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SUMMARY:

The goal of our project is to **incorporate principles of design and regulation of walking by biological sense organs into sensors for legged robots**. Both animals and robots must utilize information from sensors in the limbs to adapt walking patterns to variations in the environment. During our last funding period we have: 1) examined how patterns of muscle activities and joint movements are changed when animals walk on surfaces in which the orientation of the gravitational vector is altered and 2) characterized the activities and effects of leg sensors that monitor the transition between

the stance (foot on ground) and swing (foot lifted) phases of walking. These studies have shown that animals discretely adapt some elements of the walking pattern when the effect of the gravitational vector is changed. These adapatations most probably occur by using specific inputs from sense organs that detect load when a leg is placed on the ground. Further, the walking system uses inputs and local reflex mechanisms of joint angle receptors to insure that a stable base of support is maintained when a leg is lifted from the walking surface in swing. The latter types of sensory inputs may also be important in adjusting walking when the leg slips on an uneven or unstable substrate. These studies are forming the basis for our collaborative efforts with the group at Case Western Reserve University to incorporate our results into a functional controller for a robot leg.

OVERVIEW OF RESEARCH APPROACH

Principles of Sensory Motor Integration in Insects. In order to be successfully and efficiently performed, locomotion in both legged animals and robots must be regulated, coordinated and adaptively modified. To fulfill these functions, animals utilize inputs from sense organs, known as proprioceptors, that are located in leg muscles and joints, as integral parts of the mechanisms generating and controlling walking (Grillner, 1975; Zill, 1990, 1993). In addition, these sensors can also function to detect changes in leg loading (Zill and Frazier, 1990) and joint positions that result from variations in the terrain or irregularities in the walking substrate. The signals provided by leg proprioceptors can then reflexively adjust the forces produced by leg muscles to counter those loads and aid in changing the patterns of coordination of leg movements to ensure that a dynamically stable bases of support is maintained. In our research, we have studied these problems in insects because the receptors of the legs of those animals are anatomically and physiologically uniquely identifiable. This technical advantage has permitted us to examine the response properties and functions of individual sense organs in walking.

Basic Approach to Defining the Functions of Individual Sensory Receptors in walking. The goal of our present and previous research has been to study the ways in which individual types of leg sense organs function in the generation and adaptation of walking, in order to serve as model systems for the design of sensors and control elements that could perform similar types of functions in legged robots (Beer, Ritzmann and McKenna, 1993). To provide a description of an insect proprioceptive system that is sufficiently complete to understand its function in walking, it is necessary to have basic information about the sense organ's structure and response characteristics, to determine the types of information it provides to the walking control system. More importantly, in order to potentially reproduce elements of the system, it is necessary to know the patterns of sensory discharges that occur during actual behaviors, to be able to directly evaluate the effects that changes in inputs have upon motor outputs. When these data are relatively complete, it is then possible to simulate or emulate such a sensor in a control system to test its potential value in enhancing the adaptability or performance of the system.

In order to develop such complete sets of data for different types of sense organs, our approach has been to perform the following series of studies (Zill, 1985):

1) First, Individual identifiable sense organs of the legs are **morphologically characterized** and the pathways by which they project to the central nervous system are determined. These studies provide basic information about the potential response modalities of the receptors and details as to the ways in which the sense organs are coupled to muscle contractions or movements. Importantly, knowledge of their projections in peripheral nerves (Dresden and Nijenhuis, 1958; Nijenhuis and Dresden, 1952, 1956) permits us to record the activities of sensory neurons in restrained and in freely walking preparations.

2) Second, we establish the **specific response properties** of sense organs by the controlled application of mechanical stimuli in restrained preparations. For many sense organs such as joint angle receptors, these studies are straightforward, and varying the parameters of joint positions and movements can provide the necessary information about the types of variables that the joint receptors are encoding. However, this problem can be considerably more complex for other receptors, such as those monitoring forces acting upon the legs. The major type of receptors that encode forces in insect legs are campaniform sensilla. These sense organs essentially function as strain gauges and respond to forces as the strains they produce in the animals exoskeleton. These strains can be the result of forces of diverse origin, such as those produced by contractions of limb muscles and those resulting from the animal's weight, as well as complex interactions of these forces. The techniques that we are applying to analyze the responses of the trochanteral campaniform sensilla are directed toward resolving just this problem.

