

Visual Targeting of Forelimbs in Ladder-Walking Locusts

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Summary

Accurate limb placement helps animals and robots to walk on substrates that are uneven or contain gaps. Visual information is important in controlling limb placement in walking mammals [1–4] but has received little attention in insects [5–7]. We investigated whether desert locusts walking along a horizontal ladder use vision to control limb placement. High-speed video analysis showed that locusts targeted their front legs to specific rungs in the absence of any previous contact, suggesting that visual information alone is sufficient for targeting single steps. Comparison between the proportions of missed steps before and after monocular occlusion showed that monocular visual information was used to place the ipsilateral but not the contralateral front leg. Accurate placement also depended upon mechanosensory inputs from the antennae and proprioceptive feedback from the ipsilateral but not the contralateral forelimb. Locusts also compensated for the loss of inputs to one eye by altering their stepping pattern. Changing the rung position after initiation of a step showed that targeting of the front leg depends on visual information acquired before but not during a step. The trajectory was only modified after missing the rung. Our data show that locusts walking in environments where footholds are limited use visual and mechanosensory information to place their front legs.

Results and Discussion

Most studies of insect walking have emphasized the role of mechanosensory information from antennae and forelimbs for correct foot placement and for obstacle and gap avoidance [5, 8–10]. Although vision influences the direction of searching movements during gap crossing in fruit flies [6], there is no evidence that visual inputs are involved in directly targeting insect forelimb movements during gap crossing or walking. We walked desert locusts, *Schistocerca gregaria*, along a horizontal ladder to determine whether they use visual inputs to control leg placement. Ladder walking requires accurate leg placement on rungs [11], which in the absence of previous contact must depend upon vision. High-speed video analysis of locusts walking along a horizontal ladder showed that they made directed leg movements from one rung to the next (Figures 1A and 1B). Altering the distance between rungs caused the locusts to adjust their front leg trajectory

accordingly (Figures 1A and 1B). Because in these experiments, the locusts' antennae were waxed in an elevated position preventing contact with the rungs, we conclude that vision is sufficient to direct the front leg from one rung to the next.

Although locusts walking on a flat surface move their limbs in an alternating tripod gait [12], this gait was rarely observed in ladder-walking locusts (Figure 1C). Instead, whereas a front leg often moved in phase with the contralateral middle leg, the hind legs moved infrequently. The front and middle legs were moved to either the next rung or the one after that (omitting the intervening rung), but the hind legs often moved several rungs in one step. For any particular rung, either the left or right front leg had an equal probability of being the leading leg (G test; $G = 0.389$, $p = 0.5331$, $n = 20$). The leading leg always reached a rung before the other legs.

The legs of ladder-walking locusts missed some rungs (Figure 1D; see also Figure S1 available online), primarily as a result of the underestimation of the rungs' distance. During these errors, the leg continued downwards, below the level of the rungs, before being retargeted correctly (Figure 1D). The proportion of steps resulting in errors during ladder walking provides a measure of limb placement accuracy. If errors are random events, however, a small sample of steps may give a biased estimate of the proportion of steps resulting in an error (hereafter referred to as error rate). We established whether these errors were random events and assessed the reliability of our measurements by comparing the error rates in each leg after different numbers of steps. Because antennal inputs may also be important for leg placement while walking on uneven substrate, in these and subsequent experiments, unless stated otherwise, the antennae were not waxed as in the initial experiments but were free to move. The error rates of the front and middle legs were assessed because vision could influence the placement of these legs, whereas error rates of the hind legs were not assessed because hind legs are not used consistently during ladder walking (Figure 1C).

The mean error rate of each leg remained almost constant from 10 to 40 steps ($n = 30$ animals), suggesting that this is a robust measure of accuracy (Figure 2A). We used 30 steps to estimate all subsequent error rates and, to avoid any potential effects of "handedness" in leg use, randomly assigned ipsilateral and contralateral sides. The proportion of errors was 0.25 ± 0.01 (mean \pm standard error; $n = 30$ animals; $n = 30$ steps per animal, unless stated otherwise) for the front ipsilateral leg (FIL), 0.27 ± 0.01 for the front contralateral leg (FCL), 0.30 ± 0.02 for the middle ipsilateral leg (MIL), and 0.31 ± 0.02 for the middle contralateral leg (MCL) (Figure 2A). Comparison of the error rates revealed that there was no significant difference between legs (analysis of variance [ANOVA]; $F_{3,116} = 1.829$; $p = 0.1458$).

