

Load sensing and control of posture and locomotion

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Abstract

This article reviews recent findings on how forces are detected by sense organs of insect legs and how this information is integrated in control of posture and walking. These experiments have focused upon campaniform sensilla, receptors that detect forces as strains in the exoskeleton, and include studies of sensory discharges in freely moving animals and intracellular characterization of connectivity of afferent inputs in the central nervous system. These findings provide insights into how campaniform sensilla can contribute to the adjustment of motor outputs to changes in load. In this review we discuss (1) anatomy of the receptors and their activities in freely moving insects, (2) mechanisms by which inputs are incorporated into motor outputs and (3) the integration of sensory signals of diverse modalities. The discharges of some groups of receptors can encode body load when standing. Responses are also correlated with muscle-generated forces during specific times in walking. These activities can enhance motor outputs through reflexes and can affect the timing of motoneuron firing through inputs to pattern generating interneurons. Flexibility in the system is also provided by interactions of afferent inputs at several levels. These mechanisms can contribute to the adaptability of insect locomotion to diverse terrains and environments.

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1. Introduction

1.1. Basic functions of sensory feedback

Feedback from sense organs located in the limbs plays an essential role in the control of posture and locomotion by the nervous system (Pearson, 1993; Prochazka, 1996). In arthropods, as in all other legged animals that have been studied, these sense organs precisely monitor parameters such as limb position and movements, forces exerted by skeletal muscles and loads that are placed upon or encountered by a leg (Zill, 1990; Seyfarth and French, 1994; Bässler and Büschges, 1998; Duysens et al., 2000). Inputs from limb sense organs serve common functions in both invertebrates and vertebrates and act to (1) monitor behaviors and assure that movements are successfully and efficiently performed, (2) aid in adjusting posture and locomotion to variations in the environment, and (3) detect perturbations and contribute to the development of

compensatory adjustments (Pratt, 1995). In many animals, perturbations can be passively resisted by skeletal and ligamentous elements (Alexander, 1988) but are actively countered by contractions of leg and body muscles. These active responses can occur in a variety of limb positions and body orientations, without anatomical constraints of passive elements (Zill and Frazier, 1990; Zill et al., 1992; Jacobs and Macpherson, 1996). Many of the sensory-motor mechanisms that mediate responses to perturbations can contribute to adaptation of walking in diverse terrains (Zill, 1993).

1.2. Effects of load on posture and locomotion: behavior and motor output

In this article we will particularly focus upon sense organs that detect forces and their functions in the control of standing and walking in insects. A number of recent experiments have shown that inputs from force receptors can have strong effects upon muscle contractions and the timing of leg movements. Signals of the cyclical changes in leg loading have also been demonstrated to provide essential cues for transitions in the phases of walking. The forces that act upon a limb can

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be derived from diverse sources including the weight of the body (Wendler, 1966), forces generated in propulsion (Dean, 1991; Pearson, 1972) and increases in load that occur when objects are carried (Zollikofer, 1994). Insects are readily able to adapt to large changes in loads: rhinoceros beetles can walk while carrying loads 30 times their own body weight (Kram, 1996), while ants carry large objects over considerable distances (Zollikofer, 1994). Increased loading also is readily overcome in limb movements in other behaviors, such as targeted grooming (Dürr and Matheson, 2003).

Changes in load have two basic effects on motor outputs. First, increases in load can enhance the magnitude of muscle contractions in posture and locomotion (Pearson, 1972). When standing, increments in the effect of body weight upon the legs produce rapid elevations in firing rates of leg extensor motoneurons to compensate for the added load (Kemmerling and Varju, 1981; Noah et al., 2004). Leg muscles also exhibit heightened activities in walking if the resistance to propulsion is increased, as when dragging weights or when friction is raised on a treadmill (Pearson, 1972; Dean, 1991). Similar effects can be elicited by perturbations that experimentally alter load to single legs during walking (Bartling and Schmitz, 2000; Schmitz, 1993; Gabriel et al., 2003). Changes in the magnitude of motor output during locomotion over non-horizontal terrains may also result from variations in load. For example, when the effect of gravity is reversed in walking on inverted surfaces, bursts of the tibial flexor muscle are enhanced, as the muscle then acts to pull the animal toward the substrate (Duch and Pflüger, 1995; Larsen et al., 1995). Elevation of muscle activities in specific phases of climbing may also be related to the increase in output needed to raise the body mass (Watson et al., 2002), and is also seen in vertebrates (turkeys: Roberts et al., 1997; cats: Carlson et al., 1998).

Second, in walking, loading can alter the timing of muscle contractions and leg movements. When subjected to loads, most animals increase the duration of the stance phase of walking (Graham, 1985; Tang and Macmillan, 1986). This effect can be elicited both when loads are increased tonically and when sudden loads are applied in stance. This strategy has the advantage of increasing the duty cycle of muscles that are active in support and propulsion, and may lead to higher force outputs due to prolonged synaptic facilitation at the neuromuscular junction (Iles and Pearson, 1971). An increase in stance duration (and minimization of the duration of swing) also occurs when traversing unstable surfaces, as in walking on inverted substrates when the effects of gravity are reversed (Larsen et al., 1995). Prolongation of extensor firing is seen when walking patterns are adapted in climbing over an obstacle (Watson et al., 2002). Less well studied is the fact that increasing stance duration usually produces changes in gait so that time

of multiple leg support is increased (Graham, 1985; Tang and Macmillan, 1986).

1.3. Multimodal integration

Many of the effects of load require integration of information from load and angle sensors. For example, the transition from stance to swing is influenced by two variables in both vertebrates and invertebrates (Duysens et al., 2000). First, the leg must be unloaded to enter the swing phase. Second, a leg will be more likely to enter swing when it is close to its posterior extreme or extended position. The timing of swing onset and the position reached by the leg are affected by both variables. In stick insects, loads that resist leg extension decrease the velocity of movement and increase the step period (Dean, 1991). There is also a shift in the range of movement of the leg that depends upon the magnitude of load. In some cases, different strategies are used at different times in development in responses to increased loads: human infants predominantly show increases in stance duration while adults overcome loads mainly by increases in the amplitude of muscle contractions (Stephens and Yang, 1999). Independent control of the amplitude and timing of motor outputs can give the nervous system greater flexibility in compensating for changes in load.

1.4. Modulation of the effects of afferent inputs

In some behaviors, the nervous system may be able to extensively modulate or reduce the effects of load. For example, responses of stick insects to perturbations of single legs during walking depend upon the mechanical properties of the terrain. Compensatory reactions to sudden forces, elicited at short latency, are much larger when animals walk on stiff vs. compliant substrates (Bartling and Schmitz, 2000). Furthermore, in some postures, load perturbations elicit 'stepping' responses, in which legs are lifted and repositioned, rather than compensatory reactions (Zill et al., 1992). The occurrence of these responses may be related to the effectiveness of muscles in generating compensatory forces, which depends upon their mechanical advantage (Zill, 1993). Last, it has been argued that during rapid movements sensory feedback may be inappropriately timed to elicit activities by simple reflex actions (Zill and Moran, 1981b). This conclusion is supported by observations that partial leg amputations can disrupt leg use in slow walking but have little effect upon motoneuron bursting during rapid walking (Delcomyn, 1990). Thus, the system is able to alter and potentially override the effects of afferent feedback during certain behaviors.