3) We also test the effects of sensory inputs on motor outputs in restrained preparations by mechanically stimulating receptors while recording activities of leg muscles to test for potential **reflexes**. Such reflex effects can occur as simple modulations of the levels of motor activities or represent more complex sequences or combinations of muscle activations that can be incorporated as components of walking patterns.

4) Lastly, experiments are performed to **record the discharge patterns of individual sense organs in freely walking animals** (Zill and Moran, 1981b). In these studies, we also record the activities of leg muscles and videotape animals so as to subsequently measure changes that occur in the angles of leg joints. Those recordings and measurements permit us to evaluate the exact phases of the step cycle in which afferent firing occurs during normal walking. In the proposed studies, these data can also usefully be compared with recordings in which animals walk over surfaces that are not horizontal or smooth. In those circumstances, sense organs can potentially provide the nervous system with specific information about the parameters of the substrate that are changing

or about the effects those changes are producing in the animal's own muscle contractions and walking movements. These types of recordings also serve as 'natural' control experiments, in that, one can test whether reflexes elicited in restrained preparations are active during walking by examining whether changes in sensory inputs are followed by modulations of the levels of activities in leg muscles.

As reported in the section below, we have performed such a series of experiments in our previous funding period to characterize some of the receptors of the cockroach tarsus (foot) that regulate and potentially serve to adapt walking. In the studies of the present proposal, we will apply and considerably expand such investigations to those and other proprioceptive sense organs in all three sets of legs. The techniques we have devised and instrumentation we have acquired through our past ONR grant will be readily utilized in the proposed experiments. In addition, our experience in resolving some of the methodological problems inherent in these types of studies should substantially facilitate their application to these new and continued investigations. Furthermore, we feel that our ongoing communications with the neurobiology and robotics groups at Case Western Reserve have given our work more definition and focus as those groups progress in the implementation of biological principles into the evolving design of legged robots (Espenschied, 1994; Full and Ahn, 1995).

REPORT OF COMPLETED RESEARCH

1) Activities of tarsal receptors in freely walking animals: the tarso-pretarsal chordotonal organ

In conjunction with our anatomical studies that have mapped sense organs of the distal segments of the leg, we have recorded the activities of receptors of the tarsus in freely walking animals (**SEE APPENDIX I, ATTACHED**). These recordings show discrete patterns that are correlated with particular phases of the step cycle. In walking on flat upright surfaces, the discharge of most afferents occur during the stance phase. This period of activity is delineated by two discrete bursts that occur near the beginning and end of stance. The first burst is nearly coincident with the time when the leg and tarsus make contact with the substrate and weight is initially placed upon the leg. The second burst occurs at the point of transition between stance and swing, when the leg is lifted from the walking surface and then brought forward to a new point of application.

Despite the fact that our recordings of tarsal sensory activities were multi-unit and derived from a number of different types of receptors, we have been able to identify the source of the afferent burst that occurs late in stance as originating from the tarso-pretarsal chordotonal organ, a joint angle receptor that has not previously been characterized. The criteria we established for this identification are important, as they have shown that with appropriate controls and a knowledge of the anatomy of the sense organs and their axonal projections, it is possible to unequivocally determine the activities of identifiable receptors recorded in nerves containing sense organs of diverse types and properties.

The tarso-pretarsal chordotonal organ consists of about 20 sensory neurons which are located near the end of the leg, that monitor the positions and movements of the tarsal claws and arolium (together these form the pre-tarsus). Recordings from the nerve to the chordotonal organ indicate that most sensory units are activated when the claws are **disengaged** from the walking surface. Tests of the reflex effects of the organ (by mechanically lifting the claws) indicate that it vigorously excites motoneurons to the tibial flexor muscle in the same leg. The same stimulus also produces excitation of the tibial extensor motoneuron in the opposite hindleg.

High speed videotapes of walking animals, taken close up to show the movements of the claws and legs, have shown how this reflex could function to adapt and coordinate leg movements in walking over irregular terrains. These video images show that at the end of stance, the tarsal claws and arolium are first disengaged from the substrate, movements that would produce a discharge in the chordotonal organ. Tarsal disengagement is followed, typically within one videoframe (16 msec.), by the **onset of swing**, in which the flexor muscle is activated to lift the leg and pull it forward. The onset of flexion would therefore be assisted by the reflex effects of the organ's discharge to tarsal elevation. It is of interest to note that the other component of the reflex effect of the chordotonal organ is to activate the extensor muscle of the opposite hindleg. That reflex would function to enhance muscles activity to **counter the increased load** that the **opposite leg would bear** when swing was initiated in the first leg.