Errors in one leg may evoke subsequent errors in the same leg or other legs as a result of coupling between legs or changes in stability. We assessed the temporal correlation of errors within and between legs across all locusts and all steps. The errors made by a single leg showed no temporal correlation, being distributed randomly across all steps (Figure S2). Likewise, the errors made by one leg were not temporally correlated to those made by other legs (Figure S3).

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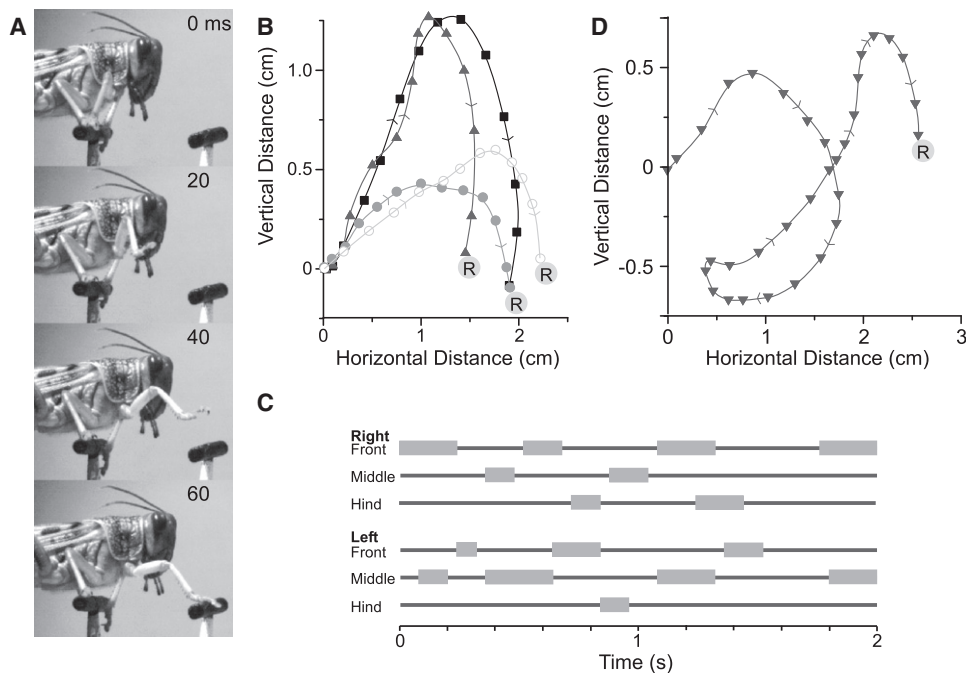


Figure 1. Targeted Limb Placement during Ladder Walking

- (A) A typical sequence of high-speed video images showing a locust making a targeted forelimb movement from one rung of the ladder to the next.
 (B) The trajectory of the tibiotarsal joint during four targeted movements of the forelimb by the same individual to a rung placed different distances away. The starting position is (0,0) for each step.
 (C) A typical sequence of steps made by locusts walking on a ladder with rungs 1.3 cm apart. Light gray indicates the swing phase of a step; darker gray indicates the stance phase.
 (D) The trajectory of the tibiotarsal joint during an error. The forelimb undershoots the rung, producing the error, but is rapidly retargeted following the error.

Locusts could target footholds by using sensory information to match their stride length to the spacing of the ladder's rungs. However, the spacing of the ladder's rungs may also coincide with the stride length of locusts walking on a flat surface. We measured the stride length distribution for the front and middle legs of locusts walking on a flat surface (front, 2.16 ± 0.03 cm; middle, 2.21 ± 0.03 cm; $n = 178$) (Figure S4). During a step, each front or middle leg starts from one rung and targets either the next rung on the ladder or the one after that. Therefore, there are two regions of the distribution where the locusts' stride lengths match the rung spacing, predicting an error rate of 0.70 for the front legs and 0.65 for the middle legs without sensory information. Because the error rate of the front or middle legs of ladder-walking locusts was ~ 0.3 compared to the 0.7 expected if the stride length distribution was the same while walking on a ladder as on a flat surface, sensory information must be used to adjust stride lengths.