In the following sections, we will discuss recent findings on how forces are detected by leg sense organs in insects and how this information is integrated in the control of posture and walking. Studies in insects, like those of other invertebrates, have the advantage that neuronal elements

can be individually identified. Recent advances have been made in studies of sensory receptors (campaniform sensilla) in several insect species and provide examples of principles and attributes of sensors that could be useful to consider in control of walking machines. These sections are not intended as complete literature reviews but rather to discuss selected recent experiments in the field of sensory-motor integration. The reader is referred to several more complete reviews that have discussed load detection (Duysens et al., 2000; Prochazka, 1996) and the mechanisms of sensory integration (Burrows, 1996; Büschges and El Manira, 1998; Fouad et al., 2002).

2. Specificity of sensory signals detecting force

A number of types of receptors can detect loading of legs in insects, including sense organs that encode forces at muscle tendons and receptors that monitor exoskeletal strains. Other types of receptors can signal the effects of forces on legs, such as receptors that detect kinematic parameters or tarsal contact. However, sense organs that are specialized to encode forces in the legs can provide the system with detailed data about the direction, rate and magnitude of loads (Ridgel et al., 2000). Two basic types of receptors detect forces in insect legs: campaniform sensilla are sense organs that monitor forces via strains that occur in the cuticle (Pringle, 1938). Multipolar receptors found in direct association with muscle tendons (apodemes) can signal tensions developed by some leg muscles and potentially encode external loads (Guthrie, 1967; Bässler, 1977; Matheson and Field, 1995). However, much less is known about the effects of apodeme receptors in posture and locomotion.

2.1. Campaniform sensilla monitor forces as strains in the exoskeleton and can encode force increases and decreases

A campaniform sensillum consists of a sensory neuron whose dendrite inserts into a cap at the surface of the cuticle (Fig. 1A). Forces applied to the exoskeleton, or developed by contractions of leg muscles, generate strains that produce mechanical distortion of the cap and discharge of the sensillum. In the legs, individual receptors are directionally sensitive and responses are correlated with the orientation of the cuticular cap. The discharges of sensilla depend upon their location and the vectorial direction of the imposed or self generated forces (Zill and Moran, 1981a; Cocatre-Zilgien and Delcomyn, 1999; Kaliyamoorthy et al., 2001). In contrast to muscle apodeme or tendon organs, the coupling of campaniform sensilla to muscle tension is indirect and the distribution of strain depends upon joint position (Flannigan, 1998; Ridgel et al., 2001).

Campaniform sensilla are found in groups whose arrangement is similar, but not identical in different insects (Pringle, 1938; Hofmann and Bässler, 1982; Hustert et al., 1981) (Fig. 1B). The largest number of groups is found on

the trochanter (Groups 1–4 in cockroaches, Groups 1–3 in stick insects) (Hofmann and Bässler, 1982; Delcomyn, 1991). Another group (fCS) is also found on the proximal femur, adjacent to the trochantero-femoral joint (Bässler, 1977; Schmitz et al., 1991), which is functionally a fused joint in stick insects but mobile in cockroaches. Smaller aggregations of sensilla are found on the tibia and individual or pairs of receptors occur on the tarsal segments (Kendall, 1970; Petryszak and Fudalewicz-Niemczyk, 1994).

In the tibial group of sensilla of cockroaches, the receptor caps have two mutually perpendicular orientations (proximal and distal subgroups) (Spinola and Chapman, 1975; Zill and Moran, 1981a). Forces applied in directions and magnitudes that mimicked loading in upright posture showed that proximal sensilla respond to force increases and distal sensilla discharge when forces decline (Ridgel et al., 1999, 2000). Discharges during releases from applied forces are evident in studies of campaniform sensilla in other insects (Delcomyn, 1991; Newland and Emptage, 1996) and regularly occur in crustacean mechanoreceptors (cuticular stress detectors, Marchand et al., 1995) but mechanisms underlying these responses are presently unknown. However, these studies showed that the system has active signals both for loading and unloading of the leg.

2.2. Tibial campaniform sensilla are particularly sensitive to body load

The sensitivities of the tibial campaniform sensilla to changes in load have been tested by recording their activities in freely standing and walking animals. In one set of experiments, perturbations were imposed by horizontally displacing the substrate upon which the animal stood (Ridgel et al., 2001). Sensilla showed bursts of activity that exhibited strict directional sensitivity. These discharges were initiated immediately following the onset of displacement and prior to large changes in joint angles. Afferent firing rates accurately reflected the rate of platform movement. These discharges could serve as early indicators that perturbations were occurring, even before they had destabilizing effects on body position. However, most bursts were abbreviated and displacements at higher rates or amplitudes produced complex firing patterns due to apparent swaying of the body.

A number of earlier studies have concluded that insects use sensory receptors to monitor the effects of body load on the legs in walking and climbing (Wendler, 1966; Krämer and Markl, 1978). To increase the effect of body weight upon the limbs small magnets were attached to the body and forces were generated by applying currents to a coil placed below the substrate (Fig. 1C) (Noah et al., 2004). The tibial sensilla showed vigorous and prolonged discharges in these tests when animals stood upon their legs and actively supported the body mass (Fig. 1D). Proximal sensilla fired to force increases while distal receptors discharged to decreasing force,

