**Active tactile exploration for adaptive locomotion in the stick insect**

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Insects carry a pair of actively movable feelers that supply the animal with a range of multimodal information. The antennae of the stick insect *Carausius morosus* are straight and of nearly the same length as the legs, making them ideal probes for near-range exploration. Indeed, stick insects, like many other insects, use antennal contact information for the adaptive control of locomotion, for example, in climbing. Moreover, the active exploratory movement pattern of the antennae is context-dependent. The first objective of the present study is to reveal the significance of antennal contact information for the efficient initiation of climbing. This is done by means of kinematic analysis of freely walking animals as they undergo a tactually elicited transition from walking to climbing. The main findings are that fast, tactually elicited re-targeting movements may occur during an ongoing swing movement, and that the height of the last antennal contact prior to leg contact largely predicts the height of the first leg contact. The second objective is to understand the context-dependent adaptation of the antennal movement pattern in response to tactile contact. We show that the cycle frequency of both antennal joints increases after obstacle contact. Furthermore, inter-joint coupling switches distinctly upon tactile contact, revealing a simple mechanism for context-dependent adaptation.

**Keywords:** insect antenna; tactile sensing; sampling strategy; reaching-movement; inter-joint coupling

1. **INTRODUCTION**

Insect antennae are highly complex, multi-sensory organs that receive and transmit information about smell, taste, humidity, temperature and various mechanosensory cues about touch events, including contact location, bending and vibration [1]. As such, antennae are of great relevance to a wide range of behavioural contexts. Staudacher et al. [1] have distinguished the role of antennae in passive and active sensing according to whether or not antennal joints are being actively moved to acquire sensory input: passive sensing behaviours of insects include avoidance reflexes, graviception, course control and the initiation of escape; active sensing behaviours include near-range exploration, tactile pattern recognition, tactile learning and communication. The present study will focus on active tactile exploration behaviour and its relevance to the adaptive control of locomotion, particularly in climbing and negotiation of obstacles.

Active, exploratory movements of antennae during terrestrial locomotion have been studied in crickets [2,3], cockroaches [4–6] and stick insects [7–10]. In these and a number of other insect groups, shortening or complete removal of the antennae (antennectomy) was shown to affect motor performance during locomotion. From ablation studies and various behavioural analyses, it has been concluded that antennae signal information about the presence and height of obstacles [11–13], direction of turning [14–16], gap width [17] or the relative height of a shelf that could either be tunnelled or surmounted [6]. Concerning the kinematic analysis of antennal movements, all of these studies were confined to measuring polar coordinates of antennal orientation. Owing to the morphology of antennal joints, azimuth and elevation, i.e. the angles of polar coordinates, either do not correspond to the antennal joint axes (as in stick insects [7]), or do not allow a unique reconstruction of two redundant joint angles (as in antennal elevation in cockroaches [1]). As a result, no study has yet analysed tactile sampling movements of an insect antenna at the level of single joints. Therefore, neither timing nor magnitude of antennal sampling movements are understood in terms of joint kinematics or muscle activation patterns. In a first attempt to change this, the present study pursues two objectives: first, we want to show that antennal touch events can elicit fast, goal-directed reaching-movements and, thereby, initiate climbing behaviour; second, we investigate how antennal touch events affect the antennal movement pattern itself.

With these objectives in mind, we chose to study tactually elicited climbing behaviour of the Indian
stick insect, *Carausius morosus*, a nocturnal, canopy-dwelling herbivore. *Carausius morosus* is a well-established model organism of hexapedal locomotion [18–23]. As in all insects, its antennae are true limbs of the second head segment, exhibiting a skeletal, sensory and muscular infrastructure that bears many similarities to the walking-legs of the thorax [1]. Indeed, it is commonly thought that the antennae are serially homologous to the walking-legs, and that they lost their role in propulsion during evolution to become dedicated sensory limbs. In stick insects, this view is supported by homeotic regenerates, where amputated antennae regenerate as a part of a walking-leg [24,25]. As in all higher insects, the antenna of *C. morosus* consists of three functional segments (figure 1a): the scape, which is the only part of the antenna that carries muscles; the pedicel, which is equipped with a set of specialized sensory organs, e.g. Johnston’s organ; and the flagellum, which carries the majority of sensory hairs [1]. The antenna can be moved by means of two joints, the head-scape joint (HS joint) and scape-pedicel joint (SP joint). Both HS and SP joints of stick insects are non-orthogonal, slanted revolute joints [26] (figure 1b), a character combination thought to improve tactile acuity [10,26]. The junction between pedicel and flagellum is passive and does not allow active, i.e. actuated movement. The fact that both antennal joints are simple revolute joints with only a single degree of freedom is of methodological significance, too: the joint axis orientations can be measured, allowing the calculation of joint angles from the pointing direction of the flagellum (by means of inverse kinematics [10]). In many insect species, such as cockroaches or honeybees, this is not possible.

