

Sensory Signals of Unloading in One Leg Follow Stance Onset in Another Leg: Transfer of Load and Emergent Coordination in Cockroach Walking

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Zill SN, Keller BR, Duke ER. Sensory signals of unloading in one leg follow stance onset in another leg: transfer of load and emergent coordination in cockroach walking. *J Neurophysiol* 101: 2297–2304, 2009. First published March 4, 2009; doi:10.1152/jn.00056.2009. The transfer of load from one leg to another is an essential component in walking, but sense organs that signal this process have rarely been identified. We used high-speed digital imaging and neurophysiological recordings to characterize activities of tibial campaniform sensilla, receptors that detect forces via cuticular strains, in the middle legs of cockroaches during walking. Previous studies demonstrated that the distal tibial sensilla discharge when body load is suddenly decreased in freely standing animals. Sensory recordings during walking showed that distal receptors in the middle leg fired an intense burst near the end of the stance phase. We tested the hypothesis that initiation of distal firing resulted from the action of other legs entering stance. Analysis of leg movements in slow walking showed that sensory bursts in the middle leg closely followed stance onset of the ipsilateral hind leg while the ipsilateral front leg entered stance earlier in phase. Similar phases of leg movement were found in slow walking in experiments in which animals had no implanted recording wires. Those studies also demonstrated that the opposite middle leg entered stance earlier in phase. Measurements of leg positions in walking showed that the hind leg tarsus was placed closest to the middle leg, in keeping with a “targeting” strategy. Triggering of distal bursts in the middle leg by mechanical action of the hind leg could facilitate the onset of swing in the middle leg through local reflex effects and contribute to emergent coordination of leg movements in metachronal gaits.

INTRODUCTION

In walking, the body weight is repeatedly transferred from one leg to another as successive steps are taken (Alexander 2003). In humans, load transfer during slow walking occurs in the periods in which both legs are on the substrate (double support), when one leg assumes support of body weight after the start of the stance phase and another leg is unloaded before it is lifted and enters swing (Winter 1991). In both humans and other multilegged animals, the probability of initiation of swing is influenced both by kinematic parameters (leg position) and by the extent of leg loading, being inhibited if the leg is still providing support (Pang and Yang 2000, 2002; Pearson 2008). These processes are thought to be monitored by sense organs the inputs of which can strongly influence both the magnitude of muscle contractions and the timing of leg movements (Duysens et al. 2000; Büschges et al. 2008). However, it has not been clear which sensory signals reflect the transfer of load between legs.

We have studied the tibial campaniform sensilla, sense organs that detect forces through strains in the exoskeleton, and have recorded sensory activities in freely moving cockroaches (Keller et al. 2007; review, Zill et al. 2004). Campaniform sensilla are directionally sensitive and respond best to compressive strains that occur perpendicular to the long axis of the ovoid cuticular cap that mechanically couples the sense organ to the exoskeleton (Ridgel et al. 2000). The tibial sensilla are composed of two subgroups of receptors (proximal and distal sensilla) the caps of which are mutually perpendicular in orientation. The responses of the subgroups of receptors to forces and loads differ according to the cap orientation (Spinola and Chapman 1975). Studies using magnets and a coil to vary the body load in freely standing animals have shown that the proximal sensilla discharge vigorously to increases in body load while the distal sensilla fire bursts to load decreases (Keller et al. 2007). During walking, the tibial sensilla of the hind leg are active during the stance phase: firing of proximal sensilla is initiated after leg placement and continues through much of stance while distal receptors discharge several action potentials immediately preceding leg lifting in swing (Noah et al. 2001). This pattern of activity strongly suggests that the signals from the tibial receptors reflect the sequential loading and unloading of the leg during stance. However, the cause of the late onset of the burst of the distal sensilla was unclear. Studies of activities of the distal sensilla in posture have shown that they have a high threshold for firing and considerable rate sensitivity to stimuli that decrease the body weight in freely standing animals (Keller et al. 2007). Those characteristics suggest that the distal burst during walking might be produced by a discrete event that rapidly unloads the leg. In the present experiments, we utilized high-speed digital imaging and neurophysiological recordings to test whether the onset of firing of the distal sensilla of the middle legs was correlated with movements of other legs.