What contribution does vision make to the accuracy of leg placement during ladder walking? If ladder-walking locusts use vision to control leg placement during walking, then disruption of vision should increase the error rates of the legs. After measuring the error rate with both eyes intact, we occluded one of each locust's compound eyes and assessed the error rates of these 30 locusts as before. As with normal vision, the estimated error rate of each leg between 10 and 40 steps remained almost constant, suggesting that our measure, taken after 30 steps, was still valid (Figure 2B). The proportion of errors was 0.34 ± 0.02 for the FIL, 0.29 ± 0.02 for the FCL, 0.31 ± 0.02 for the MIL, and 0.28 ± 0.02 for the MCL (Figure 2B). After monocular occlusion, there was

a significant difference in the mean error rate between legs (ANOVA; $F_{3,116} = 2.798$; $p = 0.0433$) (Figure 2C).

Subtraction of the original error rate of each leg from the error rate of the same leg of the same individual after monocular occlusion (Figure 2C) showed that monocular occlusion produced a significant increase in the mean error rate of the locusts (ANOVA; $F_{3,116} = 7.5$; $p = 0.0001$). This significant increase was due to an increase in the error rate of the front leg ipsilateral to the occluded eye (Tukey honestly significant difference [HSD] test; $p < 0.0459$). Repeating the analysis with two separate cohorts of locusts also showed that monocular occlusion produced a significant increase in their mean error rate (ANOVA; $F_{1,76} = 11.276$; $p = 0.0012$; $n = 40$) as a result of an increase in the error rate of the front leg ipsilateral to the occluded eye (Tukey HSD; $p < 0.005$). The increase in the error rate of the FIL but not the FCL shows that monocular visual inputs are necessary for accurate placement of the FIL. Binocular visual inputs are not necessary for accurate limb placement because occlusion does not affect the error rate of the FCL, though this does not exclude their use in normally sighted locusts. Placement of the middle legs was unaffected by monocular occlusion, suggesting either that they are not under visual control or that monocular visual information is sufficient to maintain their accuracy.

Although the increase in the error rate of the front leg ipsilateral to the occluded eye suggests an ipsilateral visual input, other sensory cues could be used, namely inputs from the antennae (which were free to move), the contralateral eye, or the FCL if it had previously been placed on the rung. We tested the effect of antennal removal on the error rate of the front legs before and after monocular occlusion. Removal of both

Visually Targeted Limb Movements in an Insect

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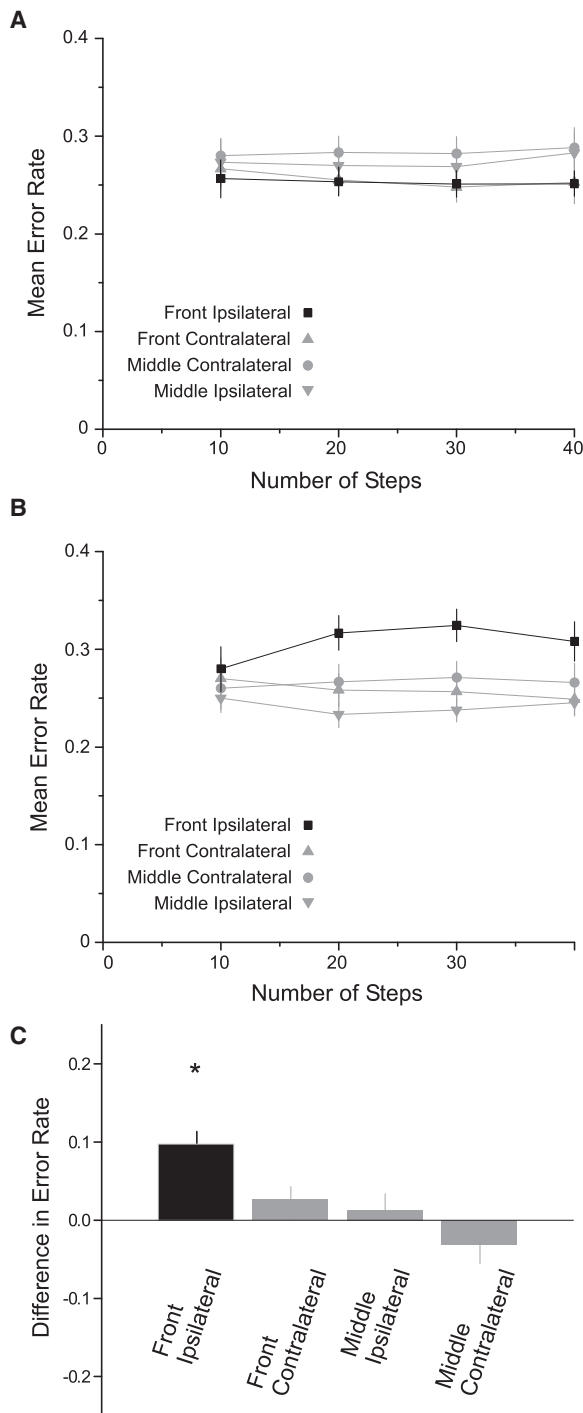