In *C. morosus*, the antennae are about the same length as the front legs. Moreover, the frontal working ranges of antennae and front legs strongly overlap, such that antennal touch events signal potential obstacles and/or touch-down locations for the next step. This is likely to be important for locomotion in spatially cluttered, unpredictable terrain. During locomotion, stick insects continuously move both antennae to sample the space ahead. The antennal movement pattern of *C. morosus* is rhythmic, and may be coordinated with the stepping patterns of the legs [7]. So far, two context-specific changes of the antennal movement pattern have been reported: first, upon loss of foothold, the antennae back-up the searching movements of the front legs by complementary action [8]; second, during visually induced turning, the working-range shifts towards the direction of heading [27]. In a detailed comparison of the antennal movement pattern and concurrent stepping movements of the front legs, it could be shown that the likelihood that an antenna touches an obstacle before a leg gets there, i.e. in time to provide contact information for guidance of leg movements, increases with obstacle height [7]. It is only 10–30 per cent for very low obstacles (less than 4 mm) but reaches 70 per cent at around 8 mm, which is equivalent to the height range at which models of the insect walking system fail to climb the obstacle without a change in motor strategy [28]. In other words, it seems as though the normal antennal searching pattern is particularly suitable to detect obstacles which are too high for the walking system to climb, at least without descending sensory information about how to adapt the motor pattern appropriately. Indeed, antennectomized stick insects drop in performance in a wall-climbing paradigm, whereas blindfolded animals do not [9].

The present study uses a narrow, vertical rod as an obstacle (figure 1c). This was for three reasons. The first reason was that stick insects appear to have an...
internal tendency to climb up twig-like structures. This made our behavioural paradigm very robust and repeatable, as stick insects tended to climb up the vertical rod whenever they found out about its presence through antennal touch. The second reason was that the rod could be placed off-midline. By placing the rod in the lateral working range of one antenna, stick insects often touch it with a single antenna only during the initiation of climbing, i.e. until the foot first contacts the rod. Finally, with a narrow rod, the analysis of touch events can be reduced to a one-dimensional variable: the height of contact. Building on preliminary results of Dürr & Krause [29], we show that the swing movement of a front leg can be re-targeted towards the obstacle upon tactile contact with an antenna. Furthermore, we show that the height of the first foot contact on the obstacle can be predicted from the preceding sequence of antennal touch events.

Finally, we report on two major changes of the antennal movement upon tactile contact with the obstacle: an increase in cycle frequency and a distinct switch in inter-joint coupling in both antennal joints.

2. MATERIAL AND METHOD

Experiments were carried out on adult female Indian stick insects C. morosus (Sinéty, 1901), bred in a laboratory culture at Bielefeld University. The entire set-up was kept in black and illuminated by a custom-built infrared flash light. During trials, room light was limited to the indirect light of a TFT computer screen; between trials, a red spotlight was switched on to allow visually guided human handling of the animals. Each trial consisted of a free walking sequence along a wooden walkway (width: 40 mm) with a vertical rod near its end (diameter: 6 mm). The rod was located between the midline of the walkway and its left margin, such that straight walking animals were most likely to contact it with their left antenna or front leg first (figure 1c).

Movement analysis was done for movements of the body axis, left antenna and front leg, using custom-made markers of retro-reflective foil (Scotchlite, Type 8850, 3M Corp., St. Paul, MN, USA). Six markers were located on the rear mesothorax, mid prothorax, distal left femur, proximal and distal left tibia and proximal third of the left antennal flagellum. Markers on thorax and leg segments were fixed with a small drop of transparent nail polish. The marker on the antenna was fixed by a knot around the flagellum. Since the load was fixed to the front leg, a mechanical effect on antennal movements was most unlikely. Nevertheless, all analyses were carried out for the pooled dataset (unloaded and loaded trials, pooled together) and for unloaded trials only.