METHODS

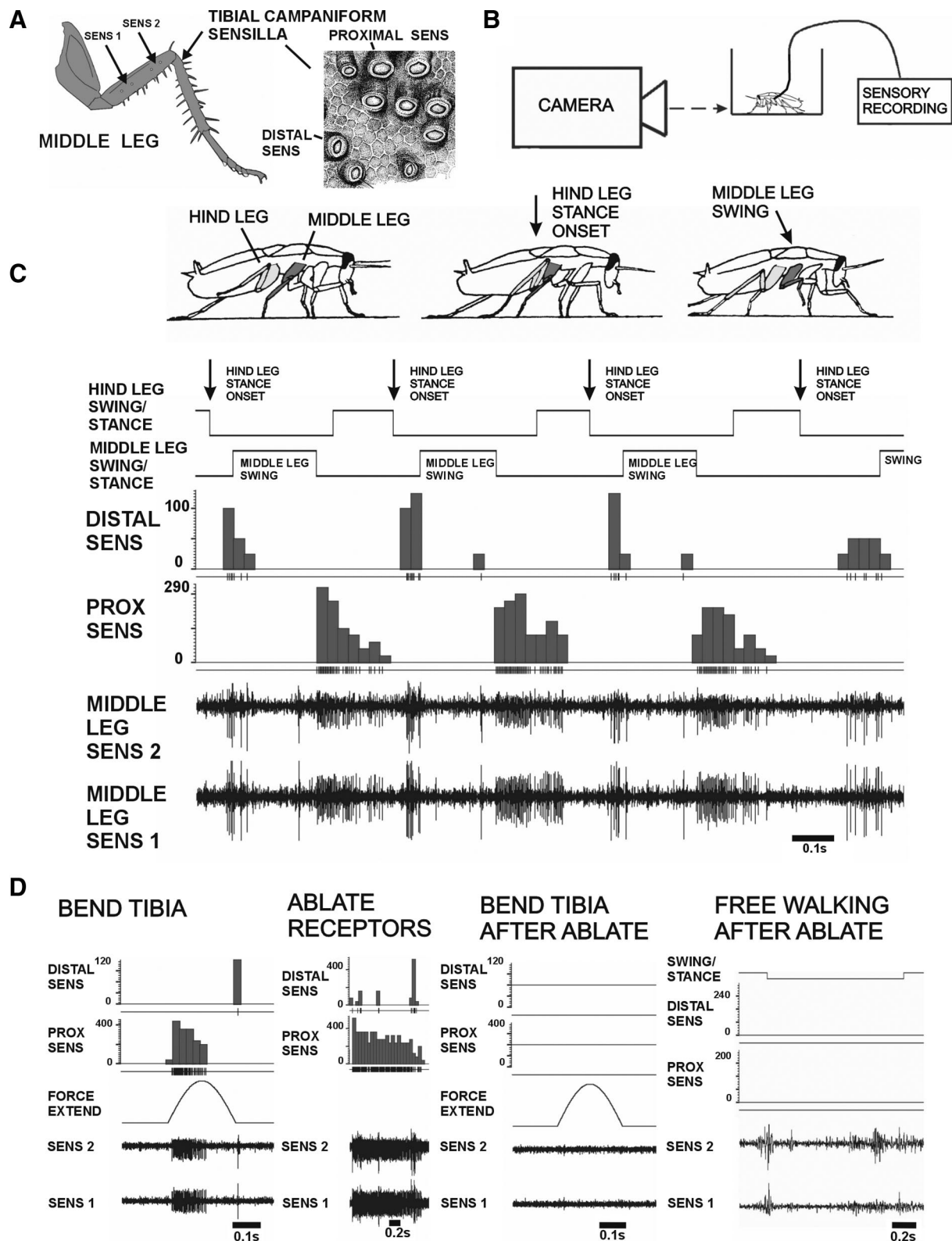
Activities of tibial campaniform sensilla in freely moving animals ($n = 15$, *Periplaneta americana*) were recorded using two pairs of fine wires implanted in the femur adjacent to the sensory nerve that contains the receptor axons (Fig. 1A) (Ridgel et al. 2000). The use of paired recordings increased the accuracy of unit identification as individual spikes occurred at fixed latencies in the pair of wires closest to the body. Animals were then released into an arena (Fig. 1B). Episodes of slow walking were imaged using a high speed camera (125 or 250 frame/s). To determine the timing of stance and swing in both the middle and hind legs, leg movements were analyzed from sequences in which the animal walked slowly in a path approximately

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perpendicular to the field of view of the camera. Kinematic data on times of onset of swing and stance were synchronized with neurophysiological recordings as in previous studies (Noah et al. 2001).

Animals were restrained after free walking sequences were recorded and tests performed to confirm that sensory units were derived from the tibial sensilla (Noah et al. 2001, 2004). Bending

forces were applied to the tibia to stimulate the campaniform sensilla. The cuticular caps of the receptors were ablated, eliminating responses to imposed bending. Animals were then released into the arena, and walking sequences were again recorded. Sensory activities derived from the tibial sensilla were absent in the sequences following ablation of the receptor caps.



In addition, we performed control experiments to assure that the implantation of wires did not affect the gaits shown by the animals. In these experiments, no recording wires were implanted in the legs, but cockroaches were simply imaged at high speed (250–500 frame/s) when they walked with very small magnets on the dorsum of the thorax (over the center of mass). The camera was placed on the side of the arena at a slight elevation from the substrate and tilted down to maximize the view of all of the legs. This allowed the positions of the tarsi (feet) on both sides of the animal to be clearly visualized as they were placed on the floor of the arena. The times of onset of swing and stance were determined for all legs in these sequences. These results were compared with measurements of leg movements from experiments in which sensory recordings were taken. In other studies, the positions of the tarsi at the start and end of stance were also digitized, and the location of the magnet was measured as a moving reference point, allowing calculation of the ranges of movements of the legs relative to the body.

Reflex effects of tibial sensilla were tested in restrained preparations by stimulation of the cuticular caps of individual receptors or by bending the tibia as in previous studies (Zill et al. 1981).

RESULTS

The pattern of activity recorded from the tibial campaniform sensilla during slow walking ($n = 15$ animals) reflected the successive loading and unloading of the leg in the stance phase (Fig. 1C). The discharges of the proximal and distal subgroups were similar to those previously demonstrated in receptors of the hind legs, but sensory discharges occurred at much higher frequencies in the middle legs (Noah et al. 2001; Zill and Moran 1981). In the sequence shown in Fig. 1C, the animal took a series of steps while the rate of walking gradually decreased from 2.2 to 1.6 step/s. The proximal sensilla fired after stance onset in each step, and the discharge continued at a high level through much of the stance phase. The distal receptors discharged in an intense burst prior to leg lifting in swing, although single spikes could occasionally occur at other times in the step cycle. The firing frequency of the distal receptors was also highly sensitive to the rate of walking (compare steps at the start and end of this sequence). Control experiments using cap ablation confirmed that sensory units were derived from the tibial sensilla (Fig. 1D).