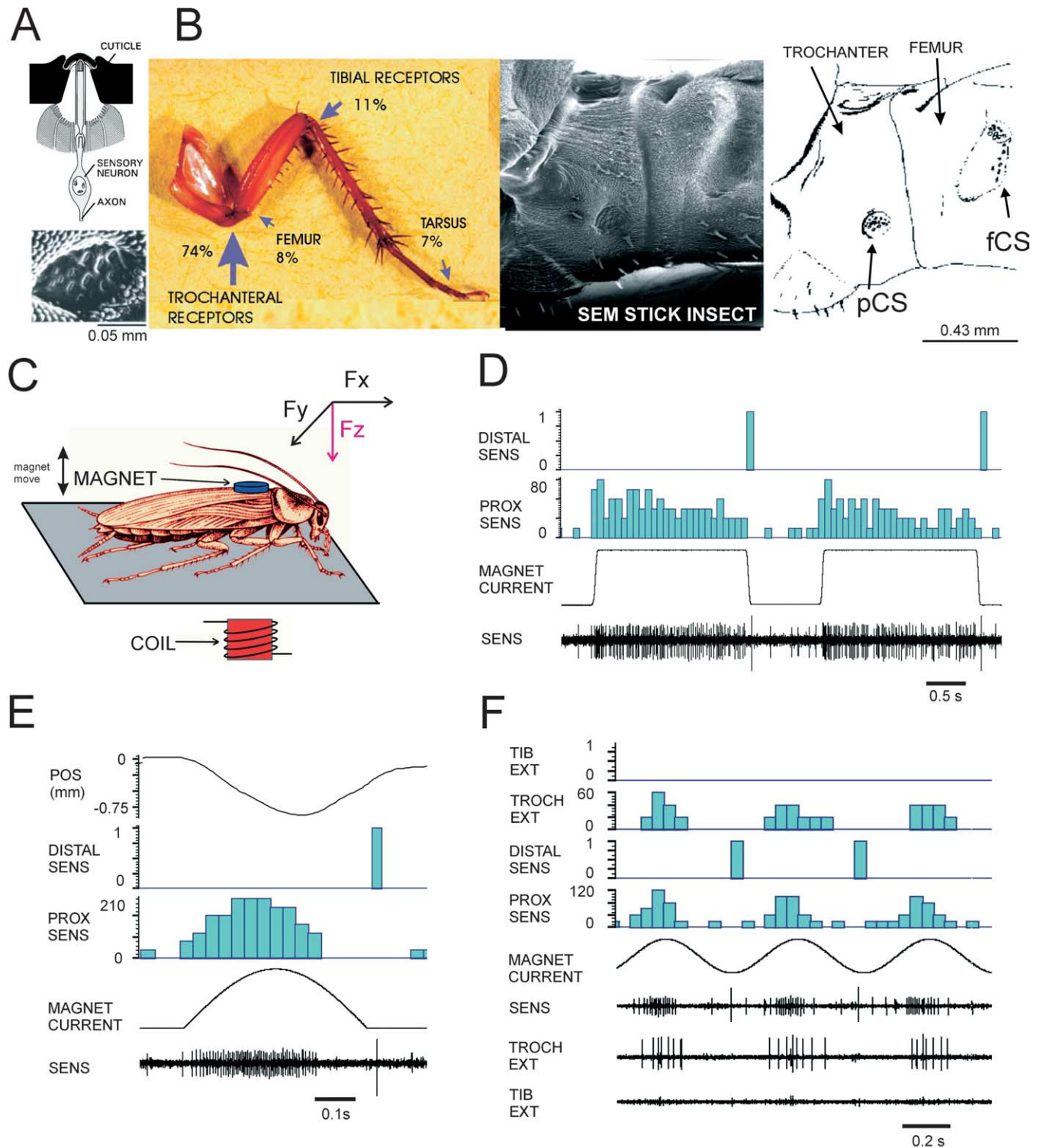


Fig. 1. Anatomy and responses of campaniform sensilla in freely standing animals. (A) A campaniform sensillum consists of a sensory neuron whose dendrite terminates in a small cuticular cap in the exoskeleton and whose axon projects to the central nervous system. The caps show consistent orientations within a group, as in this scanning electron micrograph of posterior trochanteral sensilla of a stick insect. (B) Left—campaniform sensilla are found in groups at discrete locations in the leg (photo of cockroach hindleg). Most groups are found on the trochanter and a smaller number of receptors are found on the femur and tibia. Middle and right—in stick insects, a large group is located on the proximal femur (fCS), opposite the posterior trochanteral sensilla (pCS). (C) Preparation used to study responses to changes in body load. A small magnet was placed on the back of the animal and the forces it exerted were varied through a coil placed below the substrate. (D) Increases in current produced strong firing of the proximal tibial sensilla that was maintained for the duration of the force increase. Release of load elicited single action potentials from the distal receptors. (E) Brief increases in current produced intense discharges of proximal receptors that preceded movement of the body. Release produced activation of distal receptors. (F) Sinusoidal currents produced bursts of proximal receptors and activation of the trochanteral extensor (Ds) but not the tibial extensor (SETi) muscles. Distal receptors fired during the opposite phase when loading on the leg decreased. The proximal receptors produce reflex activation of the trochanteral extensor in restrained preparations.

confirming the findings in restrained preparations. Sensillum firing also immediately followed the onset of force application at very short latency and discharges substantially preceded the peak of displacement of body position (Fig. 1E). Thus, proximal sensilla are particularly sensitive to body load and provide a rapid signal that loads are increasing, even prior to substantial changes in body position in the vertical plane.

Recordings of muscle activities in the cockroach hindleg showed that there was unexpected specificity in the activation of leg muscles in tests which increased body load (Noah et al., 2004) (Fig. 1F). Firing frequency of the trochanteral extensor (Ds) was strongly modulated by changes in load but no or only weak activation occurred in the slow tibial extensor (SETi). This may reflect use of these muscles preferentially in support vs. propulsion. The trochanteral extensor is active through most of stance, while the tibial extensor only reaches higher frequencies late in stance to generate propulsion. Simultaneous recordings of sensory and motor activities showed that, in some postures, proximal sensillum firing was followed by an acceleration in trochanteral extensor frequency consistent with a known interjoint reflex of the sensilla (Zill et al., 1981). Application of sustained forces via ramp and hold stimuli showed that sensory and motor activities could be increased for the duration of the stimulus at some joint angles. These findings provide evidence that receptors that monitor force can complement the effects of other afferents, such as joint angle receptors, and contribute to compensatory reactions to increases in load.

2.3. Patterns of activity in tibial campaniform sensilla in walking: different forces are signaled at different times in the stance phase

In walking at slow to moderate rates, proximal sensilla fire at stance onset and continue through midstance; distal sensilla fire short bursts at the end of stance when the leg is unloaded (Fig. 2A). Proximal activity in walking had been thought to result entirely from leg loading derived from body mass and tests were performed to minimize the effects of body weight upon the legs (Noah et al., 2001). Sensory activities were compared when animals walked freely in an arena and when walking upon an oiled glass plate with their body weight supported by a rigid bar. Proximal sensilla discharged following the onset of stance in all load conditions, but activity was significantly decreased in the middle of the stance phase when the effect of body weight was reduced (Fig. 2B). These results suggest that sensory discharges may result from different sources at different times in stance: firing early in stance can result from forces generated by contractions of muscles that press the leg as a lever against the substrate (Fig. 2C). Force feedback later in stance may reflect the use of the leg as a supportive strut when body weight is placed upon the limb.

3. Sensory inputs in the control of magnitude and timing of motoneuron activity

There are two basic mechanisms by which inputs that detect load are incorporated into motor outputs. First, the amplitude of outputs can be adjusted by reflex connections. Second, the timing of onset and durations of motor outputs during movements can be changed by sensory afferents that input directly into pattern generating circuits. These circuits produce rhythmic outputs at particular joints or in muscles of several limb segments (Akay et al., 2001, 2003, 2004). Data to support these ideas have been developed from extensive studies on sensory inputs in the hindleg of the cat (Pearson and Gordon, 2000) and in the middle leg of the stick insect (Bässler and Büschges, 1998). Additional new data on the processing of inputs from load detectors is reviewed below, with a particular emphasis on the stick insect walking system.

3.1. Load signals and magnitude control of motor output

Tests in restrained preparations have shown that campaniform sensilla have strong excitatory reflex effects in motoneurons to muscles that generate support and propulsion (Zill and Moran, 1981b; Noah et al., 2004). In cockroaches, Pringle (1940) first demonstrated that pressure on the trochanter could produce activation of the trochanteral extensor muscle, a finding that was confirmed by Pearson (1972). Zill and Moran (1981b) showed that the tibial campaniform sensilla have both local and interjoint effects: the proximal sensilla excite both the tibial and trochanteral extensors, while the distal receptors produced excitation of flexors at both joints. Those receptors also had inhibitory effects upon antagonist motoneurons. Thus, the campaniform sensilla of cockroaches are able to produce activation of muscles that are used in support and propulsion even in resting preparations, in contrast to inhibitory effects usually ascribed to other force receptors in mammals such as Golgi tendon organs (although see Duysens et al., 2000, p.97).