The main results of this comparison are shown in electronic supplementary material, figure S2. They justified pooling of trials for the analyses presented in this paper.

All trials were classified as either reaching-movement or re-targeting-movement. Whenever the first antennal contact occurred during a stance movement of the ipsilateral front leg, the trials were considered a reaching-movement. If, however, the first antennal contact occurred during a swing movement, the trial was considered a re-targeting movement. The original classification was based on visual inspection of the video sequences.

The cycle frequency or frequency of modulation in antennal joint angle time courses was determined by the number of peaks or troughs per unit time. Peaks and troughs were automatically detected as zero crossings of the joint angle velocity time course. The latter was obtained by smoothing the joint angle time course with a Gaussian kernel of width 50 ms (five frames),
fitting a quintic spline (based on the QUINAT 600 algorithm by J. G. Herriot and C. H. Reinsch; http://netlib.bell-labs.com/netlib/toms/) and differentiating it. Velocity between two zero crossings had to exceed an absolute value of 10^7 s^{-1} for them to qualify as distinct extreme points.

A second, independent, set of experiments was done with a further three animals, where the same paradigm was studied first in sighted and then repeated in blindfolded animals (eyes covered by black paint). The purpose of this experiment was to prove that reaching and, particularly, re-targeting movements not only occur in sighted animals that walk in near-complete darkness, but also in blindfolded animals. For these experiments, we used two synchronized digital video cameras (Basler A602f), operating at 100 fps, above and to the side of the set-up (see the electronic supplementary material).

All motion capture and analysis software was custom-written in C++ (Microsoft Visual Studio; video acquisition), MATLAB (The MathWorks; kinematic analysis), Delphi (Borland; data analysis) or R 2.1.0 (www.r-project.org; statistics), except for simple t-tests and box-whisker graphs (Microcal Origin).

3. RESULTS
(a) Adaptive leg and body movements during the initiation of climbing

A total of 98 trials from five animals were analysed. In all trials, stick insects were left to walk freely along the straight walkway (figure 1c), touched the rod with the left antenna and climbed the rod. Movement sequences were analysed from the time at which the antenna first touched the rod until the time at which the ipsilateral leg first touched the rod. In trials, where the first antennal contact occurred during a swing movement of the ipsilateral leg, the analysis was started at the time of lift-off of the left leg, i.e. the start of swing movement. Figure 1d shows typical movement sequences of a swing movement (top) and the two kinds of tactually elicited reach-to-grasp movements observed. The first kind was termed reaching-movement (‘reach’ in figure 1d) and occurred whenever the antenna touched the rod during a stance movement of the ipsilateral front leg, i.e. while the leg had ground contact. In this case, retraction of the front leg continued and the stance movement was completed before the leg was moved towards the rod. At first sight, reaching-movements appeared to be similar to regular swing movements, except for the increased height of the foot trajectory. The second type of reach-to-grasp movement was termed re-targeting movement (‘re-target’ in figure 1d). This type of movement occurred when the antenna touched the rod during an ongoing swing movement of the ipsilateral front leg. Re-targeting movements were characterized by at least one distinct upward kink of the foot trajectory.

The relative frequencies of reaching movements and re-targeting movements were 73.5 and 26.5 per cent, respectively (72 and 26 trials). This is similar to the 3 : 1 ratio of stance and swing duration at the typical walking speed of 0.05 m s^{-1} [32]. In both kinds of reach-to-grasp movements, the height of the first leg contact with the rod appeared to depend on the preceding set of antennal contact locations (see below). Note that the leg did not always touch the rod at first with the tarsus (foot), but rather at more proximal parts of the leg. In this case, the leg was retracted and lifted until foot contact was achieved.