Bursts of distal tibial campaniform sensilla were restricted to a short period in the last 20% of the stance phase although single spikes could occur at other times in the step cycle. Measurements of movements of the ipsilateral hind leg provided insight into its effect on the timing of firing of distal sensilla (Fig. 1C). The uppermost traces above the recordings in Fig. 1C show the times of onset of stance and swing in the ipsilateral hind leg. The hind leg was placed down in stance prior to the initiation of distal bursting in the middle leg in each

step. The sensory burst was, in turn, followed by lifting of the middle leg in swing.

The close association of hind leg placement and distal firing is apparent in Fig. 2A; the histogram plots the mean rate of firing of distal sensilla of the middle leg and the mean time (and SD) of the stance onset of the hind leg for steps in which the movements of both legs could be clearly seen. The firing frequency of the distal sensillum rose rapidly after foot (tarsal) contact of the hind leg as load was decreased in the middle leg. The first distal spike followed the onset of hind leg stance in 94% of steps. While the timing of initiation of the distal sensillum discharge was relatively constant, the firing frequency within a burst showed a strong dependence on the rate of walking. This is demonstrated by comparing Fig. 2B, which is a graph of the time of onset of the first spike in the distal burst at different rates of walking, and C, which plots the maximum firing frequency at different walking speeds. Thus the discharge of distal sensilla occurred at a relatively constant phase in very slow walking but was highly sensitive to the rate of progression.

We also measured the times of stance onset of other legs to see if they could have similar effects on unloading of the middle leg and the timing of bursts of distal sensilla. The histogram in Fig. 3A plots the mean phase of initiation of distal bursting and phases of onset of stance of the ipsilateral front and hind legs within the stance phase of the middle leg. The distal burst was initiated at a mean phase of 0.86, and the phase of onset of stance was 0.78 in the hind leg and 0.49 in the front leg. We also analyzed data from experiments in which animals had no recording wires implanted. Those studies assured that the recording leads did not affect walking movements and further permitted examination of steps in which movements of the contralateral middle leg could also be measured. The histogram in Fig. 3B plots the phases of initiation of the ipsilateral (left) front and hind legs and the contralateral (right) middle legs within the stance phase of the (left) middle leg. The values from these data were similar to those obtained from the experiments with sensory recordings (mean phase of ipsilateral hind leg 0.75, ipsilateral front leg 0.48). They also demonstrated that the phase of stance onset of the opposite leg was considerably earlier in time (mean: 0.61). Thus both data sets support the idea that the time of stance initiation of the ipsilateral hind leg most closely precedes the onset of distal bursting.

The positions of the other legs relative to the center of mass could also influence unloading of the middle leg. To gain insight into this problem, the positions of the tarsi of all legs on one side were measured in sequences in which the animal walked in a path perpendicular to the camera (Fig. 3C). We

FIG. 1. Activities of tibial campaniform sensilla and pattern of leg movements in walking. *A*, *left*: discharges of tibial campaniform sensilla were recorded extracellularly with 2 pairs of fine wires implanted in the femur of the middle leg adjacent to the sensory nerve that contains the receptor axons. *Right*: drawing of cuticular caps of receptors (as viewed in wholemount of cuticle) (after Schnorbus 1971). The tibial group consists of proximal and distal receptors whose caps show a mutually perpendicular orientation. *B*: animals were released into an arena. Leg movements were digitally imaged, and sensory activities were recorded during sequences of slow walking. *C*: sensory recordings and leg movements. This sequence shows sensory activities (middle leg sens 1 and 2) and the pattern of leg movements of the middle (middle leg stance/swing) and hind legs (hindleg stance/swing) in 3 steps in which the rate of walking progressively slowed. The tibial sensilla were active during the stance phase in each step. Firing of distal receptors (distal sens) occurred as a short burst near the end of the stance phase of the middle leg. Distal bursts were preceded by stance onset in the hind leg. *D*: controls for unit identification. Animals were restrained and bending forces were applied to the tibia. Forces applied in the direction of forced extension resulted in a burst of activity in proximal receptors while distal sensilla fired when the applied forces were decreased. Ablation of the cuticular caps of the receptors produced intense bursts that matched the heights of the sensory units in earlier tests and eliminated the responses to imposed bending. Activities of sensory units were also no longer recorded during walking when animals were released into the arena following the sensory ablation.