2) Walking in unstable environments: animals on inverted substrates as models for understanding principles of the adaptation of locomotion

One of the goals of our previous proposal was to examine how walking patterns are adapted to unstable or uneven terrains and to identify some of the sense organs that contribute to the compensations for changes in load that are required in these circumstances. In order to delineate the mechanisms by which the central nervous system integrates inputs related to force or load into pattern generating neural circuits, we first examined how motor outputs were altered in the extreme condition of walking on an inverted substrate (**SEE APPENDIX II, ATTACHED**). Our reasoning was that the differences seen in the extremes of upright and inverted walking might be able to be extrapolated to predict patterns of walking on surfaces of intermediate inclinations and give some general **insights into how walking could be adapted over uneven terrains**. We found, rather unexpectedly, that many of the basic parameters of joint movements and muscle activities of walking were either unchanged or only discretely altered when animals walked on a surface that was inverted. One fundamental relationship that was retained in inverted walking was the relative constancy of duration of the swing phase at different rates of walking (Grillner, 1975)(although at an even more constrained minimal value). That finding is of interest as the **constant burst durations of flexor motoneurons that generate swing movements**, has not only been noted in walking in many different types of animals but has also formed a **basis for the neuronal 'circuitry'** for Randy Beer's initial controller for legged robots (Beer, 1990). The major difference that we found in the motor pattern during inverted walking occurred in the first half of the stance phase, when muscle groups are active to support the animal's weight. During this period the effect of the reversal of direction of the gravitational vector was to switch, or more accurately, to shift the relative intensities of muscle activations among antagonist groups, from extensors to flexors. When upright, the animals weight applied to the leg tends to flex or collapse the intrinsic leg joints, an effect that is countered by extensor activation. In contrast, on an inverted substrate, the animals weight was supported by recruitment of muscles that tended to draw it upward and to flex leg joints. Essentially, the effect of load inversion could be likened to **changing the use of the limb from that commonly associated with a leg that is stood upon, to an arm, that grasps a surface to support an animal that is climbing.**

3) **Tibial campaniform sensilla contribute to load compensatory reactions during imposed perturbations**

To confirm that the flexor muscle was active to counter loads when walking on an inverted substrate, we tested compensatory reactions of insects by suddenly releasing small weights that were linked to the animal via a string tied to the dorsal cuticle or by simply pulling on the string. Each of these tests resulted in bursts of firing in the tibial flexor muscle, including the recruitment of fast flexor motoneurons, as seen in the stance phase of walking.

We have also applied similar tests to examine the potential contribution of one group of force sensitive receptors, the tibial campaniform sensilla, to load compensatory reactions in inverted postures. We recorded the activities of these sensilla by implanting wires adjacent to the dorsal nerve in the femur (n5r8) while monitoring the tibial muscle myographically (Zill and Moran, 1981a). Release of weights linked to the animal produced vigorous discharges of afferents of large extracellular amplitude in neurographic recordings that were also followed, at short latencies, by increases of firing of tibial flexor motoneurons. We were able to confirm that the receptors that were activated were distal tibial campaniform sensilla by mechanical stimulation of the cuticular caps of individual receptors, which produced bursts of action potentials of the same size as those seen in compensatory reactions. These discharges of the distal tibial sensilla are consistent with the demonstrated response properties, directional sensitivities and reflex effects of these receptors (Zill and Moran, 1981a, b). The cuticular caps of these sensilla are oriented parallel to the long axis of the tibia and they are, therefore, most sensitive to forces that bend the tibia ventrally. This type of bending could readily occur when the weight of the animal is supported by the leg while standing inverted, as opposed to the dorsal bending that occurs in upright postures. We were able, in some experiments, to quantitatively compare the responses of the tibial sensilla in load compensatory reactions to those that occur to ventral bending of the end of the tibia. Animals from which sensory and motor activities had been recorded in inverted postures were restrained, and bending forces were applied to the tibia using a stiff probe attached to a piezo-electric crystal (with movement of the femoro-tibial joint blocked by a pin). Bending forces imposed as step displacements produced discharges similar to those obtained in tests of load compensation. These bursts were phasico-tonic and consisted of an initial firing at high frequencies that adapted over several hundred milliseconds to a lower tonic level. The rate of adaptation during the first second following the onset of mechanical stimulation was less rapid in restrained preparations than in compensatory responses in freely standing animals. This finding may be the result of the reflex effects of the distal sensilla themselves. Stimulation of individual distal tibial campaniform sensilla has been shown to produce excitation of both the trochanteral and tibial flexor muscles. The contractions of those muscles, when resisted, produces dorsal bending of the tibia which mechanically inhibits the discharge of the distal sensilla. Thus the more rapid rate of adaptation seen in sensory discharges during compensatory reactions may be the result of bending forces being generated by the reflex activations of the flexor muscle.