Whereas, in principle, reaching-movements could be pre-planned before their execution, re-targeting movements certainly could not, because the tactile information about the presence of the obstacle was obtained only after the initiation of swing movement. Although it was unlikely that the stick insects could see the black rod in front of a black curtain under the low-light conditions of the experiments, we repeated the experiment with blindfolded animals in order to rule out visual cues in triggering and/or controlling a re-targeting movement. Indeed, blindfolded animals also showed re-targeting of ongoing swing movements in response to antennal touch events (see figure 1e and videos in the electronic supplementary material). The foot trajectory and schematic of the leg movement in figure 1e illustrate the temporal and spatial relationship of two antennal touch events and corresponding actions of the reaching leg. During the first touch event (‘touch I’ in figure 1e), the antenna contacted the rod during an upward movement, causing considerable bending of the flagellum. Shortly after antennal contact, the foot trajectory exhibits an upward kink, followed by an even stronger kink shortly after termination of antennal contact (in this condition, the flagellum snaps back to its normal shape). A second, brief contact occurred during the subsequent downward movement of the antenna (labelled ‘II’ in figure 1e), followed by a forward bend of the foot trajectory. In the example shown, first leg contact occurred above the first, elongate antennal contact region and below the second antennal contact region. We conclude that re-targeting can be elicited by tactile cues alone and does not require additional visual information.

The existence of tactually mediated re-targeting movements reveals that antennal mechanosensory information, which enters the nervous system at the level of the deutocerebrum, has access to the motor networks of the prothoracic ganglion that controls movements of the front legs. In order to estimate the speed of information transmission from the antenna to the front leg, we measured the latency of the onset of a re-targeting movement at the single-joint level. For this, we differentiated twice the time courses of all leg joint angles and determined the shortest delay of the first turning point after the onset of antennal touch, i.e. the zero-crossing of the second derivative. Shortest delays were observed in leg protraction (thorax–coxa joint angle) and femoral levation (coxa–trochanter joint angle), where the median delays were 39 and 44 ms, respectively. Taking into account the original sampling frequency of 100 fps and inaccuracies owing to kinematic calculations and differentiation, it is reasonable to assume a typical latency of 40 ms.

Before the leg made contact with the rod, the antenna touched the rod up to five times. The most common number of antennal touch events prior to leg contact was three (n = 37), followed by two (n = 27; see also...
A reaching-movement trial with four concurrent antennal touch events is shown in figure 2a, b. As depicted in figure 2a, b, antennal touch events tended to occur in an upward sequence, with the first antennal contact in the sequence being lower than the last. In order to determine the extent to which the reach-to-grasp movements were aimed at the contact locations of the antenna, we conducted two kinds of statistical analyses, one concerning the mean antennal contact height, and one concerning individual contacts. The first analysis suggested that the average contact location of the antennal touch sequence could be used to predict the location of the first leg contact in the initiation of climbing (see electronic supplementary material, figure S1). This analysis was refined further by the use of multiple linear regression models, in which the predictive value of individual events of the antennal touch sequence was evaluated. First, we tested linear models that took into account exactly three antennal touch events prior to leg contact \( (n = 37) \), or the pooled data of all trials with at least two antennal touch events prior to leg contact \( (n = 85) \). In both cases, the model explained more than 86 per cent of the total variance, and regression coefficients for the last contact height were highly significant \( (p < 0.001) \). The coefficient of the second-last contact was weakly significant if only trials with exactly three antennal touch events were considered \( (p = 0.013) \), but non-significant if all trials with at least two events were considered \( (p = 0.0523) \). Coefficients of the linear models indicate that, on average, the first leg contact occurred at approximately 70 per cent of the height of the last antennal touch event (see also the electronic supplementary material, tables S3 and S4). To test for effects of contact duration, spatial spread of the contacted area and the load added to the front leg, we normalized these variables to the range \([0,1]\) and added them as further regression parameters to the model with two antennal touch events. None of these parameters proved to have a significant effect (duration: \( p > 0.27 \); spatial spread: \( p > 0.65 \); load: \( p = 0.0538 \); \( r^2 > 0.86 \), and \( n = 85 \) for all three models). For further details about the statistical analyses mentioned, see the electronic supplementary material, part II. In summary, the last antennal touch event prior to leg contact has a strong predictive value for estimating the height of the
During this sequence of antennal contacts, stick insects also changed their body attitude, such that the latter effect was non-significant if only unloaded trials were considered; see the electronic supplementary material, figure S2). This shows that, in addition to the reaction of the antennal joints, the body axis, too, is actively levated in reaction to antennal touch. Also, animals showed a tendency to turn clockwise, i.e. towards the midline with respect to the contacting left antenna.