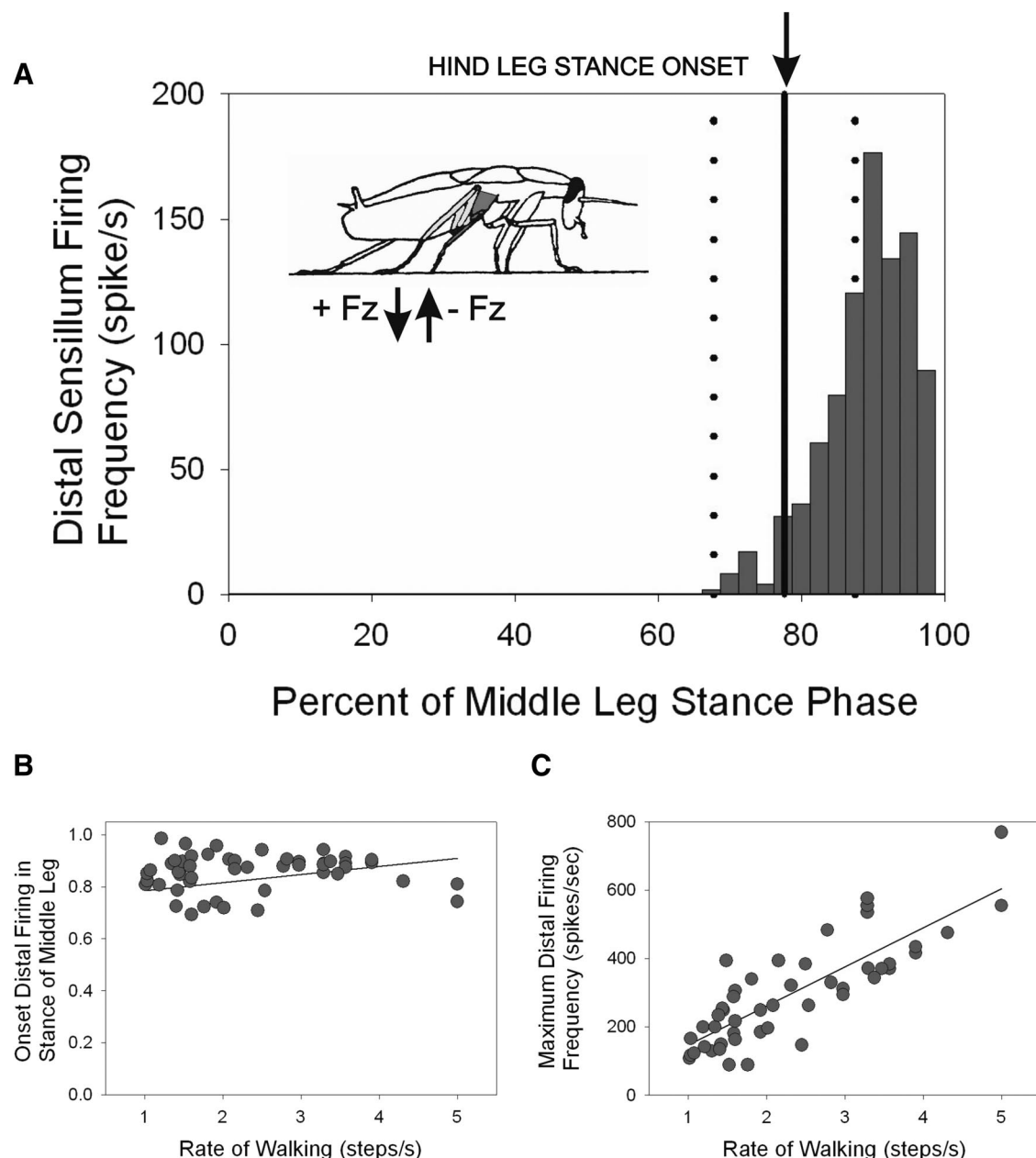


FIG. 2. Sensory discharge follows stance onset of the ipsilateral hind leg. *A*: histogram showing the mean rate of discharge of distal sensilla of the middle leg occurring during the stance phase of the middle leg from walking sequences in which the movements of both legs could be clearly seen (50 steps at mean rate of walking 2.34 step/s from 5 preparations). The solid vertical lines indicate the mean time of onset (and dotted lines standards deviations) of stance of the hind leg. Distal sensillum firing greatly accelerated following hind leg placement consistent with the idea that force exerted by the hind leg (+Fz) supported body load and unloaded the middle leg (-Fz). *B* and *C*: plots of the phase of onset of bursting (*B*) and maximum firing frequency (*C*) of distal sensilla at different rates of walking (from the same data set as *A*). Distal bursts are initiated at a relatively constant phase of the step cycle but the maximum firing frequency depends strongly on the rate of walking.

also tracked the position of the center of mass (see METHODS) and calculated the positions of the legs along the body axis relative to the movements of the animal as a whole (Fig. 3D). The graph in Fig. 3E shows the ranges of movements of the front, middle and hind legs ($n = 3$ animals): movements of the hind leg bring it closest at the start of stance to the posterior extreme position of the middle leg.

To evaluate the possible effects of the distal discharges on motor outputs, we tested the reflex effects of distal receptors on activities of motor neurons to muscles of the middle leg ($n = 5$ animals). Simulation of distal receptors by bending of the leg

in the direction of forced flexion produced rapid inhibition of the activities of the slow motor neuron of trochanteral extensor muscles (Fig. 3F). Similar results were obtained from indentation of the caps of individual distal receptors.

DISCUSSION

Sensory discharges of distal tibial campaniform sensilla of the middle legs during walking

These studies have shown that the distal tibial campaniform sensilla of the middle legs fire in intense short bursts that are