Thus the major findings of this study are that 1) **the distal tibial campaniform sensilla are activated during load compensatory reactions** and 2) those sensilla produce reflexes that could aid in compensation through a negative feedback system, in that the muscles that are reflexively excited tend to produce bending forces that oppose the increase in load and inhibit sensory discharges. While the participation of campaniform sensilla in load compensation has also recently been demonstrated in stick insects (Schmitz, 1993), the potential functions of these types of receptors in positive, as well as negative feedback systems is further discussed below. It is important to note that **different groups of campaniform sensilla have different response sensitivities and effects in walking.**

4) 'Peg' Leg experiments and the Determination of Leg Use and Coordination by Trochanteral Campaniform Sensilla

Some of the earliest experiments done in the study of insect walking examined the **effects of leg ablations on the patterns of limb movements**. In von Buddenbrock's (1921, 1953) studies and those of Wendler (1964, 1966), the middle legs of stick insects were severed in the proximal part of the femoral segment of the leg. This type of amputation left each leg as a stump that contained the proximal leg muscles and the trochanteral segment of the leg. These stumps could not contact the walking substrate but could still be moved and potentially provide the animal with sensory inputs from the trochanter about movements of the proximal segments. These **partial ablations produced immediate changes in the coordination** of the remaining, intact legs during walking. In general, the effect of middle leg amputation was to change the pattern of support **from the alternating tripod gait**, seen in intact animals, **to a 'diagonal' gait**, similar to that observed in quadrupeds (Hughes, 1952, 1957). For example, in normal coordination of animals with intact legs, the front and hindlegs of one side are swung forward and then placed down in support in stance almost simultaneously, as two legs of the tripod. The phase relation of the two legs is then close to 1.0. After the ablations, swing movements of the front legs generally alternate with those of the hindlegs of the same side so that the phase is closer to 0.5 producing a 'diagonal' gait. In order to evaluate whether these changes were due to the loss of sensory inputs from the middle legs, **small prosthetic 'legs' were attached to the stumps** that allowed them to contact the walking surface. The pattern of leg coordination was then dramatically changed and the phase relationships of the front and hindlegs **returned to the pattern of nearly synchronous use seen in the tripod gait** in intact animals (phase = 1.0). This restoration of a normal gait was not simply due to the fact that the protheses provided mechanical support for the animal's weight, as similar changes occurred when the stumps merely contacted a small platform attached to the animal's thorax. Instead, these experiments implied that when the stumps could be pressed against a substrate, they produced activities of sense organs in the remaining, proximal leg segments (trochanter or coxa) and that these sensory cues were sufficient to change the overall pattern of use of the legs in walking. The idea that these effects were due to inputs from receptors detecting forces were supported by Wendler's (1964) observations that ablations of joint angle receptors, such as the trochanteral and coxal hairplates, did not alter leg coordination. He also noted that the leg stumps in the ablation experiments still moved through appreciable joint angles with and without the prosthetic limbs. It appears, therefore, that the effects of leg contact and the subsequent changes in leg coordination that are induced are mediated by receptors detecting forces that act upon a leg.

