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Characteristics of dynamic postural reactions in the locust hindleg

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Summary. The use of the locust *(Schistocerca americana)* hindleg in postural control was examined in animals that stood on a repeatedly swayed vertical substrate. Myograms were recorded from leg muscles and the angle of the femoro-tibial joint was monitored photographically. Two discrete strategies were observed; in compensatory reactions the hindleg was held in place, while in "flexion" reactions, the leg was moved, most often to complete flexion of the femoro-tibial joint. Tightly coupled, rhythmic bursting occurred in the flexor and levator muscles of the leg during compensatory reactions. Bursting was initiated repeatedly when the substrate was being pulled away from the animal. Bursting was correlated with subsequent decreases in the rate of change of the femorotibial joint angle. Compensatory and "flexion" reactions occurred preferentially in different ranges of joint angles: most often, compensatory reactions occurred in the midrange, while "flexion" reactions were elicited in the extremes of joint angle. These differences may be due to the mechanical advantages of the tibial muscles and the leg may be moved to full flexion because of a locking mechanism of the flexor muscle tendon. These reactions are compared with known reflexes of hindleg proprioceptors and contrasted with similar responses of vertebrates.

Key words: Postural control – Insects load compensation – Joint angle – Chordotonal organ

Introduction

Many animals have been shown to exhibit dynamic postural control. In the literature on motor control in vertebrates, this term has been used to describe the sequence of muscle contractions and movements that humans and animals make to maintain postures when mechanical perturbations occur in their physical environment (Duncan et al. 1990). These types of reactions have been extensively and systematically studied in vertebrates using a variety of paradigms and have been utilized to evaluate the potential functions of proprioceptive sense organs.

In the paradigm first developed by Nashner and colleagues (Nashner 1976, 1977; Nashner et al. 1979), human subjects stand upon a platform that is suddenly rotated, longitudinally translated or vertically displaced. Humans react to displacement of the substrate upon which they stand by using discrete motor strategies. For example, small to intermediate rotational displacements produce swaying of the ankle and hip joints, accompanied by stereotyped contractions of groups of limb and trunk muscles (Nashner et al. 1979). In these compensatory reactions the subject's foot remains stationary upon the substrate. Similar adaptive postural reactions have also been demonstrated in other vertebrates, such as cats (MacPherson 1988).

Another paradigm, recently developed by Wolfson and colleagues, is the postural stress test (Wolfson et al. 1986). In this test, postural perturbations are produced by dropping a weight that is attached via a pulley and wire to a padded belt placed around a subject's waist. As the person tested stands facing away from the pulley, this paradigm measures an individual's ability to counter destabilizing forces that pull the center of gravity behind the base of support (Duncan et al. 1990). Human subjects respond to sudden applications of small weights with swaying movements at joints of the lower extremities as they do in the platform tests of Nashner (Wolfson et al. 1986). However, larger weights and greater forces produce "corrective" reactions, in which the foot is lifted from the substrate and re-positioned to produce a more stable basis of postural support (Chandler et al. 1990). Such movement or "corrective" stepping strategies have been demonstrated to occur during walking in humans (Dietz et al. 1984, 1986, 1987) and have also been shown in previous studies in which forces were applied to individuals standing in unstable initial postures (Do et al. 1982). Similar corrective reactions have also been dem-

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onstrated to occur in walking in a variety of animals (Forssberg 1979). Thus, dynamic postural control has been demonstrated in vertebrates to consist of discrete responses: compensatory or swaying reactions which occur at low levels of postural perturbations and forces and "corrective" or stepping responses which occur at higher levels of force or at initial unstable postures.

While these motor reactions have been well characterized, there is little agreement in the vertebrate literature on the relative contributions of different sensory modalities in the detection of perturbations and in the generation of appropriate postural responses (see Nashner and McCullom 1985, for review; Cohen and Keshner 1988; Keshner and Cohen 1988). In vertebrates, inputs from proprioceptive, visual or vestibular systems can all contribute to elements of dynamic postural control (Cohen and Keshner 1988). The early studies by Nashner and colleagues suggested that proprioceptive inputs from limb mechanoreceptors were primarily responsible for generating compensatory reactions (Nashner et al. 1979). For example, ankle muscles were activated in postural swaying tests at latencies similar to those seen in studies of long latency stretch reflexes in non-standing subjects, suggesting that leg proprioceptors such as ankle muscle spindles or joint receptors mediated postural responses (Nashner 1977). However, recent experiments in which the activities of neck, spinal and abdominal muscles have been recorded during swaying tests have shown that those muscles are also recruited at similar latencies, suggesting that other, non-proprioceptive pathways were also active (Keshner et al. 1988). Thus, the contributions of particular types of receptors to the various components of dynamic postural control have remained unresolved.

While these paradigms have been applied in vertebrates, few studies have examined the responses of invertebrates to postural perturbations. Earlier studies on crustacea have shown that crabs (Barnes et al. 1972) and lobsters (Chasserat and Clarac 1983) can produce compensatory activities in leg muscles when external forces are applied during walking. However, few studies have examined this problem in insects or other invertebrates. Many insects are of interest for studies of postural control as they lack receptors corresponding to the vertebrate vestibular system (Keshner and Cohen 1988) or the crustacean statocyst organs (Neil 1975). Previous studies have suggested that these animals utilize information derived from leg proprioceptive sense organs in behaviors such as gravity orientation (Markl 1971; Wendler 1971). Insects, therefore, provide an interesting system for studying how dynamic postural control mechanisms could operate based upon information provided solely by limb proprioceptive sense organs.

We have developed a paradigm for studying postural responses in the locust hindleg that represents primarily an adaptation of the paradigm of Nashner (1976), utilizing a swaying chamber (Zill and Frazier 1990a). In the studies reported here we also add elements adapted from the paradigm of Wolfson et al. (1986), in combining the use of additional weights to stress postural reactions. We have demonstrated that these animals show discrete patterns of motor activities during tests of dynamic postural responses which we discuss as analogies to the compensatory and "corrective" reactions of vertebrates.

Methods

The basic methods and apparatus we used to test the responses of grasshoppers to postural perturbations are described in detail in a previous paper (Zill and Frazier 1990a). Briefly, in order to record the myographic activities of leg muscles, animals were restrained and the ends of long lengths of 50 μm diameter silver wires were inserted as pairs into 3 of the following muscles of the hindleg: the trochanteral levator (TrLe) and depressor (TrDe), the tibial flexor (FlTi) and extensor (ETi) and the tarsal levator (TaLe) and depressor (TaDe) muscles (Fig. 1B). All wires were then tied and glued to the external cuticle of the femoral segment of the leg using cyanoacrylate adhesive.

Animals were subsequently released into a plexiglass chamber that was mounted on a platform (Fig. 1A). This platform was supported by swivel joints and linked to a d.c. motor. Activation of the motor (via a stimulator and a series of relays) produced swaying of the chamber. We monitored the angle of the floor of the chamber relative to the horizontal plane by applying a voltage to a potentiometer attached to the swivel rod. We were also able to vary the rate of displacement of the chamber via a potentiometer configured as a voltage divider in line with the power source. We covered the inner sides of two walls of the chamber with fine wire mesh and many animals spontaneously climbed those walls and stood upright at the top of the screen with their body long axis oriented vertically and their head end up. This arrangement generated forces during repetitive displacements so that animals were being forced toward or away from the chamber wall. The angle of the chamber and all myographic activities were recorded on tape for subsequent transcription and analysis. Histograms of muscle activities were plotted on an IBM computer using a Modular Instruments interface system (MI2). We have plotted the data in these histograms from the phase of movement in which the wall of the cage was in a vertical plane (phase = 0) and being moved toward the animal. In addition, we calculated the initiation of bursting either by measuring the smallest recordable junctional potentials in multiply innervated muscles (such as the tibial flexor) or by using a window discriminator (MI2) in muscles that have single slow excitatory axons (such as the tibial extensor).