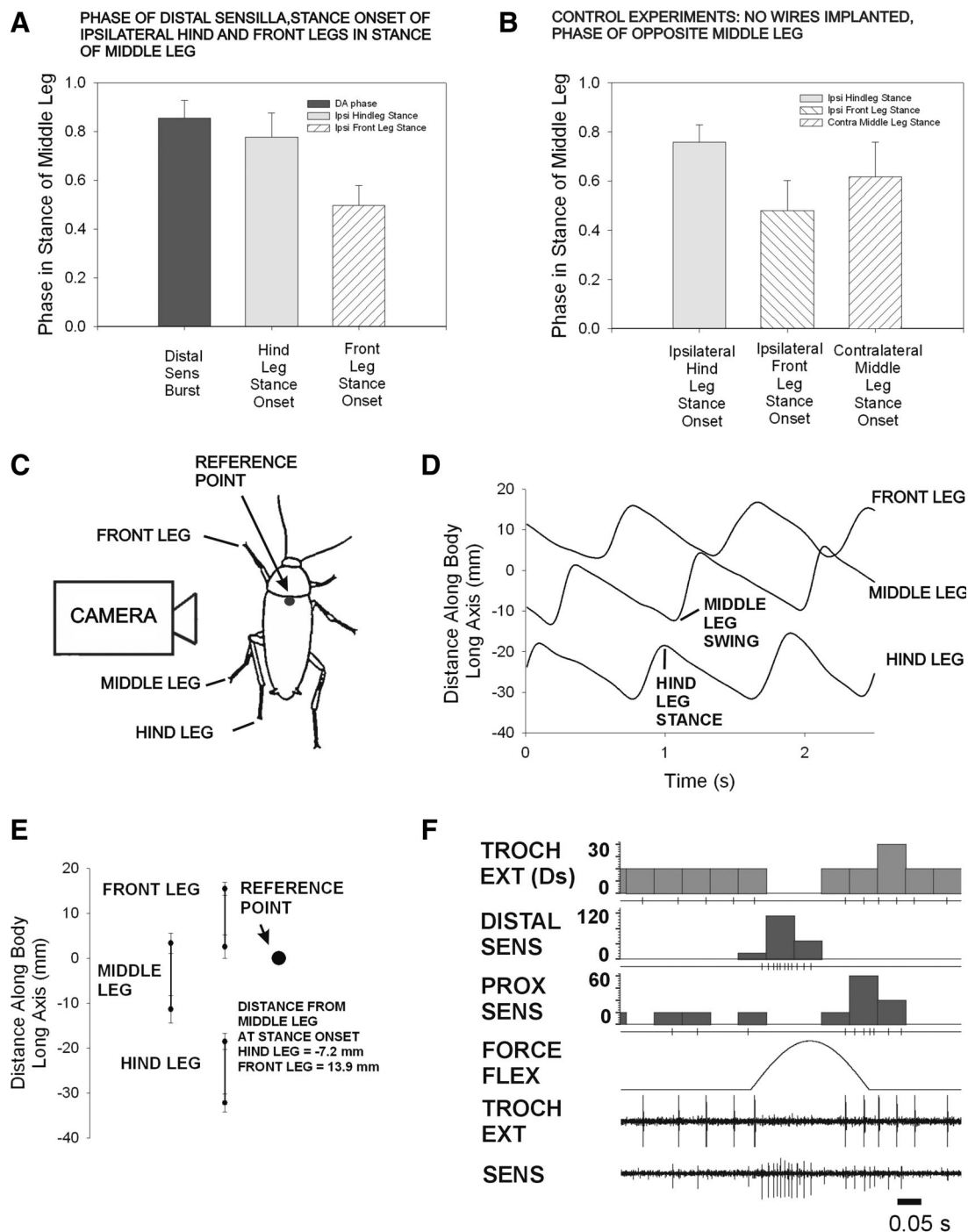


FIG. 3. Effects of other legs on sensory discharges. *A*: mean phase of sensory discharge and leg movements—This histogram plots the mean phases (and SDs) of onset of distal bursting and initiation of stance of the ipsilateral hind and front legs within the stance phase of the middle leg (49 steps of 3 animals from the same data set as Fig. 2*A* in which all ipsilateral legs could be seen). The phase of stance onset of the front leg is earlier in phase than the hind leg in very slow walking. *B*: animals walking without recording wires—histogram (as in Fig. 3*A*) from sequences of animals walking without recording leads (40 steps from 3 animals.) Similar phases of stance onset occur in ipsilateral legs. The opposite middle leg is also earlier in phase as movements alternate within a segment. *C*: influence of leg position. The positions of the tarsi at the start and end of stance (along the body long axis) were imaged with a camera placed perpendicular to the direction of progression. A small magnet on the dorsum of the animal was digitized as a moving reference point. *D*: continuous tracings of tarsal positions of the front middle and hind legs relative to the center of mass. The legs are retracted along the body during stance (declining values) and protracted in swing (rapidly rising values). The hind leg at stance onset is in close proximity to the middle leg before it is lifted in swing. *E*: plot of the ranges of movements of legs on one side of the animal show that the hind leg at the start of stance is brought closest to the middle leg. *F*: distal sensilla reflexively inhibit support of body load—discharges of distal sensilla was generated by bending the tibia in the direction of forced flexion (with movement resisted) in a restrained preparation. This produced rapid inhibition of activity of the slow motor neuron to the trochanteral extensor muscle. Activity of this motor neuron has been shown to support body weight in walking.

initiated near the end of the stance phase in slow walking. The discharge frequencies within a burst rise rapidly and are followed at short latency by leg lifting in swing. This pattern of activity is similar to that recorded in distal tibial receptors of the hind leg (Noah et al. 2001; Zill and Moran 1981), but the maximum firing frequencies are considerably higher in the middle legs, a finding that is consistent with their proximity to the center of mass (Quimby et al. 2006). These results are in agreement with the sensitivities of the receptors to decreases in body load in posture that have been demonstrated in tests of freely standing animals (Noah et al. 2004; Keller et al. 2007) and support the idea that firing of the distal receptors of both middle and hind legs can indicate unloading of the leg in standing and walking.

