^\circ$  as found in the experiment). Body rotation in experiment II could better be described by application of a gain of 1 for the coxa-trochanter joint and a gain of 0.6 for the femur-tibia joint (Fig. 3b, open circles). The body height decreased by about 1% (compared to about 3.5% in the experiments) (SD of body height is about  $\pm 9\%$ ), and the movement to the side was somewhat smaller (about 0.5 mm) than observed in the experiment (about 2 mm, SD =  $\pm 1.2$  mm). In order to simulate the results of animals standing on a tilted platform (exp. Ib), a gain of 1 for the coxa-trochanter joint and a gain of about 1.7 for the femur-tibia joint was necessary to describe the deviation of  $\delta = 0.4^\circ$  ( $\lambda = 60^\circ$ ).

#### Experiment III: Leg trajectories during swing movement

In these experiments the animals walk along a path and are filmed in top view and side view. For five animals and 10 steps for each leg and animal the spatial position at three extreme positions have been evaluated. These are i) the posterior extreme position (PEP), *i.e.*, the tibia end point of the leg in the last frame before the leg lifts off the ground to start swing movement, ii) the anterior extreme position (AEP),

*i.e.*, the corresponding position in first frame after the leg has touched ground to begin a stance movement, and iii) the swing extreme position (SEP), *i.e.*, the position when the tibia end point has reached its most dorsal (highest) position during swing. The values are given in body (leg) centered coordinates (Fig. 1). The results (mean values  $\pm$  SD) for the extreme positions are given in Table 1 for front, middle and hind legs. For the inclined path ( $\lambda = 60^\circ$ ), values for uphill and downhill legs are shown separately. Considering changes along the x-axis, only small effects are found for middle legs and hind legs. In the front legs, however, the AEP is shifted by 2.7 mm and 3.4 mm for both the uphill and the downhill leg respectively. The PEP of the uphill front leg is shifted by 2.7 mm to the rear. Therefore the step amplitude of the uphill front leg is increased by 5.3 mm. For the downhill front leg, the PEP shifts by 4.9 mm to the front, decreasing its step amplitude by 2.2 mm. In transversal direction (y-axis), there is a general tendency for all legs to increase the uphill distance and to decrease the downhill distance. This is to be expected as a result of the effect of gravity pulling the body downhill. This shift to the side varies with respect to extreme position and leg, but in general is in the order of 2 mm (SD =  $\pm 3.1$  mm). As mentioned above, the simulation predicted a shift of about 1 mm. The greatest effect can be found along the z-axis. For the uphill legs, the extreme positions are shifted between 3.1 mm and 8.3 mm in upward direction and for the downhill legs by 0.7 mm to 5.3 mm downward. However, this change in absolute values essentially is due to the rotation of the body. Considering the lift amplitude of the legs, *i.e.*, the difference between SEP and the mean of AEP and PEP, projected onto the y-z plane, gives the following mean values for uphill and downhill legs, respectively: front legs 13.1 and 14.3 mm, middle legs 10.5 and 11.1 mm, hind legs 10.0 and 8.0 mm (with SDs in the order of  $\pm 3$  mm). Therefore, there is no large difference between uphill and downhill leg pairs with respect to swing amplitude.

The results, however, indicate that the slope of the plane of swing movement appears to be different in uphill and downhill legs. Does this difference result from changes in only the coxa-trochanter joint (Fig. 1,  $\beta$  joint) or is it in addition or mainly due to changes in the femur-tibia joint (Fig. 1,  $\gamma$  joint)? To answer this question, complete trajectories for front, middle and hind legs have been registered from 22 to 25 steps for each leg (3 animals). These data were used to calculate the joint angles during swing and stance movement. The results show that during stance angle  $\beta$  is always more negative in the uphill legs compared to their downhill partner legs which means that the femur is more elevated in the uphill legs. Angle  $\gamma$  is mostly higher in the uphill legs (except for the final part of stance in the hind leg) which means that, during stance, femur-tibia joint is more flexed in the uphill legs. Our main interest however, concerns the swing movement. As the leg angles during stance are differ-