Similar results have also been obtained in stick insects. Bässler (1977) showed that continuous stimulation of the trochanteral campaniform sensilla arrested the middle leg in stance and blocked the transition from stance to swing phase after it had reached the posterior extreme position. This finding, taken together with the results of Cruse (1985), implied that decrease in load may be crucial information for the release/initiation of the swing. Other studies have demonstrated that strain applied to the cuticle of the trochanterofemur strongly affects the motor output generated in the middle leg at the thoraco-coxal and femur-tibia joints, both in the resting and in the walking stick insect (e.g. Akay et al., 2001, 2003; Schmitz, 1993). Schmitz (1993) showed that a posteriorly directed increase in load on the middle leg femur is monitored by one subgroup of the trochanteral campaniform sensilla (pCS). This stimulus

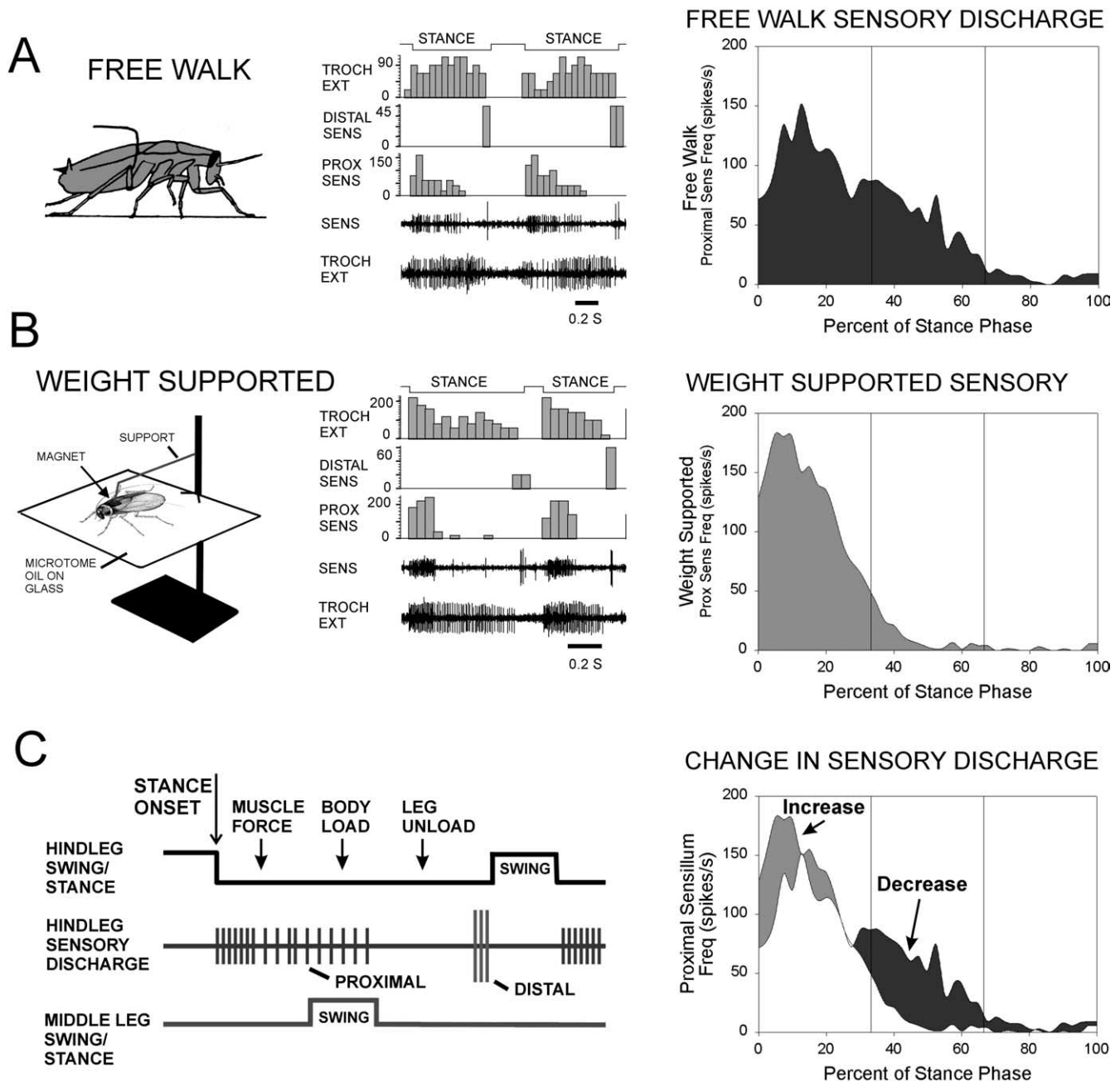


Fig. 2. Effects of decreases in body load on sensory discharges in walking. (A) In free walking animals, proximal sensilla fire at the onset of stance and discharges continue through the middle of the stance phase. Distal receptors are active immediately prior to the onset of swing. (B) Activities were recorded when animals walked on an oiled glass surface with their body weight supported by a rigid bar. The proximal receptors still discharged, but bursts were limited to intense firing after the onset of the stance phase. (C) Composite histogram showing changes in sensory discharges in free walking vs weight supported animals. The firing of the proximal sensilla persisted when body weight was supported. The discharge was higher early in stance, possibly due to the resistance provided by the support bar. Firing significantly decreased in the middle of the stance phase. Model of forces encoded by tibial sensilla: the early discharge of the receptors apparently results from forces generated by leg muscles that act to engage the substrate and generate support. Afferent firing in the middle of stance may reflect the support of body load. Distal receptors provide a signal that the leg is unloaded and may aid in the initiation of the swing phase.

excites the retractor and inhibits the protractor muscles of the thoraco-coxal (TC) joint. The reverse response is elicited by anteriorly directed loads. Similarly, activation of the femoral campaniform sensilla (fCS) (by increased leg loading) has been found to excite flexor and inhibit extensor motoneurons innervating muscles of the femoro-tibial (FT) joint (Akay et al., 2001). The tibial flexor is active during

stance and this activity was decreased in stepping of the single middle leg preparation upon removal of the fCS (Akay et al., 2001).