While ground reaction forces have not been measured in slow walking in cockroaches, studies in rapidly running animals have demonstrated that vertically oriented forces (F_z along the gravitational vector) peak in the middle of the stance phase and decrease gradually before leg lifting in swing (Full et al. 1991). We postulated that the rapid onset and high frequency of firing of distal sensilla that occurs very late in stance in slow walking resulted from other legs being placed in support and showed that the discharge of distal receptors of the middle leg closely follows the onset of stance of the hind leg on the same side. As no direct efferent modulation is known to occur in campaniform sensilla, these sensory bursts appear to be produced by mechanical forces exerted through the substrate.

To produce unloading of the middle leg in the intervals found in the present study, muscles in the hind leg that support the body weight must exert their effects rapidly after stance onset. In cockroaches, body load is supported by the trochanteral extensor muscle in all legs (Quimby et al. 2006). This muscle, one of the largest in the leg, becomes active during walking late in swing and then shows a peak of activity after leg placement in stance (Watson and Ritzmann 1998). While the plane of action of the extensor muscle in the hind leg is nearly horizontal through much of stance to generate forceful propulsion, the leg is rotated more vertically during swing so that the muscle can effectively produce support of body load at stance onset. (Hughes 1952; Noah et al. 2001; Quimby et al. 2006). The trochanteral extensor could, therefore, readily generate the rapid force increases needed to unload the adjacent leg. The firing frequency of the extensor motor neuron is also closely correlated with the rate of walking (Watson and Ritzmann 1998). Further experiments are planned to test whether firing of the distal sensilla of the middle legs, which shows a strong dependence on the rate of walking, is correlated with the rate of discharge of the hind leg trochanteral extensor motor neuron, the prime generator of forces that unload the middle leg.

It is important to note that other factors could also contribute to the onset of distal bursting. The tibial sensilla are sensitive to contractions of tibial muscles and potentially muscles located more proximally in the leg (Zill and Moran 1981). Imposition of movements against the resistance of muscles can also produce strains to excite the sensilla: stiffness in the extensor muscle, for example, could contribute to the single spikes that can occur during swing (as in Fig. 1C). However, these discharges do not reach the firing frequencies that occur in the vigorous bursts of activity of the distal sensilla near the end of the stance phase.

Transfer of load in metachronal gaits

The close temporal association of stance onset of the hind leg and lifting of the middle leg is integral to the metachronal gait, which many insects show during very slow walking (cockroaches, Delcomyn 1971; stick insects, Graham 1972; Dean 1991) including those that exhibit predominantly tripod gaits at more rapid speeds (ants, Zollikofer 1994). In these gaits, legs are lifted in swing in a caudal to rostral sequence, producing the appearance of a wave moving in time along one side of the body. The metachronal gait of cockroaches was first described by Hughes (1952) as obeying the rule “no foreleg or middle leg is protracted (enters swing) until the leg behind has taken up its supporting position.” In a description of coordination of leg movements in stick insects, Cruse (1990) formulated a similar “influence” in which “the start of a power stroke excites the start of a return stroke” in the more anterior leg. The regular occurrence of distal firing and swing in the middle leg following onset of stance in the hind leg is consistent with this pattern.

We also demonstrated that, in slow walking, stance onset in the ipsilateral front leg preceded the onset of stance in the hind leg. Insects are often described as using a tripod gait in walking and running (Zollikofer 1994). Although definitions vary, this gait is often envisioned as involving the precise, synchronous movements of the front and hind legs on one side of the animal. While few authors have studied leg coordination in very slow walking, Delcomyn (1971) demonstrated that cockroaches show metachronal gaits at these rates of stepping with phases of movement similar to those found in the present study (see Delcomyn 1971; Fig. 3). Similar timing of leg movements has also been observed in slow walking in stick insects (Wendler 1966). In a metachronal gait, swing in the front leg follows stance onset of the middle leg and is short in duration so that in slow walking, it is terminated about halfway through the stance phase of the middle leg. As the rate of walking increases, the delay between the onset of swing of the front and hind legs is reduced, and swing movements of those legs become more closely synchronized with swing of the middle leg of the opposite side. This mechanism has been termed “gliding coordination” (Wendler 1966) and can produce a tripod of movements at more rapid walking speeds. However, legs of a single segment alternate at all rates of stepping, consistent with the findings of the present study.

The effectiveness of the hind leg in unloading the middle leg should be enhanced by their physical proximity (Cruse 1990). We have shown that the hind leg tarsus is placed at stance onset closest to the position of the tarsus of the middle leg. Similar results are seen in walking in a number of insects (Fig. 5 of Hughes 1952) and may reflect use of a “targeting” strategy, in which movements of a leg in swing are “aimed” toward the position of the tarsus of the adjacent anterior leg (Cruse 1979; Cruse et al. 2006). This mechanism is thought to optimize stability of leg placement as the posterior leg reaches toward the “known” point of contact of the anterior leg. However, this strategy also directly affects the transfer of load. Vectorial analysis of the forces exerted by legs, which is now widely used in algorithms for force distribution in walking machines (Nelson and Quinn 1999), shows that the effectiveness of forces generated by individual legs in countering body load are related to their distance from the center of mass. Preliminary

measurements of leg positions from video data in the present study support the idea that cockroaches use this strategy and bring the point of contact of the hind leg close to that of the middle leg (further studies are planned using two cameras to study the use of this strategy more precisely.) These findings suggest that another consequence of targeting strategies is that they effectively facilitate the transfer of load during walking. It is also important to note that the ipsilateral hind leg should be most effective in unloading the middle leg even when the animal assumes a tripod gait due to targeting and its proximity to the middle leg. However, the effectiveness of these mechanisms is probably greatly reduced or absent in rapidly running cockroaches when the phases of muscle activities substantially precede the movements that are produced (Zill and Moran 1981) and targeting mechanisms may be less prevalent (Sponberg and Full 2008).