Figure 2. Error Rates within the Front and Middle Legs during Ladder Walking before and after Monocular Occlusion

(A) The estimated mean error rate of each leg initially remained constant between 10 and 40 steps.

(B) The estimated mean error rate of each leg initially remained constant between 10 and 40 steps following monocular occlusion.

(C) The difference between locusts with normal vision and after monocular occlusion in the number of errors made by each leg after 30 steps. The number of errors made by the front ipsilateral forelimb increased significantly (asterisk), but the other limbs were unaffected.

All data are mean \pm standard error (SE) from $n = 30$ animals. Ipsilateral and contralateral are defined relative to the eye in which vision was occluded (see main text for details).

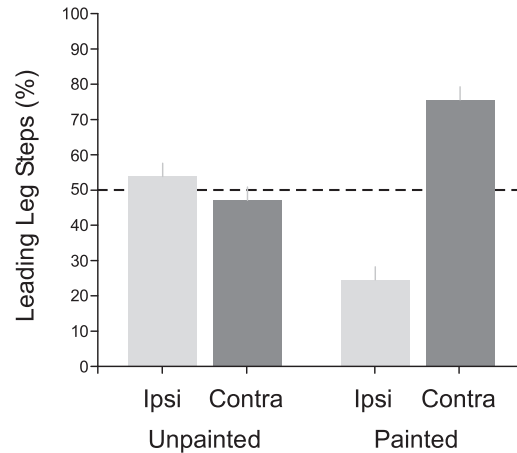


Figure 3. Loss of Vision in One Eye Reduces the Proportion of Steps in which the Ipsilateral Forelimb Leads

The proportion of steps in which each forelimb was used as the leading leg in locusts before (unpainted) and after (painted) monocular occlusion. The dashed line indicates the expected 50:50 ratio. After monocular occlusion, there is a significant decrease in the use of the front ipsilateral forelimb. Data are mean \pm standard error from $n = 30$ animals. Ipsi (light gray) indicates the front ipsilateral leg; contra (dark gray) indicates the front contralateral leg. Ipsilateral and contralateral are defined relative to the eye that was occluded (see main text for details).

antennae caused a significant increase in the error rate of the front legs (before removal, 0.22 ± 0.02 ; after removal, 0.32 ± 0.02 ; ANOVA; $F_{1,78} = 10.704$; $p = 0.0016$; $n = 40$) (Figure S5). After monocular occlusion, removal of both antennae caused a significant increase in the error rate of the FIL (before removal, 0.37 ± 0.02 ; after removal, 0.51 ± 0.04 ; ANOVA; $F_{1,78} = 12.383$; $p < 0.0007$; $n = 40$) (Figure S6). Thus, antennal as well as visual inputs contribute to accurate limb placement.

Following monocular occlusion, the contralateral eye could still provide information about the rung position on the ipsilateral side because the frontal visual field of locusts contains a region of binocular overlap [13]. We tested whether visual inputs from this region contributed to the accuracy of the ipsilateral leg by painting over the facets in this region. Occlusion of this binocular region did not, however, significantly affect the error rate of the FIL (data not shown), suggesting that inputs from the eye contralateral to the forelimb do not contribute to its targeting.

Loss of ipsilateral visual inputs for targeting the front leg could be compensated for by leading with the FCL. We assessed the proportion of steps in which the FIL or FCL was the leading leg before and after monocular occlusion of the ipsilateral compound eye (Figure 3). Before monocular occlusion, the FIL and FCL were used equally often as the leading leg, but afterwards, the proportion of steps in which the FCL was the leading leg increased significantly (G test; $G = 55.094$, $p < 0.0001$, $n = 40$) (Figure 3). This suggests that locusts alter their walking pattern following monocular occlusion, thereby reducing the number of limb targeting errors, emphasizing the importance of visual inputs for selecting the leading limb.