3.2. Timing of motor output in particular leg joints

A number of investigations demonstrated that load

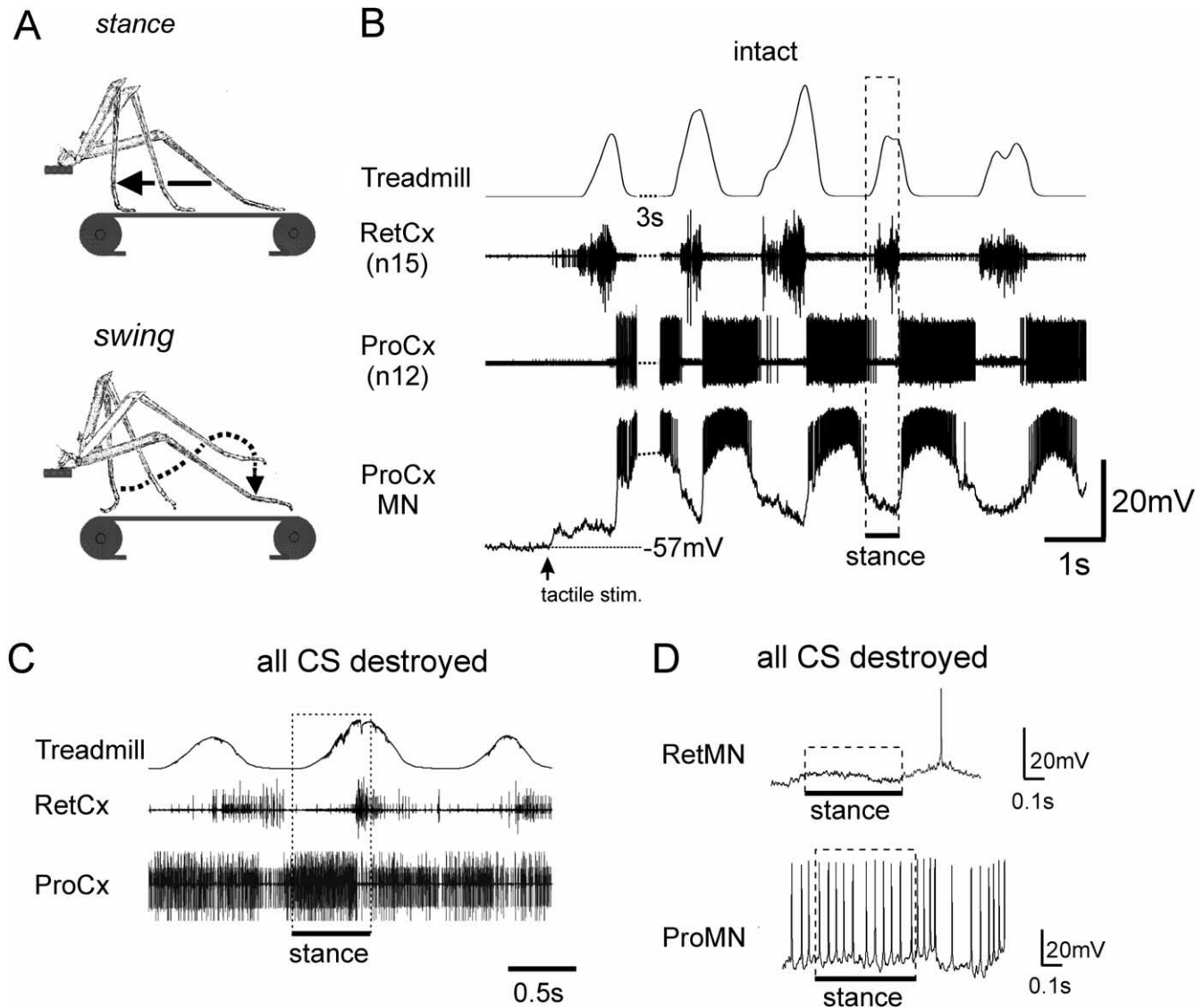


Fig. 3. Effects of trochanteral campaniform sensilla upon interjoint coordination. (A) Diagram showing the movements of the stick insect middle leg during stance and swing in the single leg preparation walking on a treadmill (see also Fischer et al., 2001). (B) Recording of activity in TC-joint motoneurons during single leg stepping. In this preparation the TC joint is immobilized. However, the activities of retractor coxae (RetCx, second trace) and the protractor coxae (ProCx, third trace) motoneurons are coordinated with the stepping movement performed by the more distal leg joints, as indicated by movements of the treadmill (see text, first trace). During stance (trace deflection upward) the band of the treadmill is pulled towards the animal. The bottom trace shows an intracellular recording of a ProCx motoneuron. (C) Recording of activity of RetCx and the ProCx motor nerves after removal of the campaniform sensilla (all CS destroyed). Ablation of the campaniform sensilla (CS) greatly reduces coupling of coxal motoneuron activity to the stepping movement of the distal segments. (D) Intracellular recordings of the membrane potential of a RetCx and a ProCx motoneuron during stance after ablation of the CS. The stance of the single leg is indicated by a horizontal bar. The RetCx (top) motoneuron does not show depolarization during stance and the ProCx motoneuron (bottom) is not inhibited during stance.

signals may also affect the timing of motor activity during walking (Dean, 1991; Bässler, 1977, 1986; Wendler, 1966). There is now considerable evidence that the activity of central pattern generating circuits contributes to the generation of timing of leg movements (see also Bässler and Büschges, 1998; Akay et al., 2003, 2004 for a more detailed account). Previous studies in the stick insect middle leg have shown that reciprocal bursting in motoneurons to antagonist muscles can be generated in the absence of sensory feedback (Büschges et al., 1995). This activity closely resembles bursting seen during walking and can also

occur independently among antagonists at each leg joint. These results strongly suggest that there are individual central pattern generating networks for each of the three main leg joints (Bässler and Wegner, 1983), the thoracocoxal (TC) joint, the coxa-trochanteral (CT) joint and the femur-tibia (FT) joint. Recent experiments have shown that signals from specific subgroups of the trochantero-femoral campaniform sensilla can aid in coordinating activities of motoneurons innervating muscles of different leg joints. These effects are produced through inputs to central pattern generating networks (Akay et al., 2004).

Sensory signals from the femoral campaniform sensilla (fCS) are able to induce transitions in activity between tibial motoneuron pools. A posterior or upward directed increase in load on the femur initiates flexor tibiae activity and terminates firing in the extensor tibiae (Akay et al., 2001). Furthermore, signals from the fCS are able to reset the rhythm of reciprocal bursting in extensor and flexor tibiae motoneurons in the otherwise deafferented mesothoracic segment. There is, however, a considerable amount of variability in the resetting effect. Additional experiments using the semi-intact single middle leg walking preparation (Fischer et al., 2001) indicated that this stimulus contributes to maintaining flexor tibiae motoneurons activity during the stance phase (Akay et al., 2001).

Other experiments have shown that sensory signals from the trochanteral campaniform sensilla (trCS) affect the timing of leg motoneuron activity at the more proximal thoraco-coxal joint. An increase of strain on the leg signaled by the trCS applied during bursts of the protractor coxae terminates the protractor activity, in an otherwise deafferented leg. This stimulus also initiates retractor coxae activity, resulting in a resetting of the rhythmic activity of both motoneuron pools (Akay et al., 2003, 2004). In the cockroach, similar resetting of bursting activities of motoneurons has been shown to be elicited by pressure on the trochanter (Pearson, 1972). Furthermore, in stick insects, ablation of the trCS in the middle leg in a semi-intact preparation produces a massive deterioration of the coordination during walking of activity in motoneurons of the thoraco-coxal joint with the stepping of the distal leg joints (Fig. 3).

Two conclusions can be drawn from these results: (i) sensory signals from the trochanteral campaniform sensilla affect the timing of the central pattern generator governing thoraco-coxal motoneurons; (ii) signals from the trochanteral receptors play a primary role in the coordinating activities of thoraco-coxal motoneurons with the movements of the distal leg joints (Akay et al., 2003, 2004). These findings indicate that when the locomotor system is active load signals from the leg are used to support the initiation of specific phases of motoneuronal activity in the locomotor cycle, i.e. load signals assist in the generation of

flexor tibiae and retractor coxae motoneuron activity during stance.