Concerning the timing of reactions in both antennal joints, figure 3b shows the contact durations of the first touch events per trial, together with the latencies of the first local minima and maxima of the corresponding joint angle time courses. Local minima corresponded to a transition from depression to levation (labelled ‘up’ in figure 3b), whereas local maxima corresponded to a transition from levation to depression (‘down’ in figure 3b). Median contact duration was 90 ms. Median latencies of the four transitions indicated that the typical sequence of events is HS levation (20 ms after contact), followed by SP levation (50 ms after contact), followed by HS depression and SP depression (after 100 and 140 ms, respectively). This is illustrated in the schematic in figure 3c. The short latencies of alternating joint actions suggest an increased cycle frequency of both antennal joints. Since the analysed time sequences were relatively short, we estimated the cycle frequencies from the number of local minima and local maxima per observed time period (electronic supplementary material, figure S3). Taken together for both maxima and minima, the median cycle frequencies before antennal touch were 1.7 s⁻¹ for the HS joint and 1.4 s⁻¹ for the SP joint.
1.2 s\(^{-1}\) for the SP joint (this difference was weakly significant; Wilcoxon’s test for matched pairs, \(p = 0.041\)). After the first antennal touch event, median frequencies were 7.8 s\(^{-1}\) for the HS joint and 5.6 s\(^{-1}\) for the SP joint (Wilcoxon’s test for matched pairs, \(p < 0.001\)). In both joints, the increase in cycle frequency was strongly significant (Wilcoxon’s test for matched pairs, \(p < 0.001\) in all four cases; median increases: HS: 6.6 and 6.5 s\(^{-1}\) for minima and maxima, respectively). In summary, antennal cycle frequency increased approximately fourfold after the antenna touched the obstacle.

Finally, we were interested to see whether and how the coupling of the two antennal joints was affected by antennal touch. In order to quantify inter-joint coupling, we used the same approach taken by Dürr [33] to quantify coupling strength in hexapedal leg coordination. For this, we discretized the joint angle velocity time courses into two states: one denoting depression (state 0) and the other denoting levation (state 1). Then we calculated the likelihood of the SP joint to be in state 1, given a certain delay relative to a switch in HS movement. Error bars indicate 95% confidence intervals. For reference, dotted lines show likelihood of HS joint levation (see also the electronic supplementary material, figure S3b). (a,c) HS switches from depression to levation; (b,d) HS switches from levation to depression. Before first antennal contact, the SP joint tends to couple to HS joint depression. Later, it tends to couple to HS levation. Grey shading marks periods near time zero with strong coupling (likelihood of SP levation significantly deviates from \(p = 0.5\)).

Before antennal touch, SP depression tended to follow HS depression (compare solid and dotted lines in figure 4; note their similarity below 0.5). By contrast, SP levation did not reliably follow HS levation. After antennal touch, this situation nearly reversed. Now, SP levation tended to follow HS levation (likelihood values > 0.5), whereas SP depression did not follow HS depression. This shows that the strength of inter-joint coupling changes after the first antennal touch event, indicating a tactually induced switch in motor pattern in association with active tactile sampling.

4. DISCUSSION

Stick insects use their antennae as active, tactile near-range sensors during locomotion. When one of the antennae touches the vertical surface of an obstacle, the animal often initiates climbing behaviour. In the present study, the obstacle was a thin, vertical rod, which the animals antennated and climbed. The transition from straight, horizontal walking to vertical climbing involved a reach-to-grasp movement of the ipsilateral front leg and a concurrent change in antennal movement pattern. Concerning reach-to-grasp movements, we show (i) that there are two types (reaching and re-targeting, figure 1d), (ii) that they are tactually elicited (figure 1e), (iii) that the response latency of re-targeting movements is 40 ms, and (iv) that the height of first leg contact is significantly correlated with and, hence, well predicted by parameters of the preceding antennal touch sequence. This shows that stick insects use antennal tactile information for the control of adaptive locomotion. Concerning the
change in antennal movement pattern, we show (v) that the antenna repetitively samples the obstacle with up to five touch events prior to first leg contact, (vi) that antennal contacts tend to occur in an upward sequence (figure 2 and electronic supplementary material, figure S1) and at increasingly levated antennal posture (figure 3a), (vii) that both antennal joints tend to respond to touch with short-latency levation (figure 3b) and an increase in cycle frequency (electronic supplementary material, figure S3), (viii) that the HS joint tends to lead the SP joint during tactile sampling (figure 3c), and (ix) that the inter-joint coupling of HS and SP joints undergoes a distinct change once the antenna touches the rod (figure 4). This suggests that stick insects adapt the antennal movement pattern from a strategy that is efficient for near-range searching to one that is efficient for repetitive tactile sampling of an obstacle.