Does mechanosensory information from the leading leg contribute to the targeting of the other front leg? The femoral chordotonal organ (FeCO) is the major proprioceptive sense organ monitoring the movement of the tibia [14]. We disrupted mechanosensory feedback by cutting the tendon of the FeCO of the leg contralateral to the monocular occlusion, disrupting

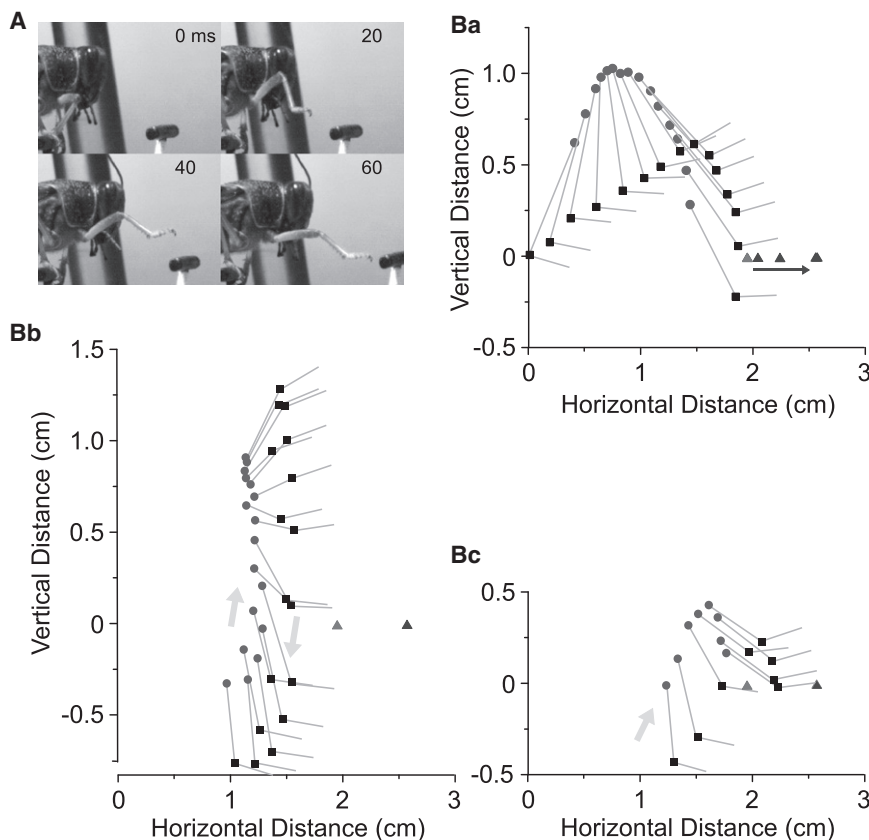


Figure 4. Visual Control of Forelimb Targeting

(A) A sequence of high-speed video images showing a locust making a targeted forelimb movement to a rung. The displacement of the rung during the forelimb movement does not affect the initial trajectory, and an error occurs. The forelimb is retargeted following the initial error.

(Ba–Bc) The trajectory of the femorotibial (gray circle) and tibiotarsal (black square) joints and the rung (gray circle) during three different epochs of the movement shown in (A). The starting position of the rung is indicated by a light gray triangle.

(Ba) The initial trajectory toward the rung triggers movement of the rung away from the original position and causes the leg to miss.

(Bb) The leg continues to search the region of space near the original position of the rung.

(Bc) The leg is retargeted to the new rung position.

mechanosensory feedback. This disruption significantly increased the error rate of the operated limb in comparison to sham-operated animals (operated, 0.27 ± 0.02 ; sham, 0.21 ± 0.02 ; ANOVA; $F_{1,35} = 4.216$, $p = 0.0475$, $n = 18$). However, the error rate of the leg ipsilateral to the monocular occlusion was not affected (operated, 0.24 ± 0.2 ; sham, 0.25 ± 0.3 ; ANOVA; $F_{1,35} = 0.002$, $p = 0.9618$, $n = 18$), suggesting that mechanosensory information about the position of the distal segments of one leg is necessary for the accuracy of that leg but not of the other legs. Thus, visual inputs play a role in targeting leg movements in combination with mechanosensory inputs from the antennae and proprioceptive feedback from the FeCO, but not feedback from the FeCO of the FCL.