We used several techniques to monitor animals' behaviors during postural perturbations and to permit measurement of the angle of the femoro-tibial joint. In early experiments ($n = 14$), animals were photographed at the time of onset of repetitive displacements using a 35 mm still camera. To coordinate photography with the time of initiation of movement of the chamber, an electrical switch was attached to the shutter cable of the camera and was used to trigger the voltage from the stimulator which activated the motor. The behaviors of animals during these tests were evaluated by visual observation.

In later experiments ($n = 12$), we videotaped animals during displacement tests using an RCA camcorder equipped with a macro lens. In order to measure the changes in the angle of the femoro-tibial joint of the hindleg we attached two miniature light emitting diodes (LEDs) to the proximal femoral and distal tibial segments of the hindleg (Fig. 1B). We measured the joint angle by subsequently playing back the tapes on a videocassette player (Mitsubishi model HS-413R) which permitted single frame freeze and advance. While some slight blurring of the image of the LEDs occurred in these recordings (approximately 30% increase in size) we were repeatedly able to detect changes in their relative positions with a resolution of 1 mm.

To calculate the change in joint angle, the positions of the leading edges of the LEDs in each frame (30/s) were marked upon acetate sheets attached to the surface of the monitor and the distance between them measured with a micrometer. We subsequently

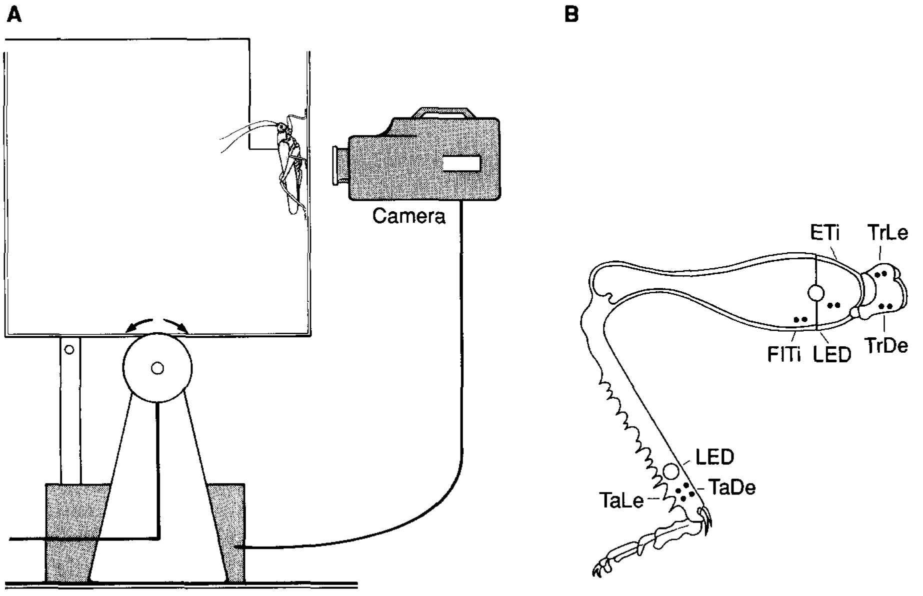

Fig. 1A, B. Experimental setup. **A** Locusts were placed in a chamber that was repeatedly swayed by a motor. Animals climbed screening on the inner wall of the chamber so that they were swayed toward and away from the substrate. In some experiments, animals were photographed at the onset of displacement tests or videotaped throughout the cycles of movement. **B** Myographic recordings were taken from 3 of the following muscles: the trochanteral levator (*TrLe*) and depressor (*TrDe*), the tibial flexor (*FlTi*) and extensor (*ETi*) and the tarsal levator (*TaLe*) and depressor (*TaDe*) muscles. In some experiments, miniature light emitting diodes (*LED*) were attached to the leg to permit subsequent measure of the angle of the femoro-tibial joint

entered these data into a spread sheet computer program (Lotus) and calculated the femoro-tibial joint angle by a triangulation formula. Histograms, other graphs and regression calculations were done on a standard graphics program (Sigmaplot).

In 3 of the experiments in which we videotaped animals, myographic activities were also recorded from the tibial flexor muscle. We correlated the changes in joint angle with parameters of muscle bursting in those animals by comparing the locust's position and the location of the wall of the cage on the videotaped image with the signal from the potentiometer which recorded the position of the chamber relative to the horizontal plane.

To further stress postural reactions, we attached a small weight (2.75 g) to locusts by tying it tightly to a surgical thread sewn through the junction of the thorax and abdomen. The effect of this procedure was to increase the animal's weight as a whole and did not effect the behavior of the abdomen in these tests (as judged from the videotaped image). In 5 experiments animals were also videotaped to measure the femoro-tibial joint angle, while in 3 other experiments we also recorded myographic activities of leg muscles during swaying tests with weights.

We performed a series of control experiments to insure that the wires which were attached to animals in the preceding experiments did not alter the use of the hindleg. In those experiments, ($n = 14$) animals were simply placed in the chamber with no wires attached and their behaviors at the onset or during displacement tests were photographed or videotaped. In addition, we performed several control experiments to limit the modalities of sensory information available to animals during displacement tests in which myographic activities were recorded: we covered the compound eyes and ocelli with nail polish (3 experiments) and cut nerves to the tympanal organs (3 experiments).

Results

Behavioral observations

The metathoracic legs were used in two general patterns of behavior during repetitive displacements of the chamber, as judged by visual observation and examination of videotaped reactions. In the first pattern, termed compensatory reactions, the tarsus (terminal segment of the hindleg) and tarsal claw remained stationary upon the surface on which the animal stood and the animal's body merely swayed relative to the wall of the chamber. In the second pattern, which we term movement or "flexion" reactions, the hindleg and tarsal claw were lifted from the surface and moved to a new position. Each of these types of responses and the patterns of myographic activities and changes in joint angle that accompanied them are discussed below.

Muscle activities during compensatory reactions

The major criterion for assigning responses of animals to this group was that the position of the tarsal claw of the hindleg did not change and the leg as a whole was not moved by the animal during a displacement test. In most of these trials, the position of the animal's body relative to the surface upon which it stood could be seen to sway in phase with the movement of the chamber.

