

Simple rules governing leg placement by the stick insect during walking

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Abstract

Finding adequate footholds on a patchy substrate is an important task in walking. When one leg of the stick insect has a foothold, it guides the swing of an adjacent leg to this location. An analytical solution for this interleg coordination involves two non-linear coordinate transformations. Physiological experiments suggest that the nervous system uses an approximate algorithm based on comparing the joint angles of the standing and moving legs. Simulations with artificial neural networks trained using back-propagation show that such a mechanism can produce the observed level of accuracy. Placement errors in which the moving leg strikes the target leg lead to a simple feed-forward correction behavior. The underlying mechanism again appears to represent an approximate rather than an exact algorithm.

Introduction

The natural walking substrate of the stick insect is an irregular environment of leaves and branches, not the smooth laboratory surfaces where walking is usually studied. Finding a suitable foothold under such conditions is not trivial. The stick insect simplifies the problem by using a spatial coordination between adjacent ipsilateral legs. Cruse (1979) showed that when a middle is standing on a fixed platform as the insect begins a walk, the first step of the adjacent rear leg carries its tarsus to a position close behind the tarsus of the middle leg. If the platform is moved to different positions, the rear leg adjusts its swing so that the end point maintains the same position relative to the new position of the target leg (Fig. 1). This interleg coordination or targeting behavior also occurs during steady walking both for middle and rear legs and for front and middle legs (Dean and Wendler 1983).

Several proprioceptors on the leg are known to provide information on leg configuration which influences the movement of the leg itself. For example, Wendler (1964) found that hair plates which measure the angle at the subcoxal joint, the basal joint where the leg inserts in the thorax, contribute to a negative feedback control which limits the forward swing of the leg. These hairs are increasingly excited as the leg swings forward; their ablation causes overstepping. However, the targeting behavior requires that the control centers for the moving leg also receive information about the configuration or tarsus position of the target leg. In part, this information comes from the same proprioceptors (Cruse et al. 1984, Dean and Wendler, 1983). However, the results from ablation experiments indicate that the influence is quite non-linear.

An analytical description of the targeting behavior focuses on the coordination of the tarsus positions because this is the appropriate measure of success. However, the insect's nervous system does not have direct information about tarsus position. Instead, it receives information about joint angles. Thus, an exact algorithm for the targeting behavior leads one to expect that the thoracic centers controlling the movement of the target leg first integrate the afferent sensory information to compute the position of its tarsus and then send this target information to the thoracic centers controlling the adjacent leg. The latter must find suitable joint angles and corresponding motor commands to place the tarsus at the desired position at the end of its forward swing. Thus, the exact algorithm requires the nervous system to solve first the direct kinematic problem for the target leg, using joint angles to find the position of the middle leg's tarsus, and then the inverse kinematic problem, finding appropriate joint angles to place the tarsus of the rear leg at the target. The present report summarizes physiological and modeling experiments designed to test this hypothesis. The results suggest that the insect's nervous system relies on a simpler approximate algorithm.

Although learning has not been demonstrated in the stick insect, the algorithm

may incorporate several simple rules relating to the success of the targeting. One is a behavior which can be regarded as an error-correcting procedure in case the moving leg actually hits the target leg. This behavior, the treading-on-tarsus reflex or TOT reflex (Graham 1979), causes a readjustment in the swing end point of the moving leg.

Neural elements which may mediate the targeting behavior

As indicated above, the spatial coordination of adjacent middle and rear legs, for example, requires that the centers controlling the forward swing of the rear leg receive information about the position of the middle leg's tarsus and this information ultimately must be derived from proprioceptors measuring the joint angles of the middle leg. Morphological evidence suggests the network shown in Figure 2a. In insects, each pair of legs is controlled by a separate segmental ganglion containing a core of neuropile in which synaptic integration takes place and an outer rind of neuron cell bodies. These ganglia are joined by paired connectives containing the axons of neurons passing between segments. Stains applied to leg proprioceptors show that the primary sensory fibers project only as far as the ipsilateral side of the segmental ganglion (Schmitz et al. 1991), so the information on middle leg configuration initially travels only into the mesothoracic ganglion. For their part, the motoneurons controlling movement of the rear leg are confined to the metathoracic ganglion, so there must be intersegmental interneurons which receive information from the proprioceptors of the middle leg and transmit it directly or indirectly to the motoneurons of the rear leg.