Locusts could use motion parallax and/or looming as monocular cues to estimate the distance between rungs. Stereotyped peering movements involving head rotations are made by locusts and mantids to obtain motion parallax [15, 16]. We did not observe these movements in ladder-walking locusts, and the error rates of the front legs were unaffected by fixing locusts' heads with glue to prevent rotation (ANOVA; $F_{1,70} = 0.379$, $p = 0.5401$, $n = 36$). Instead, head movements in ladder-walking locusts were generated during walking. These head movements could produce both parallax and looming cues. In fruit flies, vertical edges on the front surface of the opposite side of the gap carry sufficient visual cues for initiating climbing [6]. Ladder rungs, however, provide only a small front surface (approximately 5° at the beginning of a step), and only the ends of the rungs provide vertical edges, suggesting that the motion of these small vertical edges generated during walking provides a distance cue for rung distance estimation.

Visual information obtained before and/or during the onset of a step may be used to target a rung. To distinguish between

these possibilities, we tested whether locusts could target a rung accurately if that rung was moved further away after the step was initiated. If the rung position (which was randomly varied from 1 to 2 cm) is estimated before the onset of a step, then the locusts cannot account for the movement of the rung; however, if the position of the rung is updated during the step, then rapid

retargeting may be possible. Rung movement was triggered by an infrared beam that crossed the path of the locust. When the leading leg broke the infrared beam, it triggered a movement of the targeted rung away from the locust. In all cases, movement of the targeted rung during a step caused the leg to miss, producing a forced error (Figures 4A and 4B). The error may be due to the time taken to transmit a signal from the visual system to the muscle or may be due to the properties of the muscles themselves [17, 18]. This suggests that visual information was obtained either before the onset of a step or early in the swing phase of the step. The leading leg then began rhythmic searching movements in the space that the rung had occupied before being retargeted to the new rung position (Figure 4B). In many cases, the locust appeared to stumble when the leading leg failed to contact the rung in the original position (data not shown), emphasizing the importance of vision to the stability of walking locusts.

Persistent searching in the original rung position and the absence of modification during a step suggest that a memory of the rung position is maintained until an error is detected. A similar memory has also been proposed to maintain information about the distance across a gap in walking fruit flies [6], though whether these object memories are retained in similar neural circuits is unclear. Mammals also use visual inputs obtained before the onset of a step to generate the initial trajectory of a leg toward a specific target; however, visual inputs obtained during the step are also capable of modifying the trajectory of the leg [2, 3, 19, 20]. The absence in locusts of visual control of leg targeting during the step may be because insects, which walk close to the substrate and have an exoskeleton and a low body mass, are less susceptible to injury than mammals.

The extent to which visual inputs are used by other insect species to control limb placement during walking remains unclear. Stick insects and cockroaches primarily use antennal inputs or searching movements of the front leg for controlling leg placement while making their way through complex environments [8–10, 21]. Mechanosensation may be more reliable than vision under the low light conditions in which many stick insect and cockroach species, being either crepuscular or nocturnal, are active [22]. During walking, vision in stick insects and cockroaches may be more important for orientation and turning [7] than for directly influencing forelimb trajectories. Fruit flies use visual inputs during gap crossing to detect the opposite side of the gap, but these visual inputs appear to direct rhythmic “leg over head” searching movements rather than directly targeting the trajectories of the front legs [6]. Thus, the only other evidence that insects can use visual inputs to directly target front leg movements is in the raptorial strikes of the praying mantis and mantispid [23–25].

Conclusions

Our experimental results show that when walking over uneven terrain, locusts use monocular visual inputs to accurately place their front legs. Mechanosensory inputs from antennae also contribute information about the distance between rungs. We find that visual and antennal mechanosensory inputs are used to generate the motor pattern targeting the front leg to a rung before the onset of the step. Accurate limb targeting also requires proprioceptive sensory information from the FeCO. The mechanism by which errors are detected remains unclear but is probably an overrotation of the coxal leg joint. In the absence of visual inputs from one eye, locusts adjust their pattern of limb movements during walking to ensure that the contralateral front leg, which receives inputs from the unoccluded eye, is used more often as the leading leg in each step. The reconfiguration of the stepping pattern occurs immediately upon monocular occlusion, suggesting that it is produced by the intrinsic flexibility of neural networks controlling limb movements and does not require long-term changes in neural circuits. The rapid induction of a shift in stepping pattern emphasizes the importance of vision for the control of limb placement during walking in the locust.