In recordings of the myographic activities of the tibial muscles of the hindlegs during compensatory reactions, most animals showed rhythmic bursting in the tibial flexor, the trochanteral levator and tarsal levator muscles (Fig. 2A, B). This is the same group of muscles that we have previously found are also active in the mesothoracic legs during displacement tests (Zill and Frazier 1990a). Discrete bursts and definable accelerations of firing frequency of muscles of the metathoracic legs were also coupled to displacements of the chamber and occurred at relatively fixed phases in the cycles of movement. Also, bursting in metathoracic flexor and levator muscles was not altered when the compound eyes and ocelli were covered or when tympanal nerves were cut. Activities of the antagonist muscles at the joints were also similar to those found in the mesothoracic leg: when the animal stood on the side of the cage, activities were generally not seen in myograms of the tibial extensor, trochanteral depressor or tarsal depressor muscles (Fig. 2B, C), although discharges in these muscles were recorded when

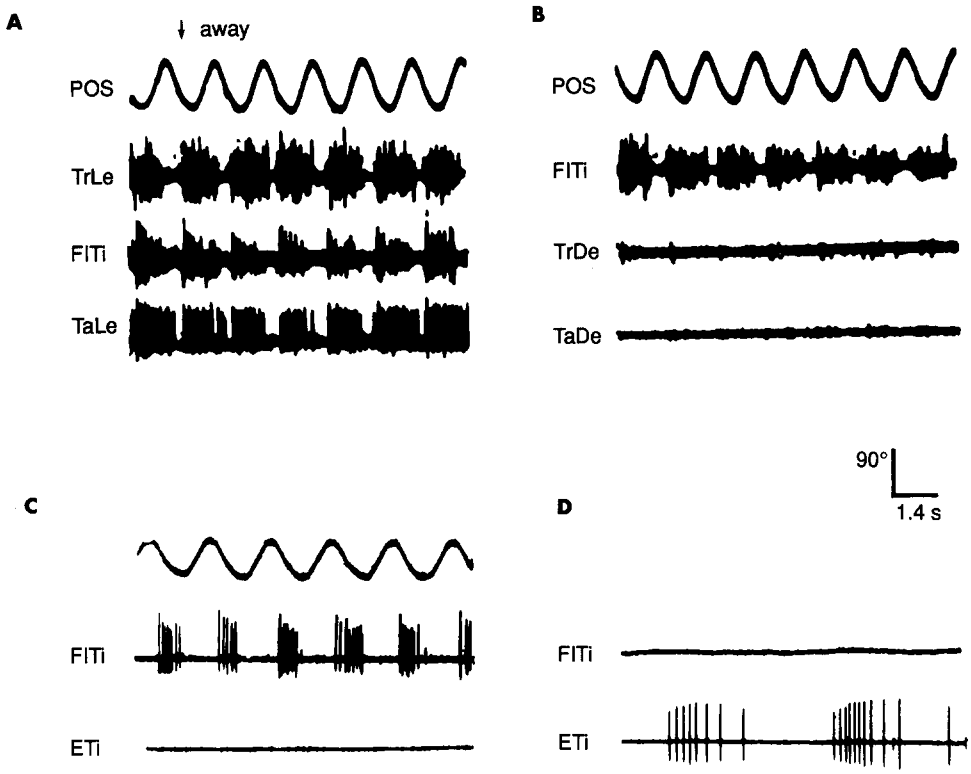

Fig. 2A–D. Myographic activities during compensatory reactions when animals stood on the side of the cage. **A** In this posture, locusts showed rhythmic bursts of activities in the tibial flexor (*FlTi*), trochanteral levator (*TrLe*) and tarsal levator (*TaLe*) muscles. Bursts of activity were regularly initiated in these muscles during the phase when the wall of the cage was being pulled away from the animal. **B** and **C** The antagonist trochanteral depressor (*TrDe*), tarsal depressor (*TaDe*) and tibial extensor (*ETi*) were generally not active in this position although activities in these muscles could be recorded by stroking the animal (**D**) or when locusts walked

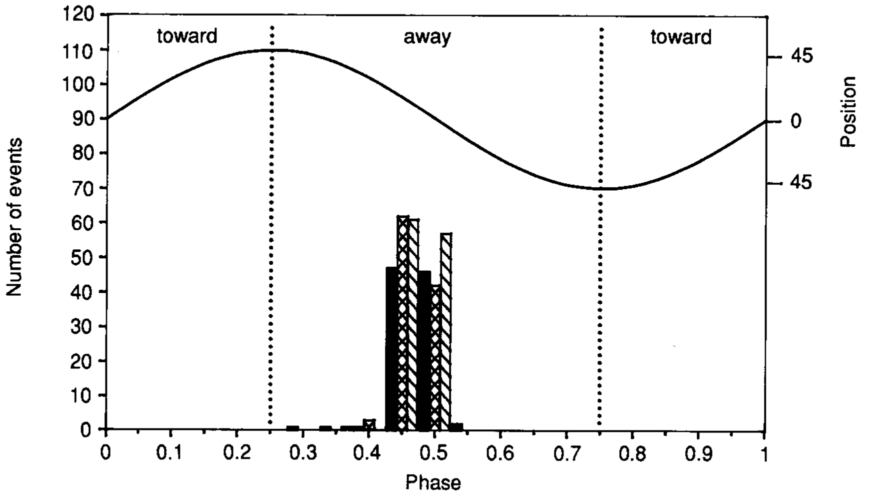

Fig. 3. Phase of cycle of movement in which bursting was initiated. Data from myograms of compensatory reactions were normalized according to whether firing was initiated during the phase of movement in which the substrate was being forced toward or away from the animal when locusts were standing on the wall of the cage. A plot of the time of occurrence of the initiation of bursting (in bins of phase = 0.05 indicated by minor tics) versus the phase of movement shows that bursts in the trochanteral levator (*TrLe*), tibial flexor (*FlTi*) and tarsal levator (*TrLe*) were tightly coupled and bursting began during the phase in which the substrate was being pulled away from the animal. ■ TrLe, ▩ FlTi, ▧ TaLe

animals walked or were stroked with a brush (Fig. 2D). Those muscles also did show bursting activities in other postures, such as when the animal stood upon the floor of the cage.

We normalized data taken from animals standing on either side of the cage according to whether the surface upon which the animal stood was being pulled away or pushed toward it. Figure 3 shows a histogram which plots the mean phase in which discrete bursts were initiated in the trochanteral levator, tibial flexor and tarsal levator muscles. All animals showed initiation of bursting during that period of the cycle when the substrate was being pulled away from the animal (phase 0.25–0.75). The mean phase value of all animals was remarkably close to the mid-range of that period (mean phase tibial flexor = 0.495 ± 0.02 S.D., trochanteral levator = 0.496 ± .3, tarsal levator = 0.497 ± 0.03). Thus, locusts showed a uniform response pattern in compensatory reactions when standing on the wall of the chamber.

Changes in the femoro-tibial joint angle during compensatory reactions

Utilizing our recording system, we were able to detect changes in the angle of the femoro-tibial joint during a number of, but not all, displacement tests (see Discussion). Changes in joint angle were largest and most reliably detected when the leg was held in positions away from the mid-range of angle. When these changes were