ent in uphill and downhill legs, a comparison of the absolute values is not sensible. Instead, we concentrate on the angular change during the first half of the swing, *i.e.*, between leg positions at PEP and SEP. Comparing the angular change in the middle legs, results show that the extension in the  $\gamma$  joint in uphill legs is  $17.9^\circ$  greater than in downhill legs ( $P < 0.002$ , *t*-test). Concerning the movement in the  $\beta$  joint, the swing movement starts with a brief elevation which is then followed by a depression. Near SEP the depression in the downhill legs is stronger than in the uphill legs by  $10.7^\circ$ , but the difference is not significant. What does this result mean? During swing, the leg could be lifted by both elevation of the  $\beta$  joint and/or extension of the  $\gamma$  joint. However, the results show that in uphill legs and in downhill legs elevation in the  $\beta$  joint and extension in the  $\gamma$  joint are applied in a different way. The uphill leg is lifted more by an extension movement in the  $\gamma$  joint (femur-tibia joint) whereas in the downhill leg the levator of the  $\beta$  joint (coxa-trochanter joint) appears to be more active. Corresponding effects are found in the front legs and in the hind legs.

#### DISCUSSION

Control of body orientation, in particular roll movement of the body, is observed in many animals and is considered as to aim at two tasks, to keep balance and to improve vision (see Hengstenberg, 1988, for a comprehensive overview). Most investigations concentrated on head movement. An intensively studied question concerns the sense organs which are involved in this behavior. This question is particularly interesting with respect to insects as for these animals no statocysts are known to exist to measure the direction of gravity. In dragon flies, rotation of head relative to the body is used to stabilize body position during flight (Mittelstaedt, 1950). In Hymenoptera, joint receptors of head and legs are used as gravity receptors (Lindauer and Nedel, 1959; Markl, 1962, 1974). Crickets use specialized sensory hairs at their cerci (Horn and Bischof, 1983; Nicklaus, 1968).

In the fly, *Calliphora*, head control is influenced by antennal gravity receptors (Horn and Keßler, 1975) and also by other, most probably leg joint receptors (Horn, 1982; Horn and Lang, 1978). Interestingly, this influence is only found for the tethered walking fly, but not for flying animals (Hengstenberg, 1988), and not for standing animals (Horn and Lang, 1978). In the flying *Calliphora* roll motion is controlled by using the halteres (Hengstenberg, 1988). In the tethered walking blowflies, a  $60^\circ$  body rotation results in a head rotation between  $10^\circ$  and  $15^\circ$ , compared to  $8^\circ$  body rotation of free walking stick insects on a  $60^\circ$  inclined surface. As the flies in the experiment of Horn and Lang (1978) and Horn (1982) are tethered, it is not known whether a body roll compensation could also be observed in free walking flies. The to our knowledge only investigation, where animals walk along an inclined surface is the work of Frantsevich *et al.*

(1993). For a 60° inclination, the body rotation of the beetles investigated (*Geotrupes* sp.) was about 12° and the head rotation was about 26°. We have not investigated head rotation in stick insects, but qualitative inspection revealed that in stick insects head rotation is stronger than body rotation, too.

Our results have shown small, non significant body rotation when a standing animal is tilted (experiment Ib). Body rotation has however been observed when the animal walks along an inclined surface (experiment Ia). This shows that the effect depends on the behavioral context which is in agreement with findings of Horn and Lang (1978) who have shown that in blowflies roll compensation of head occurs only in walking, but not in resting animals. What might be the reason for the change of the vertical axis of the body? For the stick insect it is probable that both antennal receptors and leg joint receptors contribute to gravity perception (Bässler, 1962, 1965, 1967; Wendler, 1964, 1969, 1972) when walking uphill or downhill. Wendler (1969) discusses the possibility that not only receptors measuring joint position, but also load receptors may play a critical role. Our results with the animals standing on horizontal plane and being pulled to the side by weights show that antennal receptors and other possible receptors fixed to the body cannot alone be responsible for the observed body rotation. This leads to the hypothesis that this effect of gravity acts basically via a mechanical effect on the position of the leg joints. One possible hypothesis is the following. It is known from a number of earlier investigations that negative feedback controllers stabilize the angles in the different leg joints (standing leg: review Bässler, 1983; Wendler, 1964, 1972; walking animal: Bartling and Schmitz, 2000; Cruse, 1981). These control systems attempt to oppose the effect of gravity or other externally applied forces. It might be that the combined effects of these control loops are responsible for the rotation of the vertical body axis and that no further mechanisms are necessary to explain the observed body rotation. This hypothesis has been tested using a simulation that is based on a kinematic, 2D version of an insect. Application of proportional position controllers in each joint leads to the following conclusions. To stabilize body posture in different body positions (varying substrate inclination, more or less sprawled leg position) a higher controller gain is required for the coxa-trochanter joint compared to that of the femur-tibia joint. Furthermore, body rotation found in the different experiments can at least qualitatively be described as to result from the combined activity of all four control systems (two in each leg). A more quantitative description of body rotation is possible when we assume that the gain of the femur-tibia controller is increased when the body is pulled to the side by an additional weight compared to the situation when the animal is walking freely on an inclined surface. Concerning the lateral shift of the body, in both cases the movement to the side was somewhat smaller in the simulation than in the experiments.