The majority of studies on insect visual systems have concentrated on the control of flight, orientation, and homing. To our knowledge, our experiments provide the first evidence for visual targeting of front legs during walking in an insect. Leg targeting places demands different from those of flight control upon the insect visual system, requiring that visual information about the target be transformed into a motor pattern that coordinates the movements of multiple leg joints. The neural mechanisms for this transformation of visual information into motor patterns for limb targeting in locusts are currently unknown.

Experimental Procedures

Animals

Fifth-instar female locusts (*Schistocerca gregaria*, Forskål) were selected at random from a crowded colony maintained at the Department of Zoology, University of Cambridge.

Video Analysis of Ladder Walking

A horizontal ladder was built with up to 90 black rungs 4 cm long and 0.1 cm wide spaced approximately 1.3 cm apart. The ladder was placed in a 45 × 85 cm white rectangular arena. Each individual was placed on the ladder, and filming began once walking had started and continued until the locust had made at least 30 steps. A high-speed video camera (Photron Fastcam-X

512 PCI) captured leg movements during walking at 250 frames per second for offline analysis of limb kinematics. A second video camera was positioned directly above the ladder to record the pattern of stepping during walking and for the detection of an error when a leg failed to reach a rung. Videos were saved and analyzed offline. Each locust was identified by a number painted onto the pronotum with acrylic paint. The paint had no effect upon the performance of the locusts (data not shown). For each individual, the number of errors in each leg and their location along the ladder were recorded and then converted into an error rate (error rate = number of errors/total number of steps). The first leg (left or right) to make contact with a rung was defined as the leading leg and was also recorded.

Once the error rate of the locusts was established, their left or right eye was occluded with black acrylic paint. The eye to be occluded was chosen randomly. These locusts then walked along the same ladder, and the error rate for each of their legs was recalculated. The frequency with which the right or left front leg was used as the leading leg was also recalculated.

We also built a second ladder with black rungs 6 cm long, 0.2 cm wide, and spaced 1.2 cm apart. We used this ladder to reassess the effect of monocular occlusion in two separate cohorts of locusts. This ladder was used in subsequent tests of the effects of manipulations on the error rates of the front legs.

In addition to having an eye occluded, the antennae of some locusts were removed while other locusts had the region of binocular overlap on their other eye painted with black acrylic paint. One further treatment involved cutting the tendon of the femoral chordotonal organ (FeCO) of the front leg contralateral to the occlusion. A small flap of cuticle in the front leg was pulled back to reveal the tendon of the FeCO, which was cut with minimal damage to the surrounding tissue. As a control, some locusts were randomly assigned for sham operations. In these animals, the small flap of cuticle in the front leg was pulled back but the FeCO tendon was left intact. In both operated and sham-operated locusts, the flap of cuticle was replaced and sealed. In all treatments, the error rates and leading leg frequencies were recalculated.

Stride Lengths

A video camera was positioned directly above the arena to record the pattern of stepping during walking. Videos were saved and analyzed offline. The stride length was calculated as the distance between the anterior extreme position and the posterior extreme position of the limb (e.g., the total distance of the swing phase of the step).

Movement of a Rung during Stepping

Wooden T bars were spaced as in the 1.3 cm ladder, except that one of the T bars was attached to a moveable plastic sleeve that slid over the surface of the metal base (Figure 4). This plastic sleeve was in turn in contact with a pair of solenoid coils that were activated when an infrared sensor beam was obstructed. The infrared beam was located in the gap before the moveable T bar so that the locust's foreleg would obstruct the beam and cause the T bar to move.

Analysis

Videos were analyzed either with custom-built software (MATLAB, The MathWorks) or with MotionScope (Redlake). Data were tested for independence, normality, and equal variance. Where necessary, data were arcsine transformed. The appropriate statistical tests (ANOVA, Tukey HSD test, or G test) were performed with the R statistical software package or with MATLAB (The MathWorks).

Supplemental Information

Supplemental Information includes six figures and can be found with this article online at doi:10.1016/j.cub.2009.10.079.

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