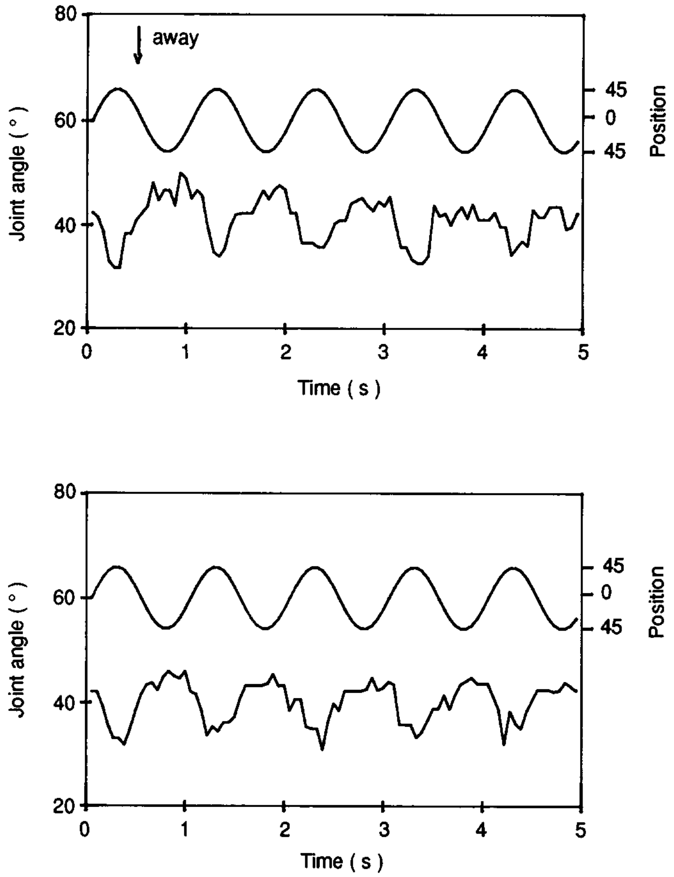

Fig. 4. Changes in the angle of the femoro-tibial joint during compensatory reactions. The femoro-tibial joint angle of the hindleg was measured by videotaping animals with light emitting diodes attached to the leg. Each point in this plot represents the mean value of two successive frames. The joint angle repeatedly increases during the phase in which the wall of the cage is moving away from the animal and decreases during the opposite phase in each cycle of movement

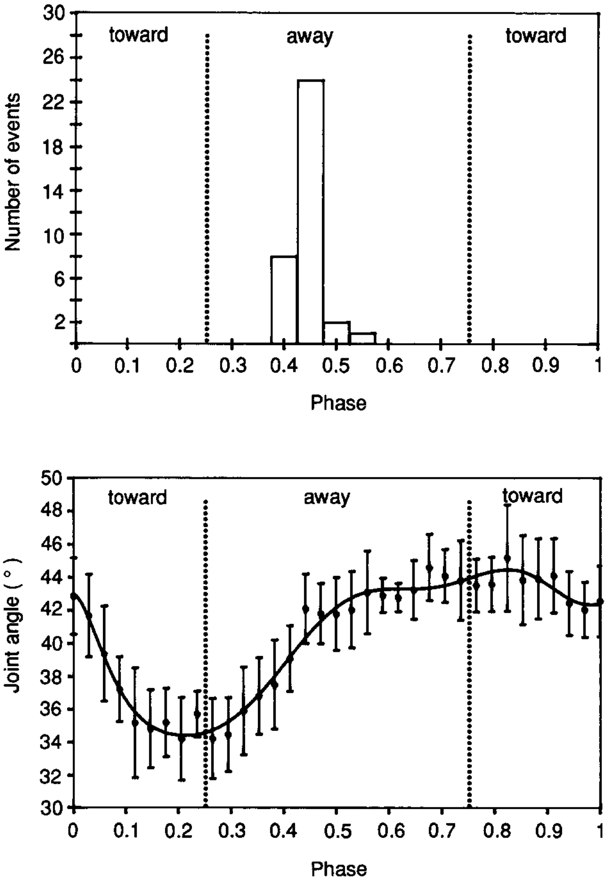

Fig. 5. Effects of muscle bursting upon the changes in joint angle. The *lower graph* is a histogram of the mean value of angle of the femoro-tibial joint in each frame over 35 cycles of repetitive swaying while the *upper graph* plots the onset of bursting of the tibial flexor muscle during the same sequence. The onset of bursting in the flexor muscle is followed by a significant dampening in the rate of change of joint angle

detected, they occurred repeatedly throughout the cycles of movement and were phasically linked to the movements of the chamber (Fig. 4). In all these tests, the angle of the femoro-tibial joint invariably increased during the phase in which the wall was being moved away from the animal and decreased during the opposite phase. In most tests there was also a significant dampening of the rate of change near the mid-range of phase, close to the point of initiation of firing of tibial muscles.

In order to confirm the potential link between muscle activities and changes in joint angle within the cycles, we recorded the myographic activities of the tibial flexor muscle while videotaping animals with LEDs attached to the metathoracic leg. The histograms in Fig. 5 show the results of one such experiment. The upper graph plots the onset of bursting in the tibial flexor muscle, while the lower graph is a histogram of the frame by frame measurement of the angle of the femoro-tibial joint over 35 cycles. Comparison of the two figures shows that the following events occur during the phase in which the wall of the chamber is being moved away from the animal: early in that phase the femoro-tibial joint angle increases; approximately midway through that phase flexor bursting is initiated followed by a decline in the rate of change of joint angle. Thus, it appears that a potential function of muscle activity during load compensatory reactions is to counter the changes in leg joint angles that result from postural perturbations.

Effects of increasing weight upon compensatory reactions

To further test this hypothesis, we attached small weights to locusts. Figure 6 shows myographic recordings of the tibial flexor and extensor muscles during tests in which the animal was not loaded (Fig. 6A) and in trials in which the locusts had attached weight (Fig. 6B, C). Prior to adding the weight, the locust showed only rhythmic bursting in the tibial flexor muscle during the phase in which the wall of the cage was being moved away from the animal, without discernable extensor firing at any time. The addition of weight produced intensification of the flexor discharge with recruitment of apparent intermediate and fast flexor motoneurons and also induced firing in the slow extensor motoneuron which could be

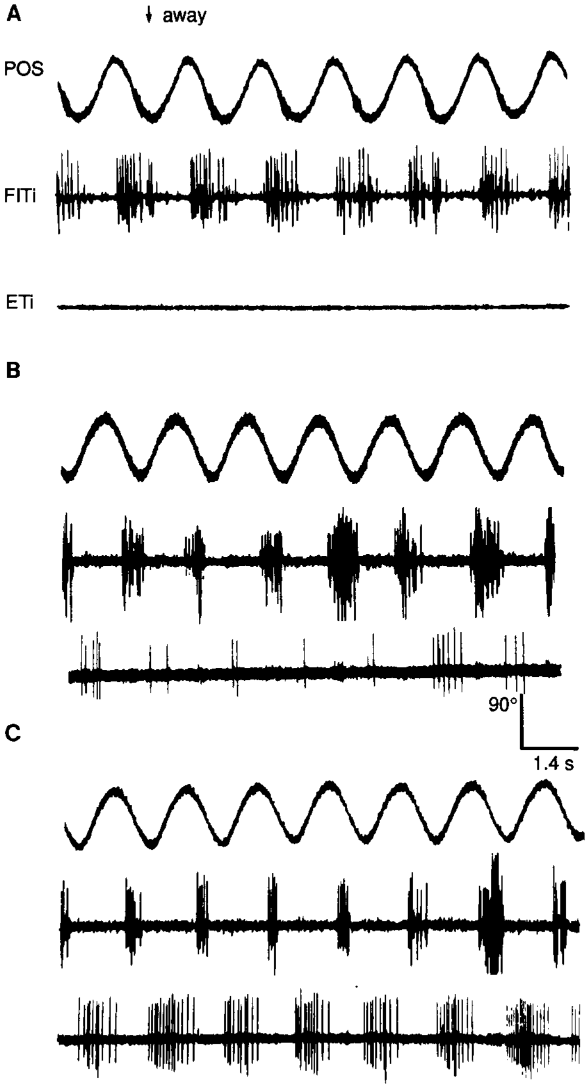

Fig. 6A–C. Effects of weight upon myographic activities. **A** In this experiment, myographic activities were recorded in displacement tests prior to and following addition of a small weight to the animal. In the absence of additional weight, repetitive bursting occurred in the tibial flexor muscle but not the antagonist extensor **B–C**. After addition of weight, reciprocal bursting occurred in the two muscles

quite intense at some joint angles. This bursting was generally reciprocal with that in the tibial flexor. Figure 7 is a histogram of the time of onset of slow tibial extensor firing during 5 sequential series of tests from this same experiment. Bursting in the extensor is always initiated during the phase in which the wall of the cage is moving toward the animal (mean phase = 0.931 ± 0.053 S.D.), nearly opposite that for the tibial flexor. We have also repeated this experiment with recordings from the tarsal depressor muscle. Thus, increasing forces acting upon the animal by increasing inertia induces motor activities in muscles that are normally silent.