Local reflexes and emergent coordination of walking movements

We demonstrated that stimulation of distal sensilla of the middle legs can produce reflex inhibition of the activities of leg extensor muscles in restrained animals. These reflexes are similar to those previously demonstrated in the hind legs: stimulation of distal sensilla inhibits the hind leg trochanteral and tibial extensors and enhances the firing of leg flexors (Zill and Moran 1981). Although direct evidence is not yet available that these effects are present in walking animals, the pattern of sensory and motor activities recorded during locomotion is consistent with the idea that the discharges of distal receptors could contribute to the onset of the stance-swing transition through reflex connections. The triggering of distal sensillum discharges by forces exerted by the hind leg would therefore facilitate an inherent or emergent coordination of leg movements in a metachronal pattern mediated by local reflexes.

The potential significance of emergent mechanisms that result from mechanical forces has been demonstrated in both physiological and modeling studies of walking. Cruse (1990) described the mechanisms that produce coordination of leg movements in stick insects as a series of “influences” or rules that legs exert on each other. Application of these rules in simulations of insect walking and in the design of controllers for walking machines have been shown to produce emergent patterns of leg coordination and “self-selection” of gaits similar to those seen in insects. These patterns can occur without additional central circuitry or supervisory command elements (Dürr et al. 2004; Ekeberg et al. 2004). However, it is important to note that in intact animals these mechanisms probably complement the neural connections (via interneurons) that have been demonstrated to mediate leg coordination (Borgmann et al. 2007), although direct interleg reflexes have not been demonstrated for the cockroach tibial campaniform sensilla (Zill and Moran 1981; Zill, unpublished observations).

Similar mechanisms that are produced by mechanical linkages and transfer of loads between the legs may be important in coordination of locomotion in vertebrates. Perturbations of a single leg during pedaling produce responses in the contralateral leg that may be due, in part, to afferent signals generated by forces in both legs (Ting et al. 2000; Zajac 1993). In recent studies of walking in rats, Giszter et al. (2008) found that apparent coordination of movements of the front and hind legs

following spinal cord transaction was probably achieved via local reflexes with some guidance through forces exerted by the trunk. In a simulation of cat walking, Ekeberg and Pearson (2005) found that stable gaits could be established in the hind legs even without direct connections between pattern generating circuits if sensory signals of load were present. They concluded that mechanical linkages between the legs, mediated by load-sensitive signals, played a significant role in establishing the alternating pattern of leg movements.

These results also suggest that there is a general advantage in the reliance of the walking system on both force and position signals in determining the transition from stance to swing, which has been considered the decisive factor in leg coordination (Cruse 1985). Forces within a leg depend on the effectiveness of forces exerted by other legs and the coordination of leg movements is inherently reflected in the signals of sense organs that detect the results of those forces. Inputs from force receptors may therefore provide the system with stability by acting as local emergent elements that reinforce and insure the performance of pattern generators within more global mechanisms of control (Rossignol et al. 2006). These emergent mechanisms may be used in animals and in walking machines to similar advantage.

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GRANTS

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REFERENCES

- Alexander RM. *Principles of Animal Locomotion*. Princeton, NJ: Princeton University Press, 2003.
- Borgmann A, Scharstein H, Büschges A. Intersegmental coordination: influence of a single walking leg on the neighboring segments in the stick insect walking system. *J Neurophysiol* 98: 1685–1696, 2007.
- Büschges A, Akay T, Gabriel JP, Schmidt J. Organizing network action for locomotion: insights from studying insect walking. *Brain Res Rev* 57: 162–71, 2008.
- Cruse H. The control of the anterior extreme position of the hindleg of a walking insect, *Carausius morosus*. *Physiol Entomol* 4: 121–124, 1979.
- Cruse H. Which parameters control the leg movement of a walking stick insect? II. The start of the swing phase. *J Exp Biol* 116: 357–362, 1985.
- Cruse H. What mechanisms coordinate leg movement in walking arthropods? *Trends Neurosci* 13: 15–21, 1990.
- Cruse H, Dürr V, Schmitz J. Insect walking is based on a decentralized architecture revealing a simple and robust controller. *Philos Transact A Math Phys Eng Sci* 365: 221–50, 2007.
- Cruse H, Dürr V, Schmitz J, Schneider A. Control of hexapod walking in biological systems. In: *Adaptive Motion of Animals and Machines*, edited by Kimura H, Tsuchiya K, Ishiguro A, Witte H. Tokyo: Springer, 2006, p. 17–29.
- Dean J. A model of leg coordination in the stick insect, *Carausius morosus*. II. Description of the kinematic model and simulation of normal step patterns. *Biol Cybern* 64: 403–411, 1991.
- Delcomyn F. The locomotion of the cockroach *Periplaneta americana*. *J Exp Biol* 54: 443–52, 1971.
- Dürr V, Schmitz J, Cruse H. Behaviour-based modelling of hexapod locomotion: linking biology and technical application. *Arthropod Struct Dev* 33: 237–250, 2004.
- Duysens J, Clarac F, Cruse H. Load regulating mechanisms in gait and posture, comparative aspects. *Physiol Rev* 80: 83–133, 2000.
- Ekeberg O, Blümel M, Büschges A. Dynamic simulation of insect walking. *Arthropod Struct Dev* 33: 287–300, 2004.