The trochanteral campaniform sensilla were also among the first receptors of the legs of insects that were demonstrated to exert **reflex effects upon motoneurons** to leg muscles. Pringle (1940) first showed that manual compression of the trochanter, presumably exciting the trochanteral sensilla (Pringle 1938a,b), reflexly **excited the trochanteral extensor motoneuron**. Pearson (1972) repeated the same experiments more extensively while recording activities of the trochanteral extensor and flexor muscles. He also found that indentation of the trochanter produced vigorous discharges in the slow trochanteral extensor motoneuron (Ds). Furthermore, Pearson (1972) postulated that this reflex formed part of a **positive feedback system** as excitation of the slow extensor should produce forces that would generate larger cuticular strains in the trochanter, further exciting the campaniform sensilla. Although this experiment has been repeated in stick insects with similar results (Bassler, 1986, 1993), it has not previously been directly demonstrated that the trochanteral campaniform sensilla were responsible for excitation of the extensor. We have recently performed that experiment by stimulating the cuticular caps of individual trochanteral campaniform sensilla. We have been able to document that some receptors of the anterior groups of trochanteral sensilla do reflexively excite both the trochanteral and tibial extensor motoneurons, although the effects of any one sensillum were weak and resulted, at best, in only a few extra action potentials in the extensor motoneurons.

We have also **repeated elements of the earlier behavioral studies** of von Buddenbrock and Wendler and have performed studies that have examined the types of inputs that can modulate extensor firing during walking. The slow **tibial extensor**

motoneuron shows a characteristic pattern within a burst during the stance phase of upright walking: firing is initiated at a low or moderate level and then shows a uniform acceleration to terminate abruptly at a much higher frequency (Ewing and Manning, 1966, Krauthamer and Fourtner, 1978; Watson and Ritzmann, 1994). We have performed a series of ablation experiments, recording muscle activities and joint angles in freely walking animals, to determine whether this acceleratory pattern could be mediated by the trochanteral campaniform sensilla.

When the **leg was ablated in the distal femur**, close to the femoro-tibial joint, the animal usually did **not** extend the femur sufficiently to allow the distal end of the leg to **contact the substrate** (Hughes, 1952, 1957). During walking, recordings of the tibial extensor and flexor muscles could show periods of reciprocal activity (Delcomyn, 1990a,b), but the slow **extensor never showed the acceleration** within a burst that was seen in intact animals, even when the extensor firing frequency was quite high. Although the remaining part of the tibia was too small to permit us to record the femoro-tibial joint angle, we were able to measure the angle of the coxo-trochanteral joint. No large excursions in joint angle were seen during walking and, in most steps, the joint movements consisted of simple irregular flexions. However, the end of the leg could **make contact on some steps** when the ablation was performed in the middle of the femur. This operation still allowed for recordings from the tibial muscles, although they effected no movements as the tibial was now completely ablated. In these preparations, the extensor did **show the characteristic acceleratory firing pattern** whenever the stump of the femur made contact with the substrate (as judged by careful visual observation of the animal from the side of the walking arena). The changes we observed in the extensor firing pattern were accompanied by equally dramatic differences in the recordings of the coxo-trochanteral joint, which showed the smooth acceleration that was characteristic of normal walking. In some sequences, steps in which contact was not made could be followed by those in which the femur touched the substrate. Again, the restoration of the firing pattern of the extensor was accompanied by vigorous extension of the coxo-femoral joint, presumably reflecting a similar increase in the firing frequency of the trochanteral extensor motoneuron as well.

Thus, we have demonstrated that contact of the stump of a leg that contains the **trochanteral campaniform sensilla, can have dramatic effects upon the firing pattern of the tibial, and presumably trochanteral, motoneurons**. The nature of the feedback loops effecting these changes is further discussed below.

5) Responses of trochanteral campaniform sensilla to imposed bending forces

We have developed a **preparation in which the activities of identifiable trochanteral campaniform sensilla can be recorded** while forces are applied to the leg, either as imposed mechanical bending of the femur or by selective activation of the coxal musculature. An animal is restrained ventral side up and all nerves innervating a middle or hindleg are crushed close to the associated thoracic ganglion. One pair of 30 micron wires, insulated to their tips, is inserted through holes made in the cuticle and placed near the main leg nerve (n5) in the coxa. Another pair of wires is either placed next to n5 distal to the first pair or is positioned adjacent to the small nerve branches that innervate the individual groups of trochanteral campaniform sensilla. To limit the number of sense organs recorded in nerve 5, the leg is severed in the proximal tibia or distal femur and the branches of n5 and 5r8 are cut just distal to the trochanter. The trochanteral segment is then immobilized by securely gluing it on its ventral edge (opposite the sensilla) to a pin placed close to the coxo-trochanteral joint. **Bending forces are then applied to the distal femur** using a blunt, stiff segment of thick tungsten wire attached to a piezo-electric crystal. In preliminary experiments, voltages have been delivered to the crystal as step functions generated by a stimulator. A second probe, of much finer etched tungsten wire, attached to another crystal is used to **stimulate the cuticular caps of individual trochanteral sensilla** to facilitate identification of units in discharges to bending forces. After a series of test are applied, individual groups of sensilla or the caps of single receptors are selectively ablated using a sharp minuten pin or etched tungsten wire. We will also confirm the adequacy and extent of our ablations by removing the trochanter after an experiment, placing it in fixative and preparing it for plastic sectioning and light microscopy or scanning electron microscopy.