We also videotaped animals during tests in which a weight was applied in order to measure the angle of the femoro-tibial joint. Muscle activities were not recorded during these tests. Figure 8A is a histogram which plots the angle of the femoro-tibial joint and the position of the chamber over 5 cycles of movement in a single test series.

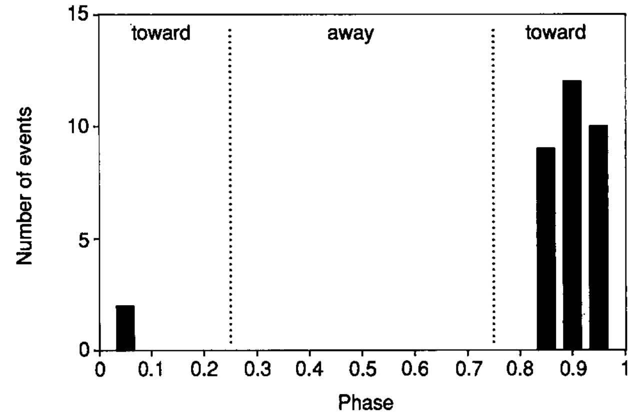

Fig. 7. Phase of onset of extensor bursting. This graph plots the phase of onset of extensor tibiae bursting for the same experiment as in Fig. 6. All bursts are initiated during the phase when the wall of the cage is being moved toward the animal, the opposite of that for flexor bursting

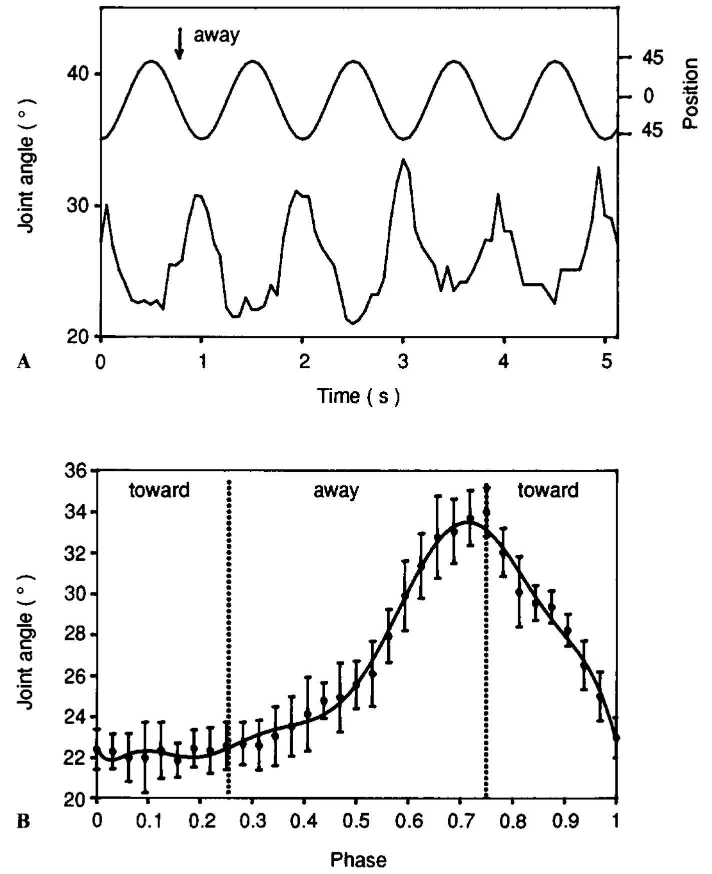

Fig. 8A, B. Effects of weight upon changes in the femoro-tibial joint angle. **A** This graph plots the mean value of two successive measurements of joint angle in a test in which the animal was weighted. Weighting produces both an increase in the magnitude and the rate of change of joint angle. **B** This is a plot of the mean value of joint angles as measured from successive frames over 14 cycles of movement in an animal carrying a weight. There is little dampening in the rate of change of joint angle in the mid-range of phase as is seen in un-weighted animals

Both the magnitude and the velocity of change in joint angle were increased in weighted animals during displacement tests. Figure 8B is a histogram which plots the angle of the femoro-tibial joint as measured frame by frame from a series of 24 cycles of movement during tests of an animal that was weighted. This graph shows greater changes in the magnitude and rate of change of joint angles than occurred in non-weighted animals during either of the two directions of movement.

Myographic activities during "flexion" or stepping reactions

Our criterion for assigning responses to this group was that the tibia and tarsus of the hindleg were observed to move at the onset or during repetitive displacements. In all of these responses, only the metathoracic leg was seen to move and not the ipsilateral mesothoracic or prothoracic legs, so the position of the animal as a whole within the chamber was unchanged. In the great majority of these cases (87%), the tibia was moved to a position of complete flexion of the femoro-tibial joint, as it would be in preparation for a jump. In a considerably smaller number of responses (13%) the tibia was moved to other positions.

In a number of experiments, we examined the possibility that corrective reactions might represent artifactual responses to visual or auditory stimuli associated with our apparatus or that these reactions were simple startle responses. These responses persisted after covering the animals' compound eyes and ocelli (Fig. 10B), and after cutting the nerves to the tympanal organs, so the former possibility seemed unlikely. Also, more convincingly, flexion responses did not occur in any particular sequence within a series of trials, but were regularly interspersed between trials in which compensatory reactions were elicited. This finding argues against the possibility that flexion reactions represent startle responses, which might be anticipated to occur more frequently at the onset of a series of tests and subsequently habituate.

Myograms of leg muscles that were recorded during flexion reactions showed intense initial activity in the tibial flexor muscle and rhythmic bursting in the trochanteral and tarsal levator muscles (Fig. 9). In most myographic recordings, it was not possible to resolve the activities of individual flexor motoneurons as the tibial flexor muscle has been reported to be innervated by up to nine excitatory motoneurons (Phillips 1980). However, in two recordings, myographic wires were fortuitously placed so as to record the discernible unit activities. In these recordings, most cycles of movement produced no modulation of activity of these units (Fig. 10), although in 3 responses slight phase linking was observed. These results suggest that in flexion reactions, the tibia is moved into a position of full flexion of the femoro-tibial joint and often held in that position by tonic, unmodulated flexor activity. It should be noted, however, that regular bursting or modulation of tonic firing still occurred in the trochanteral and tarsal levator muscles during these reactions.