The physiological experiments were undertaken to look for these interneurons and characterize the information they carry. For this purpose, stick insects were restrained on a holder with movable supports for one or more legs. The thorax was opened so that glass microelectrodes could be inserted into neurons in the metathoracic ganglion near the entrance of the anterior connective. This location was chosen in order to monitor the information arriving from the mesothoracic ganglion when the middle leg was moved in different directions.

Two intersegmental interneurons which could contribute to the targeting behavior are shown in Figure 3. The important physiological feature is that both show tonic activity which reflects the position of the middle leg's tarsus. One responds with increasing discharges as the tarsus of the middle leg is moved caudally; the second increases its discharge rate as the tarsus is moved dorsally. Both have axons in the anterior connective and neither has a cell body in the metathoracic ganglion, so the morphology is consistent with that of interneurons receiving information in the mesothoracic ganglion. Responses in both neurons also contain a phasic component: that is, as

the middle leg is moved to a new position, the change in the response rate is magnified at first and then returns to a more constant rate reflecting the new position. Whether this phasic component is adaptive is not yet clear, but it could contribute a prediction of the future position of the leg and thus help to compensate for conduction delays in the CNS and low-pass characteristics of the muscles.

Despite intensive search, surprisingly few interneurons were found to show a significant tonic response to middle leg position. In fact, the illustrated neurons are the only ones providing a tonic measure of position in the caudal and dorsal directions; a third unit appears to be the only one signalling lateral position in a tonic manner. Neurons responding in a purely phasic manner to changes in middle leg position were more frequent, but their activity does not provide unambiguous information useful for controlling the targeting.

Still more surprising was the discovery that the neurons responding tonically to changes in the tarsus position of the middle leg actually only monitor changes at a single joint of the middle leg. For example, the tonic activity of the neuron excited by caudal movement of the middle leg only signals the accompanying retraction at the subcoxal joint whereas that of the neuron excited by dorsal movement only responds to leg elevation at the coxa-trochanter joint. Similarly, neurons responding to lateral movement appear to monitor only the position of the femur-tibia joint. Thus, it appears that the metathoracic ganglion simply receives reports on the angles of the individual joints of the middle leg. To be sure, these reflect the integrated activity of many sensory cells at each joint, but they do not reflect any computation of tarsus position in abstract coordinates.

Therefore, additional recordings were made in other parts of the metathoracic ganglion in order to explore further links in the network controlling the targeting movement. Recordings were made from motoneurons and from interneurons located farther from the entrance of the connective and therefore more likely to carry results of integrative processing in the metathoracic ganglion. Figure 4 shows a particularly interesting local interneuron, i.e. a neuron with processes confined to one segmental ganglion. Like the intersegmental interneuron discussed above, this neuron is excited (depolarized) when the middle leg is moved caudally. However, it is also excited when the rear leg is moved forward, so the membrane potential represents a measure of the distance between the two tarsi. Like the intersegmental interneuron, the activation actually reflects the difference between the angles at the subcoxal joints of the two legs rather than that between tarsus positions as such. Since depolarization of this local interneuron tends to terminate the activity of protractor motoneurons, those responsible for the forward swing of the rear leg, it appears ideally suited to contribute to the targeting behavior.

Modeling studies using artificial neural networks

Because the physiological results indicated that the intersegmental signals are limited to relatively few neurons and that they are apparently related to joint angles rather than to abstract measures of tarsus position, the sufficiency of such a network was explored in a simulation using artificial neural networks (Fig. 2b, Dean 1990). The task for the network was not to explicitly solve the relationship between the middle leg's position and the appropriate end point for the swing of the rear leg, but rather to learn an equivalent association. This association was trained using 28 pairs of middle and rear leg configurations and the back-propagation algorithm. Leg configuration was defined in terms of three parameters; for different simulations, these were either the three Cartesian coordinates of the tarsus position or the angles of the three leg joints. The results for the association between pairs of configurations defined in terms of joint angles were then converted to the corresponding tarsus positions. The comparison between results from this simulation and behavioral experiments show a similar level of target accuracy (Fig. 1b), which supports the notion that the insect relies on a simple association of joint angles for the rear leg to joint angles of the middle leg.