- Ekeberg O, Pearson K.** Computer simulation of stepping in the hind legs of the cat: an examination of mechanisms regulating the stance-to-swing transition. *J Neurophysiol* 94: 4256–4268, 2005.
- Full RJ, Blickhan R, Ting LH.** Leg design in hexapedal runners. *J Exp Biol* 158: 369–90, 1991.
- Giszter SF, Davies MR, Graziani V.** Coordination strategies for limb forces during weight-bearing locomotion in normal rats and in rats spinalized as neonates. *Exp Brain Res* 190: 53–69, 2008.
- Graham D.** A behavioural analysis of the temporal organisation of walking movements in the 1st instar and adult stick insect (*Carausius morosus*). *J Comp Physiol [A]* 81: 23–52, 1972.
- Hughes GM.** The coordination of insect movements. I. The walking movements of insects. *J Exp Biol* 29: 267–285, 1952.
- Hughes GM.** The coordination of insect movements. II. The effects of limb amputation and the cutting of commissures in the cockroach (*Blatta orientalis*). *J Exp Biol* 34: 306–333, 1957.
- Keller BR, Duke EF, Amer AS, Zill SN.** Tuning posture to body load: decreases in load produce discrete sensory signals in the legs of freely standing cockroaches. *J Comp Physiol [A]* 93: 881–891, 2007.
- Nelson GM, Quinn RD.** Posture Control of a cockroach-like robot. *IEEE Control Syst* 19: 9–14, 1999.
- Noah JA, Quimby L, Frazier SF, Zill SN.** Force receptors in cockroach walking reconsidered: discharges of proximal tibial campaniform sensilla when body load is altered. *J Comp Physiol [A]* 187: 769–784, 2001.
- Noah JA, Quimby L, Frazier SF, Zill SN.** Sensing the effect of body load in legs: responses of tibial campaniform sensilla to forces applied to the thorax in freely standing cockroaches. *J Comp Physiol [A]* 190: 201–215, 2004.
- Pang MY, Yang JF.** The initiation of the swing phase in human infant stepping: importance of hip position and leg loading. *J Physiol* 528: 389–404, 2000.
- Pang MY, Yang JF.** Sensory gating for the initiation of the swing phase in different directions of human infant stepping. *J Neurosci* 22: 5734–40, 2002.
- Pearson KG.** Role of sensory feedback in the control of stance duration in walking cats. *Brain Res Rev* 57: 222–227, 2008.
- Quimby L, Amer A, Zill SN.** Common motor mechanisms support body weight in serially homologous legs of cockroaches in posture and locomotion. *J Comp Physiol [A]* 192: 247–266, 2006.
- Ridgel A, DiCaprio R, Frazier S, Zill S.** Active signaling of leg loading and unloading in the cockroach. *J Neurophysiol* 81: 1432–1437, 1999.
- Ridgel AL, Frazier SF, DiCaprio RA, Zill SN.** Encoding of forces by cockroach tibial campaniform sensilla: implications in dynamic control of posture and locomotion. *J Comp Physiol [A]* 186: 359–374, 2000.
- Ritzmann RE, Büschges A.** Adaptive motor behavior in insects. *Curr Opin Neurobiol* 17: 629–36, 2007.
- Rossignol S, Dubuc R, Gossard J-P.** Dynamic sensorimotor interactions in locomotion. *Physiol Rev* 86: 89–154, 2006.
- Schnorbus H.** Die subgenualen sinnesorgane von *Periplaneta americana*: histologie und vibrationsschwellen. *Z Vergl Physiologie* 71: 14–48, 1971.
- Spinola SM, Chapman KM.** Proprioceptive indentation of the campaniform sensilla of cockroach legs. *J Comp Physiol* 96: 257–273, 1975.
- Ting LH, Kautz SA, Brown DA, Zajac FE.** Contralateral movement and extensor force generation alter flexion phase muscle coordination in pedaling. *J Neurophysiol* 83: 3351–3365, 2000.
- Watson JT, Ritzmann RE.** Leg kinematics and muscle activity during treadmill running in the cockroach, *Blaberus discoidalis*. I. Slow running. *J Comp Physiol [A]* 182: 11–22, 1998.
- Wendler G.** The co-ordination of walking movements in arthropods. Nervous and hormonal mechanisms of integration. *Symp Soc Exp Biol* 20: 229–249, 1966.
- Winter DA.** *The Biomechanics and Motor Control of Human Gait: Normal, Elderly and Pathological* (2nd ed.). Waterloo Biomechanics, 1991.
- Zajac FE.** Muscle coordination of movement: a perspective. *J Biomech* 26 Suppl 1: 109–124, 1993.
- Zill SN, Moran DT.** The exoskeleton and insect proprioception. III. Activity of tibial campaniform sensilla during walking in the American cockroach, *Periplaneta americana*. *J Exp Biol* 94: 57–75, 1981.
- Zill SN, Moran DT, Varela FG.** The exoskeleton and insect proprioception. II. Reflex effects of tibial campaniform sensilla in the American cockroach *Periplaneta americana*. *J Exp Biol* 94: 43–55, 1981.
- Zill S, Schmitz J, Büschges A.** Load sensing and control of posture and locomotion. *Arthropod Struct Dev* 33: 273–286, 2004.
- Zollikofer CP.** Stepping patterns in ants. I. Influence of speed and curvature. *J Exp Biol* 192: 95–106, 1994.