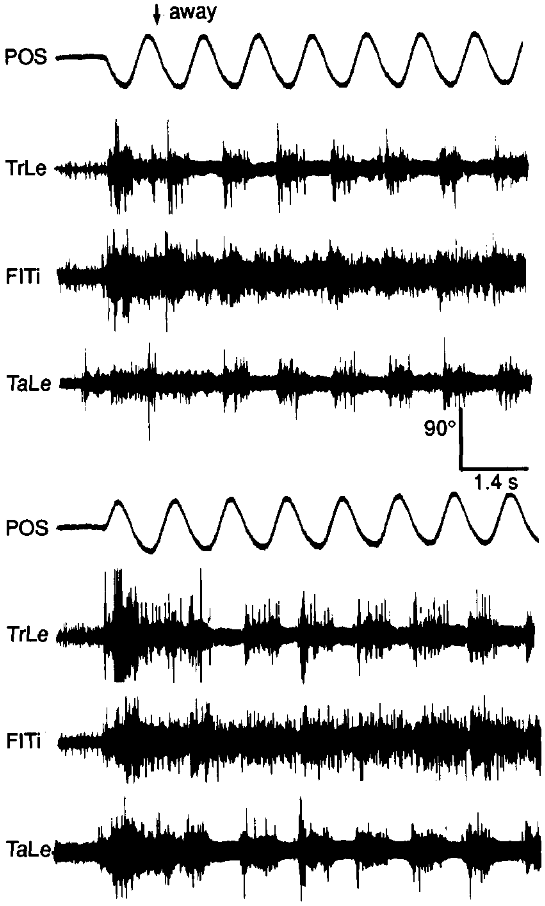

Fig. 9. Activities of muscles of the hind leg during "flexion" reactions. In "flexion" reactions the tibia was moved to a position of full flexion of the femoro-tibial joint. These movements were produced by intense firing of the tibial flexor muscle (*FlTi*) and are accompanied by rhythmic bursting in the trochanteral (*TrLe*) and tarsal (*TaLe*) levator muscles

Videotapes of animals exhibiting "flexion" reactions showed that these responses occurred at variable latencies most often close to the onset of movement of the cage (Fig. 11). In contrast with compensatory reactions, "flexion" responses occurred at approximately equal frequencies during the phases when the wall was being moved toward or away from the animal. The duration of the flexion movement was also variable, but depended upon the initial joint angle, being longer in duration at angles further away from full flexion of the femoro-tibial joint. However, the rate of change in joint angle was fairly constant during these responses (mean rate = 18.6°/100 ms ± 1.4 S.D.).

Occurrence of compensatory and corrective reactions in different ranges of joint angle

Utilizing both still photography and videotaping of animals, we measured the frequency of occurrence of compensatory and "flexion" reactions at different initial angles of the femoro-tibial joint. Figure 12 is a histogram which plots the percentage of responses of each type in

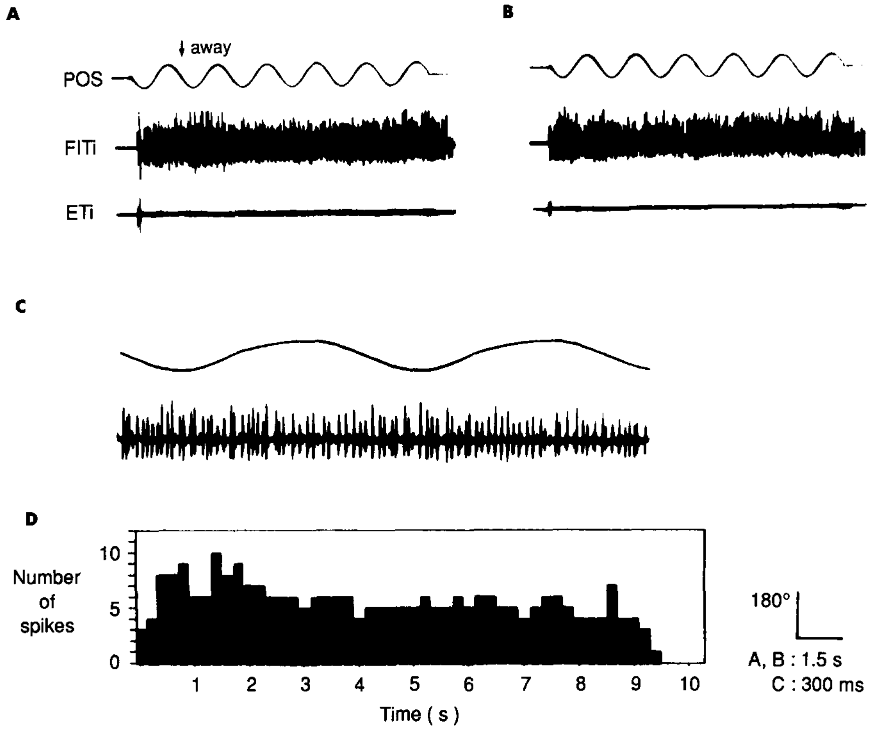

Fig. 10A–D. Myographic activities accompanying flexion reactions in the tibial flexor muscles. **A** and **B** Myographic activities recorded during flexion reactions showed intense firing of flexor motoneurons that was sustained throughout the repetitive cycles (**A**) and that persisted after elimination of visual inputs (**B**). **C** Expanded view of flexor muscle activity during two cycles of movement in **A**. **D** Histogram of flexor activity in **B**. Neither **C** nor **D** shows any rhythmic activity in the flexor myogram that was coupled to the cycles of movement of the chamber

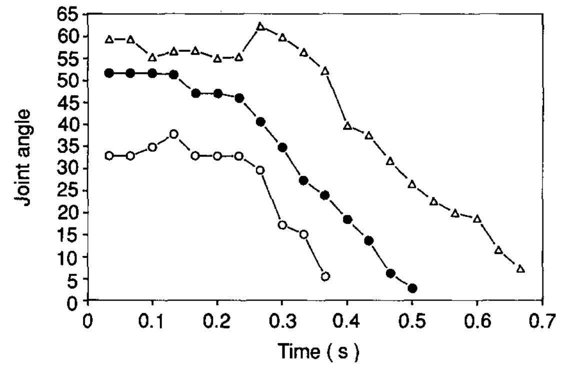

Fig. 11. Changes in angle of the femoro-tibial joint during "flexion" reactions. This graph plots the angle of the femoro-tibial joint during three "flexion" reactions as measured from successive frames of the videotape. Movements to full flexion are variable in latency and duration but tend to occur at similar rates of change of joint angle

127 tests (each consisting of at least 5 cycles of movement) in different ranges of joint angle. Compensatory reactions most often occurred in the mid-ranges of joint angle (60–120°) and were less frequent in the extreme ranges of joint angle. In contrast, "flexion" reactions more commonly occurred in those extreme ranges. These findings are of interest as the mechanical advantages of the tibial muscles has been demonstrated to be highest in the mid-range of joint angle (Heitler 1974) and considerably lower in the extreme ranges. Thus, compensatory reactions occur most frequently in ranges of joint angle in which forces generated by contractions of the tibial flexor muscle may be most effective. In contrast, "flexion" reactions appear to occur preferentially in positions of lower stability of the femoro-tibial joint.