Correcting errors in targeting

Experimental manipulations or normal variation can cause the moving leg to strike the target leg or step onto its tarsus. Such a situation disturbs normal walking because the temporal coordination is such that the target leg needs to lift and swing forward shortly after the rear leg completes its swing. This is difficult if the rear leg is standing on the tarsus of the middle leg. Graham (1979) described a behavior, the TOT reflex, which corrects this error by causing the rear leg to be lifted and replaced on the substrate a bit farther to the rear (Fig. 5). This adjustment involves a rearrangement in the normal rhythm of activity in the motoneurons controlling the protraction and retraction of the leg. Figure 5 illustrates a record of the leg movement and the underlying activity of the protractor motoneurons. During the interruption of protractor activity, an extra burst of activity in retractor motoneurons occurs to move the leg backward.

A priori such a behavior could be triggered by comparing the tactile signals from the two tarsi or by computing the position of the tarsi in order to determine whether they are at the same position. However, Graham concluded that the behavior is triggered in a feedforward manner by any tactile stimulus to the tarsus of the forward leg as long as it occurs at an appropriate time in the step cycle of the rear leg. Stimuli applied before the rear leg completes its swing shorten the swing. In other words, the nervous system does not actually check whether the rear leg hit the target leg; it assumes that the rear leg is responsible for any tarsal stimulation of the middle

leg if the former is at or near the end of its swing. Further investigation (Schmitz and Haßfeld 1989) showed that the position of the moving leg as well as its state influences the tendency to produce a TOT reflex, i.e. the moving leg is assumed to be responsible if it is in a forward position, regardless of where it is in the step cycle. The position of the front leg, which also affects the probability of a true collision, is not used. More surprisingly, when the insects are induced to walk backwards, it is still the front leg which can elicit a TOT reflex by the middle leg, although the leg that the middle leg will hit if it oversteps is now the rear leg, not the front leg. In summary, as in the targeting itself, the algorithms for the error correction also represent simple approximations to the exact solution.

Discussion

Given the normal habitat of the stick insect, a mechanism helping the legs find suitable footholds is clearly advantageous. The mechanism used by the stick insect is a kind of follow-the-leader principle which helps middle and rear legs to use any footholds found by the front legs. An exact algorithm for this spatial coordination involves rather complex trigonometric computations, but the behavior in the stick insect appears to rely on simple approximate rules. The basic control can be described as an association between appropriate final joint angles for the moving leg and the current angles at the joints of the target leg. Short-term plasticity in the targeting behavior has not been demonstrated and in fact, the stability of the ablation effects make it appear unlikely. However, errors in the coordination do lead to corrective behaviors: the TOT reflex discussed here if the leg oversteps or searching behavior if the leg fails to find a foothold. In theory, these could also help calibrate the association. In this way, the back-propagation algorithm used in the simulation could be replaced by more natural reinforcement learning. Like the association, the TOT reflex appears to rely not on exact solutions but rather on simple associations which lead to appropriate behavior under normal circumstances.

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Figure Legends

Figure 1. Modification of the rear leg's step end point depending on middle leg position as shown by the insect (left, from Cruse 1979) and by a neural network simulation (right, from Dean 1990). The figures present a dorsal view of the tarsus position of the right middle leg (o) relative to the thorax and the corresponding position of the right rear leg's tarsus at the end of its swing (+). In the simulation the network produces the three joint angles for the rear leg when given the three joint angles of the middle leg.

Figure 2. Hypothetical control network for the targeting behavior of the stick insect (left) and the form of the network used in the simulation (right). For the simulation, the three values defining a configuration of the middle leg are used as inputs and the activities in the output units are interpreted as the corresponding rear leg configuration.

Figure 3. Intracellularly recorded action potentials in two intersegmental interneurons transmitting information about the caudal (A) and dorsal (B) positions of the middle leg. The lower traces show the change in the position of the middle leg tarsus; the upper traces show the response of the neurons recorded in the metathoracic ganglion. Each change in middle leg position leads to a phasic increase in discharge frequency which then declines to a tonic position-dependent level.

Figure 4. Intracellularly recorded potential in a local metathoracic interneuron integrating information about middle leg and rear leg positions to compute a measure of the separation between the tarsi of the two legs. As in the intersegmental interneurons, the response contains both phasic and tonic changes in the membrane potential, which reflect the incoming excitatory post-synaptic potentials; the neuron does not produce action potentials in the example shown. The response to combined movement of the middle and rear legs (B) is larger than the response to either movement alone (A). Part C illustrates the recording situation and the stimulus orientations.

Figure 5. Modification of step movement (upper trace: rostral movement corresponds to upward change) and motoneuron activity (lower trace) by the moving leg in response to a tactile stimulus (triangles) applied to the adjacent rostral leg (Schmitz and Haßfeld 1989; inset after Graham 1979 in Bässler 1983).

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