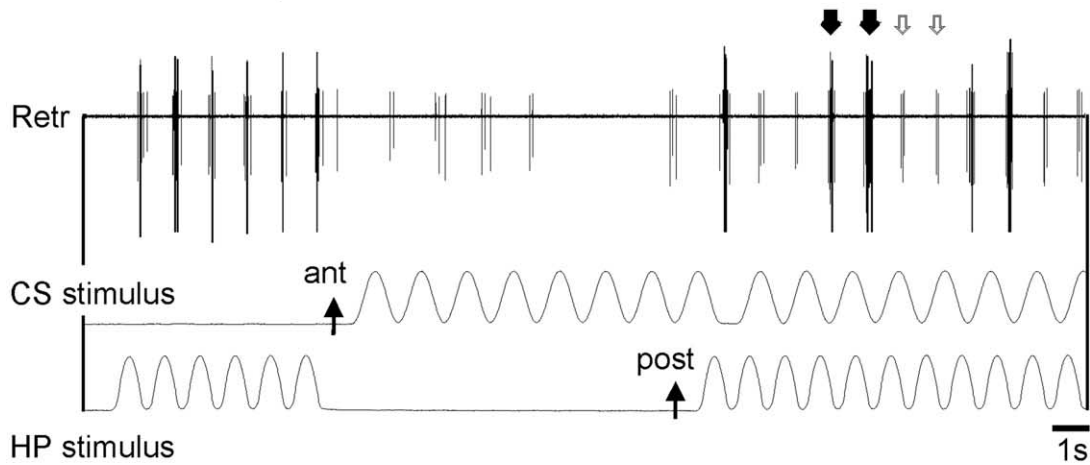
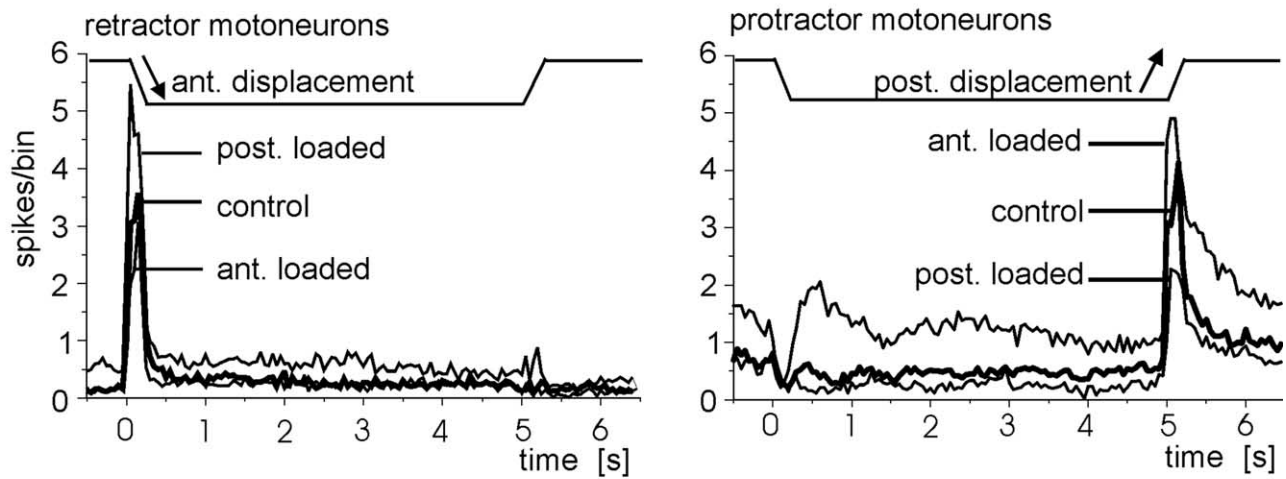
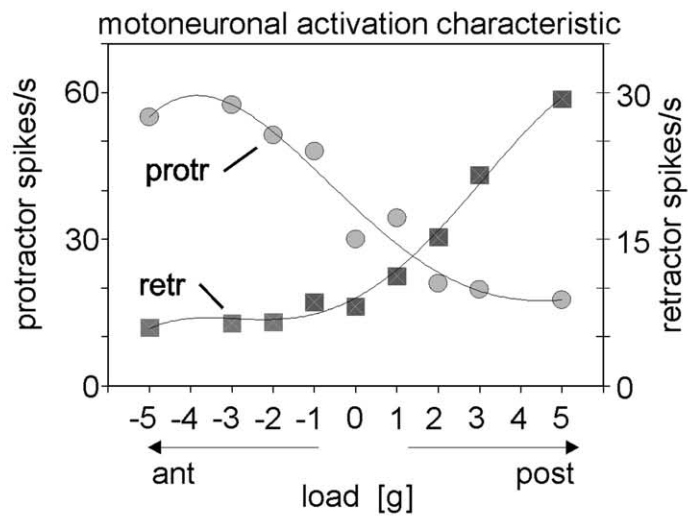
4. Integration of sensors of diverse modalities

Motor outputs produced by pattern generating circuits are adapted to specific tasks, both by direct sensory feedback and by interactions of afferent pathways within the central nervous system. Previous studies in the stick insect middle leg, for example, have shown that movement signals are processed in a distributed fashion. Information from sensors is transmitted in parallel direct and polysynaptic pathways that can have excitatory or inhibitory effects on motor output (e.g. femoral chordotonal organ: Bässler and Büschges, 1998; hair plates: Büschges and Schmitz, 1991). Sensory inputs of diverse modalities can potentially modulate motor outputs through these pathways by simply adding reflex inputs or by more complex mechanisms, such as changing the gain of sensory-motor pathways.

Recent studies on the control of the thoraco-coxal (TC) joint of the stick insect have examined the mechanisms underlying this convergence or ‘sensor fusion’ (Fig. 4). Both inputs that monitor force and those encoding movement of the leg are crucial for control of this joint during standing and walking. Position is monitored by the coxal hairplate (cxHPv) (Graham and Wendler, 1981; Büschges and Schmitz, 1991) and load is measured by the anterior and posterior groups of trochanteral campaniform sensilla (aCS and pCS) (Delcomyn, 1991; Schmitz, 1993). The primary afferents of each sense organ synapse with short central latencies onto the motoneurons innervating muscles of the TC joint. These inputs can provide both excitatory and inhibitory synaptic drive, depending on the stimulus direction (Schmitz and Stein, 2000). Stimulating both sensory modalities concurrently results in a superposition of the respective reflex responses (Fig. 4B and C). Increases or decreases in the level of load on the leg imposed as step functions or sinusoidal changes led to similar changes in reflex activities depending on direction of the loading.

However, the reflex responses did not add linearly (Fig. 4B and C). The superposition of load and movement

Fig. 4. Multimodal Integration. (A) Interactions of effects of signals of changes in joint angle and cuticular stresses. This sequence shows reflex responses of retractor coxae motoneurons to TC- joint movements and to cuticular stress (bending of trochanter-femur). Sinusoidal stimuli were first applied sequentially and then simultaneously. Left—sinusoidal stimulation of the coxal hairplate (HP) produces activation of the retractor (top trace) during the phase mimicking anterior joint movement. Middle—cuticular stresses that excite the campaniform sensilla produce weak activation of the retractor on release from anterior bending. Right—concurrent stimulation of the HP and CS produces reflex responses that are increased (filled arrowheads) when stimuli are in phase and decreased (open arrowheads) when stimuli are in antiphase. (B) Modification of the reflex response amplitude due to tonically increased cuticular stress. Post-stimulus-time histograms (PSTH) showing the averaged reflex responses of retractor (left panel) and protractor motoneurons (right panel) to stimulation of the hairplate indicating movements (upper trace direction indicated by arrows). The same stimuli were applied at different levels of loading of the leg. The thick line in each PSTH shows the response to the stimulus indicating joint movement alone while the thinner lines are the responses when the femur was loaded by 2g anteriorly or posteriorly. Loading the leg posteriorly increases the activation of retractor and decreases the responses of the protractor. Loading anteriorly has the opposite effects. (C) Effects of varying tonic level of loading. Plot of the mean amplitude of the phasic response to hair plate stimulation (during the ramp) at different levels of loading. Positive values of load are applied posteriorly, negative values indicate anteriorly directed loads. The resulting curves are sigmoidal.

A motoneuronal reflex response to individual and concurrent stimulation**B** motoneuronal displacement response with leg loaded**C**

information processing was shown to occur at several levels in the segmental sensory-motor pathway. One important point of integration is the motoneuronal membrane (Schmitz and Stein, 2000). These findings indicate that load information not only serves a protective function but also underlies a continuous mechanism of force control during standing, and most probably during walking as well (Schmitz, 1993; Pearson, 1972).