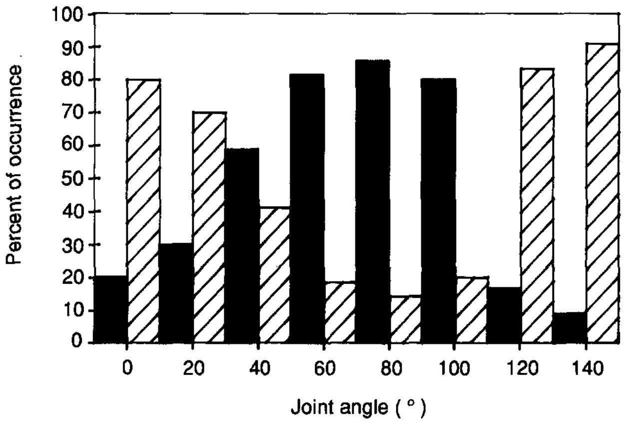

Fig. 12. Frequency of occurrence of compensatory and "flexion" reactions in different ranges of angles of the femoro-tibial joint. This is a histogram of percentages of responses that occurred as flexion reactions (in 127 tests) at various angles of the femoro-tibial joint, as monitored both by still photography at the onset of displacement tests and by videotaping animals. Compensatory reactions tend to occur more in the mid-range of joint angle where mechanical advantages of the tibial muscles is high while "flexion" reactions occur most often in the extreme ranges of joint angle, where mechanical advantages are low. However, both types of responses can occur at any given joint angle. ■ compensatory reaction, ▨ flexion reaction

These hypotheses are also supported by experiments in which we amputated one of the metathoracic legs ($n = 3$) and observed the use of the opposite leg during displacement tests. In those animals the frequency of occurrence of "flexion" reactions rose to almost 80% of all responses.

Discussion

The present studies have shown that locusts use the hindleg in distinct strategies in tests of dynamic postural control. These findings will be discussed as follows: first, the general nature and advantage of each of these strategies will be reviewed; second, these results will be compared to the reflexes elicited by known sense organs of the hindleg; last, these responses will be compared to reactions of other animals to changes in load.

Compensatory reactions

The behavioral response of many animals during repetitive displacements was to hold the hindleg in place. During such compensatory reactions, rhythmic modulation or bursting occurred in motoneurons of the tibial flexor, trochanteral levator and tarsal levator muscles when animals stood on the side of the chamber. These rhythmic bursts were not accompanied by reciprocal firing in the antagonist tibial extensor, trochanter depressor or tarsal depressor muscles in the absence of external loading. Rhythmic bursting in muscles in the metathoracic leg also occurred consistently in the phase of movement in which the substrate was being pulled away from the animal. These basic findings are quite similar to the results of previous studies of the use of mesothoracic legs in this paradigm (Zill and Frazier 1990a).

The present study has also demonstrated that regular repetitive changes in the angle of the femoro-tibial joint can occur during compensatory reactions. These changes occur as increases during the phase when the wall of the cage was being moved away from the animal and decreases during the opposite phase. While we have been able to demonstrate that these changes in joint angle can occur in many tests we were not able to invariably detect them, particularly in trials occurring in the mid-range of angles. One simple explanation for this finding may lie in the resolution of our videotape system. Because of slight blurring of the image of the light emitting diodes we estimate that the minimum change in distance between them that we could reliably detect was 1 mm. At an initial joint angle of 90 degrees, this represents a change in joint angle of approximately 3 degrees. Any changes in joint angle that were less than that value would not have been accurately detected. Thus, one possibility is that small changes in angle do occur in the mid-range of angle of the femoro-tibial joint but were not recorded by our apparatus. Future experiments are planned using a high speed video system and strobe to address that possibility.

In those cases in which we did record changes in joint angles we also found that the initiation of bursting in intrinsic leg muscles is followed by a deceleration in the rate of change of joint angle. Similar findings, that changes in joint angles or leg positions occur in response to perturbations during walking, have previously been reported in crustacea (Barnes et al. 1972; Chasserat and Clarac 1983). This finding is of interest because it may imply that one parameter that may be regulated in compensatory reactions in these systems is the rate of changes in joint angles, although related variables such as muscle stiffness and length may also be regulated in these responses. We have also demonstrated that the trochanteral depressor, tibial extensor and tarsal depressor muscles, which are antagonists of the levator and flexors, are generally not activated during compensatory reactions in the absence of external load. This finding is similar to the results of studies of compensatory reactions in the mesothoracic legs (Zill and Frazier 1990a), although in neither study have we systematically examined the effects of swaying at a number of different speeds. We should note that in our experimental set-up, animals are swayed symmetrically and forces acting upon an animal's legs should be equivalent in both directions. We have now also shown that adding a weight to animals produces increases in the magnitude and rate of change of joint angle and generates bursting activities in the depressors and extensor that are generally reciprocal with the antagonist muscles. One explanation for these findings may be that resting tensions in the extensor and depressor muscles are sufficient to counter forces acting upon the leg in the absence of excitatory motoneuron activity when animals are unloaded, but insufficient in the presence of additional weight. Evidence to support that possibility has been generated by previous studies which have examined the tension characteristics of the metathoracic tibial extensor muscle. First, it was demonstrated some time ago that this muscle has considerable "catch" properties and that considerable residual tensions can result from transient changes in firing of the slow excitatory axon (Wilson and Larimer 1968). Similar residual tensions have also been demonstrated in muscles of a number of invertebrates (Yox et al. 1982). Second, the tibial extensor muscle has also been demonstrated to have a variable and occasionally substantial amount of "basic tonus", that is, inherent tension in the absence of excitatory motoneuron activity (Hoyle 1978; Piek et al. 1979; Forman and Zill 1984). This tonus has been shown to be modulated by activities in the excitatory and inhibitory neurons which innervate the muscle (Hoyle 1983), by activities in the octopaminergic dorsal unpaired median cell (DUMETi) which innervates the tibial extensor (O'Shea and Evans 1979) and by circulating levels of octopamine and the neuropeptide proctolin (Hoyle 1983). Thus, a number of mechanisms have been demonstrated to be able to create and regulate the intrinsic tensions in the tibial extensor muscle, which may be responsible for its lack of excitatory activity in tests of postural control in the present experiments. We should, however, note that similar data are not presently available for the agonist trochanteral and tarsal depressor muscles, but the potential participation of neuromodulatory elements in those muscles remains a subject for investigation.

Flexion reactions

The second major category of response of animals to repetitive displacements was to move the tibia, most often to a position of complete flexion of the femoro-tibial joint. The control experiments we performed, eliminating visual and auditory inputs, argue against the possibility that flexion movement responses were artifacts caused by secondary sensory stimuli associated with our apparatus. These responses also do not appear to be startle reactions, as they did not occur in any particular sequence and showed no evidence of habituation in a test series.

Movements to full flexion occurred most often when the angle of the femoro-tibial joint was initially in the extreme ranges of joint flexion or extension, but not already in a fully flexed position. In these ranges of angle, the mechanical advantages of the tibial flexor and extensor muscles are quite small. Thus, locusts and grasshoppers appear to move the tibia out of these ranges rather than attempt to maintain its position by generating the requisite large muscle contractions.