Our preliminary studies have shown that this preparation is viable and that, with accurate placement of the recording wires, the **activities of trochanteral campaniform sensilla can be readily recorded**. Furthermore, the use of two sets of extracellular recording electrodes has substantially facilitated the identification of spiking activities of single identifiable receptors. In those recordings, responses to bending forces can be compared to those obtained by stimulation of the cuticular caps of single sensilla not only for their extracellular amplitude but also other parameters such as waveform shape and conduction velocity. These factors will enable us to perform detailed analysis of the activities of single sensilla (using the techniques described below) even in multi-unit recordings. Using this new preparation, we have also been able to demonstrate that a number of sensilla show vigorous responses to forces that bend the femur and trochanter dorsally, similar to the types of bend that should occur if the leg were used when walking upright. This preliminary finding supports the idea that some sensilla may participate in positive or force amplifying feedback loops. However, we have found some receptors that apparently respond maximally to forces imposed in planes in other directions and thus reflect the postulated differential sensitivity of the trochanteral campaniform sensilla (Hofmann and Bassler, 1982, 1984; Delcomyn, 1991).

Thus, all our evidence to date is that this preparation will allow us to fully characterize the sensitivities of the trochanteral receptors to external and muscle generated forces. We should also point out that this preparation can be readily used in experiments in which activities are recorded using prosthetic limbs, merely by attaching an extension to the stump of the femur. Thus, we believe we have developed a method in which the activities of the trochanteral campaniform sensilla can also be studied in freely walking animals.

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Implementation and Implications for Legged Robots

Our studies of the activities of sense organs of the tarsus during walking have demonstrated several advantages in the use of the pre-tarsal claws by cockroaches. They have also accompanied a growing interest in our colleagues at Case Western in **incorporating claw like extensions to the limbs in the next generation of legged robots**. We have found, for example, that the claws are frequently engaged with the substrate during the stance phase of walking when animals traverse discontinuous surfaces (the mesh floor of our arena). We have also noted that use of the claw is almost invariant in the American cockroach when animals climb on inclined substrates or climb barriers. Under these circumstances, the claw provides a much more firm base of support in that it actively penetrates and engages the substrate and prevents slipping of a foot by greatly increasing traction. Furthermore, our basic findings of the **reflex effects of the tarso-pretarsal chordotonal organ are also planned to be incorporated into the robotic controller**. Both the components we have demonstrated for these reflex engender behavioral advantages: first, the elevation of the claw that produces reflex activation of the flexor muscle by the chordotonal organ aids to initiate swing after the substrate has been disengaged and prevents any discoordinating or potentially damaging effects in use of the leg. Also, the cross-extension component of the reflex serves to immediately enhance the activities of the opposite legs in support, thus anticipating the increase in load will result from lifting a leg. That latter effect, which is found in leg reflexes of vertebrates as well, will be similarly effective not only in walking but other behaviors in which a leg is lifted, such as reaching to explore a terrain or picking up an object.

Our studies on inverted walking and our preliminary findings on load compensatory reactions in inverted postures have implications for the design of a neuronally based control system as well as practical applications in the uses of legs that possess claws. We found that in inverted walking the elements of walking that were basically similar to upright walking supported the idea of a **flexor burst generator** in the central nervous system that patterns the basic parameters of walking. However, we also found other attributes of the basic pattern that were changed, such as the fact that the duration of the swing movements were kept to a minimum in walking on unstable surfaces. These changes could also be considered in adapting walking to irregular terrains. However, more fundamentally, our results can be interpreted as showing that a limb with a claw can be readily used both in ways that are normally associated with a leg as well as supporting an animal in ways that bear more resemblance to an arm. For example, we found that the flexor muscle was active both during the stance phase of walking and in load compensatory reactions when animals were inverted and likened the responses to load to 'doing chin ups'. These rules could well be applicable to animals that were walking on surfaces inclined perpendicular to the body long axis. In that case one leg could be using the extensor in support to push the animal up while the other leg is flexed to grab and pull the animal toward the walking surface. Our preliminary finding that the distal tibial campaniform sensilla were activated during such load compensatory responses may indicate that **cockroaches use inputs of some groups of sensilla to effectively and directionally react to loads according to the specific mode of leg use.**