The kinematic analysis of antennal and leg movement was simplified in two ways: first, only one side of the animal was observed. This was because the obstacle was placed laterally from the midline of the walkway. Indeed, pre-test observations without kinematic analyses resulted in 40 out of 60 trials (67%, n = 3 animals) with ipsilateral-only contacts prior to first foot contact. In an additional nine trials (15%), the contralateral antenna made contact before the contralateral antenna or leg did. Under the assumption that these relative frequencies also apply to the experiments of the present study, the contralateral (right) antenna would have been involved in 32 out of 98 trials, and in 18 of these, it would have touched the rod before the ipsilateral (left) antenna did. Therefore, it is likely that contact information from the contralateral antenna contributed to the analysed behaviour, though this does not affect any of the conclusions made in the present study.

The second simplification concerned the roll component of the body axis (rotation around the rostro-caudal axis), which was neglected. This was reasonable, given the results from Diederich et al. [34], who showed that stick insects stabilize their horizontal body plane during walking on inclined surfaces by active counter-roll of the body axis, such that roll angles remain well below 10°, even for inclinations up to 60°.

Unlike previous studies on insect climbing, we can show a significant correlation between antennal touch location on the obstacle and the subsequent touch-down location of the first step on the obstacle. This is reminiscent of the targeting mechanism proposed for middle and hind legs in stick insects [38,39], where touch-down locations strongly depend on the position of the next anterior foot. The fact that the height of the last antennal contact prior to leg contact can be used to predict the height of the forthcoming leg contact suggests that front leg swing movements may be targeted towards a spatial position signalled by means of antennal tactile cues. The importance of tactual cues in reach-to-grasp movements is further supported by the finding that visual information is not necessary for eliciting re-targeting movements. Similar to the ‘targeting mechanism’ that has been used to model spatial coordination of front and middle legs (or middle and hind legs) in insect locomotion [28,40], we propose a mechanism of coordinate transfer between the antenna and the ipsilateral front leg. So far, our data indicate that such a targeting mechanism works for contact height (by weighting either last contact height or mean contact height). Future studies will have to investigate the extent to which targeting works for the remaining two spatial dimensions, too. To date, it is unclear which antennal mechanoreceptors might be involved in the coding of contact height. The most likely candidates for coding antennal elevation would be proprioceptive hair plates that are present at both antennal joints in stick insects [41], and that are known to affect tactual induced turning in the cockroach [15].

Apart from eliciting targeted reach-to-grasp movements, antennal touch also affects the movement of the antenna itself. During locomotion, the antennal movement pattern is rhythmical and the working range depends on the behavioural context of locomotion, as known for straight walking [7], searching for foothold [8] and turning [27]. In contrast to these ‘non-contact’ situations, the present results reveal a marked change in antennal movement pattern in response to antennal touch: it becomes a repetitive tactile sampling pattern with a faster, smaller-amplitude rhythm in both antennal joints. The cycle frequency increases, much as has been observed in cockroaches [14,15,35], we find only a weak tendency for tactually induced turning, at least during the period of the first three antennal contact events. It is possible that this is an effect of restrained movement of the prothorax. Indeed, this segment has been suggested to be of importance for the control of curve walking [36]. Also, the short duration of tactually induced reach-to-grasp movements (less than 1 s) compared with the timing of visually induced turning behaviour (time constants greater than 1.7 s [27]) could mean that tactually induced yaw-turning in stick insects may simply be too slow to result in a strong effect before first foot contact. Tactually induced changes in body axis inclination (pitch) during climbing have been reported for cockroaches [6,13] and beetles [37]. Here, we show that stick insects significantly incline their body axis no later than the second antennal touch event (figure 3a).
repetitively sample a vertical edge as a result of a simple pattern of inter-joint coupling (HS levation inducing a lagging SP levation), combined with slanted joint axes (that determine the movement directions and, thus, the trajectory of the antennal tip). In summary, the results show that antennal tactile cues about a touched obstacle efficiently initiate the onset of climbing behaviour, beginning with a targeted reach-to-grasp movement of the front leg, accompanied by a switch in antennal movement pattern to sample a vertical edge.

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