Although the motoneuronal membrane is one important integration point in the processing of sensory information of different sources, interactions also occur at the level of the premotor interneuronal network. Büschges and Schmitz (1991) described both supporting and antagonizing pathways in non-spiking interneurons that conveyed the information from the coxal hairplate (cxHP) onto retractor and protractor coxae motoneurons. They found that the net motor output for a given stimulus depends on the balance of supporting and antagonizing pathways. It is possible that the load information processing pathways affect this balance in parallel to the direct influences onto the motoneurons. Campaniform sensilla of the locust hindleg have also been shown to provide inputs to pre-motor non-spiking interneurons (Newland and Emptage, 1996).

Influences between different modalities of sensory inputs also occur through primary afferent depolarizations (PAD), which represent interactions at the level of the primary afferent terminations within the central nervous system (Rudomin, 1990). These PADs can originate from afferents derived from the same sense organ (e.g. chordotonal organ: Burrows and Laurent, 1993; Sauer et al., 1997; campaniform sensilla: Stein and Schmitz, 1999). Stein and Schmitz (1999) also showed that interactions of position–position, position–load and load–position sensors could occur at this very first level of processing of sensory inputs (Fig. 5).

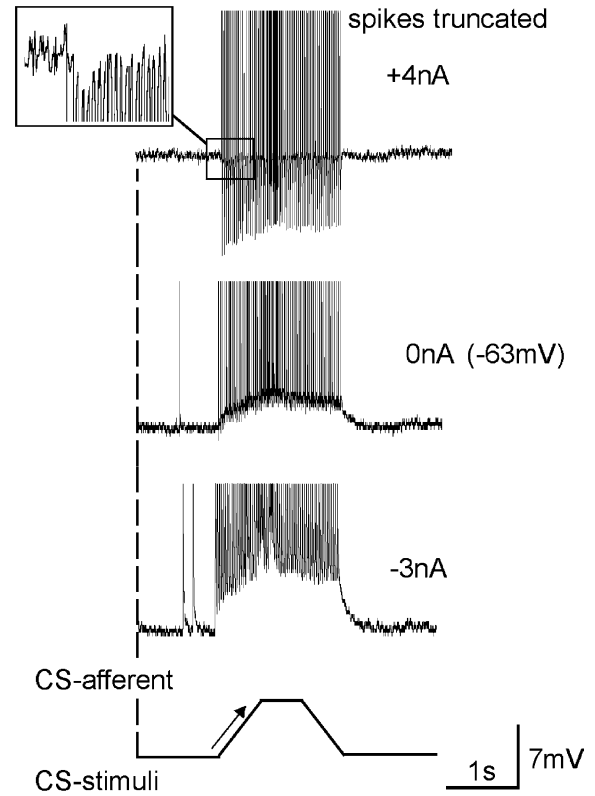
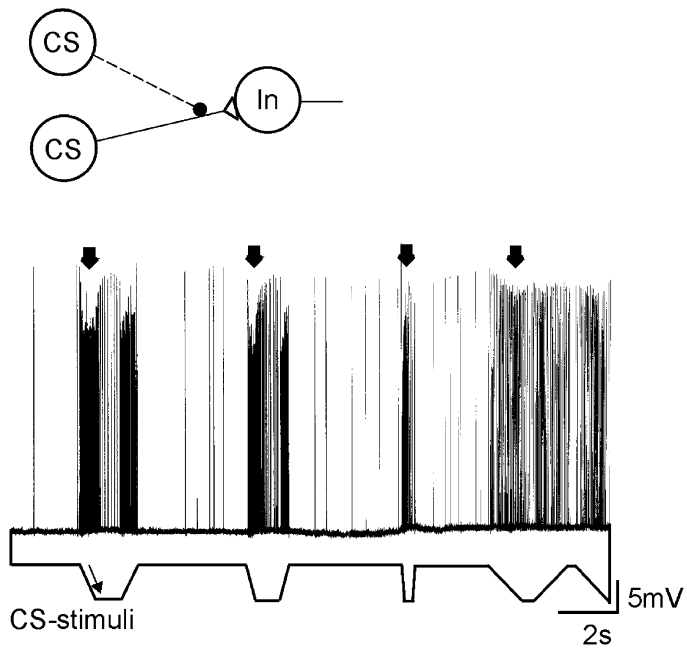
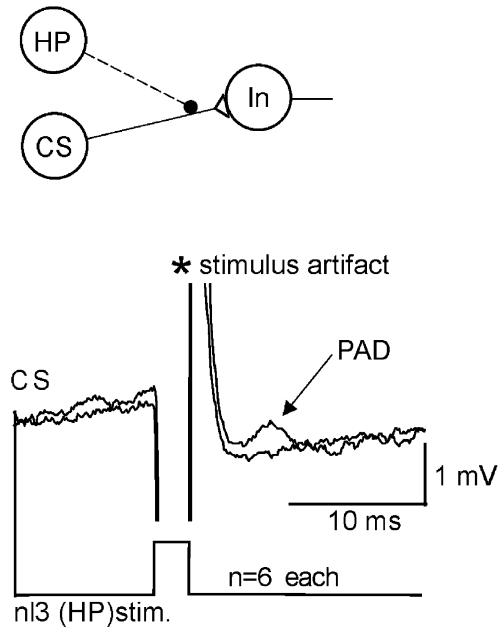
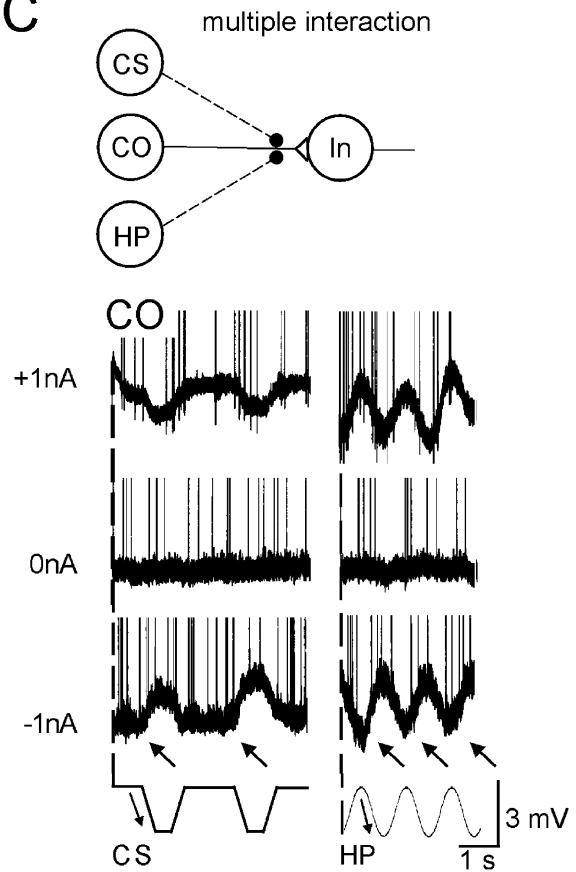
The PADs reduce the amplitude of afferent action potentials and thus also decrease afferent transmitter release and synaptic efficacy. This feedforward control of afferent input to the CNS should be viewed in the context of amplitude control of reflexes and of detection of important sensory information for the shaping and timing of centrally generated motor patterns.

Fig. 6 summarizes the sensory-motor pathways that have been described to date that underlie the control of posture and load. Several neuronal pathways of this scheme were already shown to be also active during walking. Future studies will have to resolve how such interaction of converging sensory information is modulated according to the given task of the motor system, e.g. when movement instead of posture has to be controlled during stepping of the leg.