2. PUBLICATIONS - (see APPENDICES ATTACHED)

Research Papers

Larsen, G. S., Frazier, S. F. and Zill, S. N. The tarso-pretarsal chordotonal organ as an element in cockroach walking (manuscript reviewed and re-submitted with minor revisions) J. Comp. Physiol.

Zill, S. N. and Seyfarth, E.-A. (1996) Exoskeletal sensors for walking. Sci. Am. 275:70-74.

Larsen, G. S. Frazier, S. F., Fish, S. E. and Zill, S. N. (1995) Effects of load inversion in cockroach walking. J. Comp. Physiol. 176:229-238.

Zill, S. N., Frazier, S. F., MacFarland, D. L. and Fish, S. E. (1993) Characterization of insect sense organs using a carbocyanine dye in fixed tissues. J. Exp. Biol. 175:299-303.

Zill, S. N. and Frazier, S. F. Activities of insect tibial campaniform sensilla in load compensatory reactions (manuscript in preparation for submission).

additional papers from:
Larsen, G. S. Mechanisms of sensory regulation and adaptation of cockroach walking (Ph. D. Dissertation, Department of Anatomy, Cell and Neurobiology, Marshall University, completed and accepted, July, 1995).

Books

Zill, S. N. (1993) Mechanisms of load compensation in insects: swaying and stepping strategies in posture and locomotion. pp. 43-68, in Biological Neural Networks in Invertebrate Neuroethology and Robotics. Beer, R., Ritzmann, R. and McKenna, T. eds. Academic Press, Boston.

Abstracts

Larsen, G. S., Frazier, S. F. and Zill, S. N. (1993) Strolling on the ceiling: Effects of load inversion on cockroach walking. Neurosci. Abstracts 19, Part 2, p. 1601.

Larsen, G. S., Frazier, S. F., Fish, S. E. and Zill, S. N. (1994) Activities of tarsal afferents in freely walking cockroaches. Society for Neurosci. Abstracts 20, Part 2, p. 1594.

Zill, S. N., S. E. Fish and Frazier, S. F.(1995) Knowing you have a leg to stand on: effects of trochanteral campaniform sensilla in cockroach walking. Society for Neuroscience Abstracts 21, Part 1, p. 426.

Zill S. N., DiCaprio, R. A. and Frazier, S. F. (1996) Leg design and response specificity of cuticular strain detectors. Society for Neuroscience Abstracts 22, (in press).

Research Papers in Preparation

Larsen, G. S., Frazier, S. F. and Zill, S. N. Fine structure and potential mechanisms of transduction of the cockroach tarso-pre-tarsal chordotonal organ.

Larsen, G. S., Frazier, S. F. and Zill, S. N. Anatomy and mechanisms of action of the cockroach tarso-pretarsal joint.

Zill, S. N. and Frazier, S. F. The cockroach trochanteral campaniform sensilla as a force detecting array: positive feedback and the regulation of muscle activities in walking.

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Summary: The goal of our project is to **incorporate principles of design and regulation of walking by biological sense organs into sensors for legged robots**. Both animals and robots must utilize information from sensors in the limbs to adapt walking patterns to variations in the environment. During our last funding period we have: 1) examined how patterns of muscle activities and joint movements are changed when animals walk on surfaces in which the orientation of the gravitational vector is altered and 2) characterized the activities and effects of leg sensors that monitor the transition between the stance (foot on ground) and swing (foot lifted) phases of walking. These studies have shown that animals discretely adapt some elements of the walking pattern when the effect of the gravitational vector is changed. These adapatations most probably occur by using specific inputs from sense organs that detect load when a leg is placed on the ground. Further, the walking system uses inputs and local reflex mechanisms of joint angle receptors to insure that a stable base of support is maintained when a leg is lifted from the walking surface in swing. The latter types of sensory inputs may also be important in adjusting walking when the leg slips on an uneven or unstable substrate. These studies are forming the basis for our collaborative efforts with the group at Case Western Reserve University to incorporate our results into a functional controller for a robot leg.

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