When, however, animals first walk along an inclined surface and then stop (experiment Ic), they appear to maintain the position of the vertical body axis as it has been adopted during walking. This means that the joint controllers do not follow a fixed reference value, but appear to avoid deviations from the current position as has been proposed by Bässler (for review see Bässler, 1983). This could be interpreted as an integral controller that adjusts its reference input to the actual position. The idea of the existence of an integral controller could also be supported by the results shown in Figure 3a: The different weights applied do not produce a proportional deviation in all cases as one would expect if a proportional controller was active. The results could, however, be understood if, for the smallest weight, the controller works as an integral controller, because negligible deviation is found. The two higher weights appear to produce a deviation about proportional to the weights, which indicates that a proportional controller is active if the disturbing weights are high enough. This hypothesis might explain why a high gain factor is necessary to describe the small deviation in experiment Ib (standing animals on the tilted platform). In this experiment, the load to be carried by the single leg is smaller than in other experimental situations, because here the weight of the body is distributed over all six legs. In contrast, during walking only three or four legs have to carry the body weight, not regarding dynamic effects occurring during walking. Therefore, in the standing animal, the  $\gamma$  controller might show properties of an integral controller. As an integral controller can be approximated by a proportional controller with very high gain, the high gain value of 1.7 found in this simulation can now be understood as to describe the properties of an integral controller. Taken together, these findings could be interpreted as to result from a control system that acts as an integral controller for small disturbing forces (as in experiments Ib and Ic, or in experiment II for the smallest weight). The control system acts as a proportional controller for higher forces, *i.e.*, in experiment II for high weights and in the free walking animal (experiment Ia). The gain of the proportional controller appears to be higher when the body of the standing animal is pulled sideways (experiment II) compared to the freely walking animal (experiment Ia).

Considerable variability in the gain of the femur-tibia joint has already been described by Schmitz and Heuer (in preparation) who found a strong negative feedback controller in the coxa-trochanter joint whereas in the femur-tibia joint the gain could even be zero or reverse sign to produce a positive feedback system.

The range of gain factors providing stabile posture was unexpectedly small when different leg positions were to be allowed. However, the situation may be not as critical when the system is extended from the 2D version with two legs investigated here to a 3D version



with more legs, because these legs may add further stability which was not investigated here.

Because the roll reaction found in stick insects can parsimoniously be explained as to be a necessary effect of the control systems needed to control body position, it appears to be improbable that, for stick insects, this behavior should be interpreted as to improve vision, in particular as the compensation effect is very small. However, as these control systems at least qualitatively show the appropriate property for a system to stabilize visual input it might be considered as to represent some kind of preadaptation which could have later been exploited by evolution.

The body rotation requires change of leg movement during stance and swing. In stance, as to be expected, coxa-trochanter joint is lower, *i.e.*, more depressed, in the downhill legs, but in these legs, in addition, femur-tibia joint is more extended. During swing, the coxa-trochanter joint is more elevated in the downhill legs. Conversely, the femur-tibia joint is more extended in the uphill legs which compensates the smaller lift in the coxa-trochanter joint. These effects cannot be explained by a control system as proposed by Cruse *et al.* (1998) that simply determines the rate of joint movement. This should lead to the same angular movements in uphill and downhill legs. The asymmetry found in the joint movements, however, at least qualitatively supports a hypothesis proposed recently (Cruse, 2002). Assuming a mutual inhibition between antagonistic muscle controllers would lead to a strong excitation of a swing muscle if its antagonist is strongly excited during the preceding stance. In the animal walking along an inclined surface, the reaction to gravity requires different torques in the leg joints of uphill and downhill legs during stance. According to this hypothesis the inhibitory connections should lead to different excitation of the muscles active during swing as they have been observed here.

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