5. Summary: load detection allows for flexibility in adaptation of posture and locomotion

Information about loading is integral to adaptive locomotion in animals and walking machines. We have reviewed experiments which demonstrate that campaniform sensilla of insects can detect strains due to loading of the leg and the forces produced by leg muscles in standing and walking. These signals provide cues for the generation of normal walking patterns and could contribute to adjustments in posture and locomotion over diverse terrains. The information provided by individual sense organs is highly specific and some groups of receptors may be particularly sensitive to loading derived from the weight of the body upon the legs, while other groups encode forces encountered in propulsion (Noah et al., 2004; Schmitz, 1993). Inputs from campaniform sensilla could, therefore, contribute to the regulation of forces in particular vectorial directions in the body reference frame (Jacobs and Macpherson, 1996; Kargo and Giszter, 2000; Ridgel et al., 2001). Data are provided to the central nervous system both about force increases and decreases by different receptors. The afferent bursts that occur during unloading form a discrete signal that may be used adaptively to detect leg slipping or perturbations of posture. In walking, however, the discharges of sensilla can reflect different sources of forces at discrete times in the step cycle. In upright walking, discharges of cockroach tibial campaniform sensilla early in stance are apparently derived from the contractions of leg muscles that press the leg against the substrate (Noah et al.,

Fig. 5. Modulation and interaction of sensory signals by pre-synaptic inhibition. (A) Effects due to interactions among campaniform sensilla afferents—left: intracellular recording from the afferent terminal of a campaniform sensillum (upper trace) during ramp and hold bending of the trochanter-femur at different rates (downward deflection of lower trace indicates posteriorly directed cuticular stress). The spike amplitude decreases during the ramp phase, an effect indicative of primary afferent depolarization (PAD) and attributable to inhibitory effects of other campaniform sensilla that are activated by the stimulus. Right panel: another CS afferent subject to PADs from neighboring CS sensilla. Imposed changes of the afferent's resting membrane potential shows that the PADs can be reversed. (B) Interaction of position and load afferents. The upper trace shows the average membrane potential recorded from a campaniform sensillum terminal during electrical stimulation of coxal hairplate (HP) afferents (via nerve n_3 , lower trace). The PAD (arrow) occurs when the stimulation of the hair plate nerve is above threshold to produce action potentials and indicates an inhibitory interaction between the afferents (* stimulus artifact). (C) Interactions between afferents of different modalities. Intracellular recording in an afferent of the femoral chordotonal organ (CO) during stimulation of trochantero-femoral CS (left panel, bottom trace, downward deflection indicates increased cuticular stress) and coxal HP (right panel, bottom trace, downward deflection indicates mimicked anterior leg movement). The membrane potential of the chordotonal afferent was held at three different levels and the PAD depolarizations show reversal of direction upon depolarization, indicative of chemical synaptic transmission. The diagrams in A–C illustrate the interactions between sensory afferents. A dashed line indicates an at least di-synaptic pathway with an imposed inhibitory interneuron. The interneuron (IN) shown should indicate only the level of processing of afferent information within the central nervous system and might therefore be a spiking or non-spiking interneuron or even a motoneuron. Filled circular synapses are inhibitory and open triangular synapses are excitatory.

A homonymous interaction**B** heteronymous interaction**C**

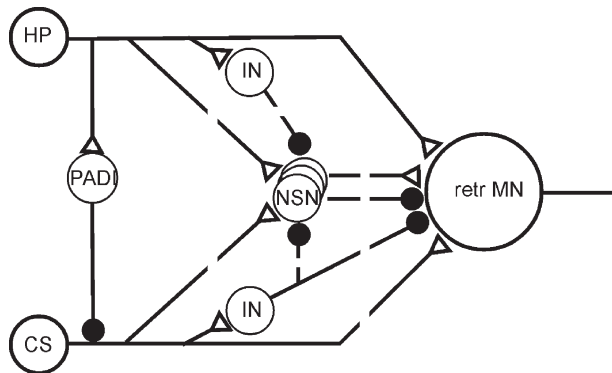


Fig. 6. Summary of pathways of sense organs detecting cuticular stress and joint angles (minimal model from data in stick insects). Most of the primary afferents provide short-latency excitatory or inhibitory synaptic drive, depending on stimulus direction, onto the motoneurons (here only one retractor coxae motoneuron is shown as an example). The layer of premotor, non-spiking interneurons (NSN) also receives and integrates information from both load and position sensors. The afferents of the different sense organs mutually interact as well as afferents of other campaniform sensilla, presumably via (yet not characterized) PAD interneurons (PADI). Broken lines indicate polysynaptic connections.

2001). The action of these muscles can unload legs already in stance and allow them to enter swing, providing the system with smooth transitions in gait.

Load signals are used to adjust the magnitude of muscle contractions through reflex activation of motoneurons. In contrast to Golgi tendon organs of vertebrates, many groups of campaniform sensilla can produce reflex activation of muscles that generate support and propulsion in restrained or 'inactive' animals (Noah et al., 2004; Akay et al., 2001; Schmitz, 1993). In some cases, these reflexes may function in negative feedback to limit the magnitude of strains produced by muscle contractions. However, in locomotion, the discharges of sensilla and patterns of motoneuron firing are consistent with the idea that they serve to enhance the activities of muscles that generate support and propulsion in the stance phase (Noah et al., 2001; Holtje and Hustert, 2003). Data from stick insects indicate that when the system is active in locomotion, the effects of campaniform sensilla inputs change, in that afferent signals can sustain the activities of stance phase muscles and aid in coordinating the pattern of activation of muscle groups at different leg joints (Akay et al., 2003, 2004). Further experiments are necessary to test whether these effects can be modeled as linear positive feedback circuits or whether the reflexes of the receptors undergo reversal or change in gain during walking.

Signals from the sense organs can affect the timing of contractions of leg muscles by inputs to interneurons that form pattern generating circuits. Furthermore, information from the receptors is integrated with inputs from sensors that detect kinematic variables both at the level of the motor output (motoneurons) and in the pattern generating interneurons. These inputs could mediate effects of load that depend both upon leg joint angles and levels of load, such as in the transition between stance and swing. These

effects could be produced by interactions in which signals from load receptors effectively change the gain of reflexes from angle sensors or by altering the occurrence of phase transitions (Akay et al., 2001). Integration of sense organs of diverse modalities in the system is also provided by inhibitory interactions that can occur at the level of primary afferent terminals in the system. The ability to make adjustments both by magnitude of muscle contractions and in the timing of movements provides the system with greater flexibility in adapting locomotion to diverse terrains and in adjusting to perturbations.

These diverse pathways and effects of load reflect the levels of adaptability of the system. A number of studies have shown that the walking system of insects is able to generate locomotion over drastically different terrains by changing the balance and timing of activation of discrete groups of leg muscles (Larsen et al., 1995; Watson et al., 2002), and similar observations have been made in vertebrates (Carlson et al., 1998). The flexibility in the circuitry of the system also allows for changes in the direction of walking and adaptations to large loads.

Future experiments will examine the specificity of these connections in individual tasks, as each sensor provides specific information that is integrated into discrete components of the behaviors. Studies in progress are also examining the effects of load changes in each of the serially homologous legs of the cockroach, which generate similar forces in support of body weight but differ in their contribution to propulsion. These studies will further elucidate how sense organs that detect loads can contribute to these elegant and efficient adaptations of walking patterns.

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