Why is the tibia moved to a position of full flexion? There are several findings in the literature that suggest that this position uniquely offers mechanical advantages to the animal. As noted by Heitler (1974), in the position of full flexion, the femoro-tibial joint possesses a locking mechanism, by virtue of the shape of the flexor tendon and a thickened mass of cuticle in the distal femur, that Heitler termed the "lump". Immediately proximal to its insertion onto the femur, the flexor tendon bifurcates into two strands which insert on either side of the tibia, leaving a pocket of connective tissue between them. When the tibia is in full flexion, the arms of the tendon slide down onto either side of the lump in the distal femur and the lump itself fits into the connective tissue pocket (Heitler and Burrows 1977a, b). In this position, only a small amount of tonic tension in the flexor muscle is able to hold the tendon down over the lump and the joint is immobilized. Considerable forces must then be applied to unlock the joint and move the tibia. Thus, this anatomical feature suggests that when locusts or grasshoppers move the tibia to full flexion during tests of load compensation they are locking and immobilizing the femoro-tibial joint.

Reflex effects of the femoral chordotonal organ and responses to tests of load compensation

The present study has shown that responses to substrate displacements persist after elimination of visual and auditory inputs. As locusts and grasshoppers have no specialized sense organs for the detection of gravity that would correspond to the crustacean statocyst or the vertebrate vestibular apparatus, it would appear that these animals utilize mechanoreceptive and proprioceptive inputs to detect mechanical forces acting upon them during repetitive displacements. A major receptor which monitors the femoro-tibial joint angle is the metathoracic femoral chordotonal organ (Usherwood et al. 1968), which has been the subject of a number of recent investigations (Burrows et al. 1988; Matheson 1990; Matheson and Field 1990). Mechanical stimulation of the chordotonal organ has been demonstrated to produce two distinct modes of reflex activation in both restrained and freely standing animals (Field and Burrows 1982; Zill 1985; Zill and Jepson-Innes 1988, 1990). In the first mode, termed the resistance mode, stimulation of the main ligament of the chordotonal organ (mimicking sudden displacements of the femoro-tibial joint) elicits resistance reflexes in tibial muscles that are directional and oppose apparent joint movement. In the second mode, termed the flexion mode, stimuli indicating movements in any direction produce activation of excitatory axons in the flexor muscle. Similar differential motor responses have also been found for the femoral chordotonal organ in stick insects (Debrodt and Bässler 1990; Bässler and Büschges 1990). The resistance mode is in many ways similar to the compensatory responses seen in the present study. Both resistance reflexes and compensatory responses are directional and act to resist changes in joint angles. However, one important difference between these two types of responses was that repetitive stimulation of the chordotonal organ in restrained preparations produced reciprocal, alternating activation of the flexor and extensor muscles. In contrast, reciprocal discharges were not obtained to repetitive displacements in the present study in the absence of external loading. This finding suggests that while resistance reflexes of the chordotonal organ could contribute to elements of load compensatory discharges, other sense organs or nervous system elements can modify some aspects of these reflexes.

The flexion reflex mode of the femoral chordotonal organ also has some characteristics similar to the initial components of flexion movement reactions to substrate displacement (Zill 1985b). Both the flexor reflex mode and "flexion" reactions are non-directional, in that displacements in any direction produce excitation of the tibial flexor. In the flexor reflex mode, movements of the chordotonal ligament in any direction produced excitation of the flexor muscle. However, flexor activation continues during "flexion" movement reactions after the tibia is moved and during this subsequent period the tibia may be held immobilized. It is not clear whether the femoral chordotonal organ could then contribute to these sustained flexor discharges. However, a number of other sensory receptors have been shown to produce excitation and these sense organs could potentially contribute to the prolonged flexor discharges (Pflüger 1980; Burrows and Pflüger 1986). In addition, some elements have been identified in the central nervous system which could contribute to these reactions: a number of local circuit spiking interneurons respond bidirectionally to chordotonal inputs (Burrows 1988; Zill and Frazier 1990b). Similar responses have also been demonstrated to chordotonal inputs in motoneurons and interneurons in stick insects (Debrodt and Bässler 1990; Bässler and Büschges 1990; Büschges 1989, 1990). Thus, in sum, the known reflex activities and connectivity of the femoral chordotonal organ suggest it could strongly contribute to elements of responses in compensatory and "flexion" reactions but additional sensory receptors, such as those on the tarsus, and other central nervous system pathways must also be activated during these global reactions.

Comparison with load compensatory reactions in other animals: are parallels valid?

The present study has shown that locusts show discrete patterns of motor activities in hindleg muscles when they are placed upon a swaying platform and when they are loaded with additional weight. While it is of interest to contrast these responses with postural reactions of vertebrates in tests using similar paradigms, there are several notable differences in the variables that bipedal and multi-legged animals can control in these responses. First, vertebrates can utilize inputs from a variety of receptors in these reactions including vestibular as well as visual and proprioceptive inputs. Second, obvious differences in postural reactions of bipedal and multi-legged animals are to be expected since swaying has disparate biomechanical consequences for these animals. Humans must maintain the center of gravity over the base of postural support either by swaying and moving the center of mass or by stepping and moving the base of support. This is clearly different from the problems encountered by an insect clinging to the side of a moving substrate. We should note that many of these differences also apply to studies comparing compensatory reactions of humans and quadrupedal animals such as cats. Lastly, the relative magnitude of forces acting upon large vertebrates are undoubtedly quite different from those acting upon a small hexapod.

Given all these differences, the elements of dynamic postural responses of locusts which are similar to those of vertebrates are actually quite interesting. First, both types of animals maintain postural stability (i.e. do not fall down) and show stereotyped activities in discrete groups of leg muscles that occur at fixed phases relative to the cycles of movement (Nashner et al. 1979). Second, swaying can cause changes in the angles of intrinsic leg joints which are resisted by muscle contractions. Third, increased weight augments both the magnitude and velocity of changes in joint angles and the intensity of motoneuron discharges (Chandler et al. 1990). Also, displacement tests that are initiated at unstable joint angles cause "flexion" reactions in which the leg is moved to positions of greater postural stability. The latter finding is a broad contrast with the widely demonstrated "correction" reactions of vertebrates, in that in vertebrates these movements shift the base of postural support, while in locusts this brings the leg to a position of inherent stability due to specializations developed primarily for jumping. Lastly, the present study supports the conclusion that inputs from leg proprioceptors may play a key role in postural reactions of invertebrates as well as vertebrates. Further studies on the locust, measuring the exact forces acting upon and developed by muscles in these reactions, are needed to determine which variables are actually controlled in postural responses. However, our findings tend to support the conclusion that both groups of animals utilize proprioceptive inputs to similar adaptive advantage.

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References

Barnes WJ, Spirito CP, Evoy WH (1972) Nervous control of walking in the crab, *Cardisoma guanhumi*. II. Role of resistance reflexes in walking. Z Vergl Physiol 76:16–31

Bässler U, Büschges A (1990) Interneurones participating in the "active reaction" in stick insects. Biol Cybern 62:529–538

Burrows M (1988) Responses of spiking local interneurons in the locust to proprioceptive signals from the femoral chordotonal organ. J Comp Physiol A 164:207–217

Burrows M, Pflüger HJ (1986) Processing by local interneurons of mechanosensory signals involved in a leg reflex of the locust. J Neurosci 6:2764–2777

Burrows M, Laurent GJ, Field LH (1988) Proprioceptive inputs to nonspiking local interneurons contribute to local reflexes of a locust hindleg. J Neurosci 8:3085–3093

Büschges A (1989) Processing of sensory input from the femoral chordotonal organ by spiking interneurons in stick insects. J Exp Biol 144:81–111

Büschges A (1990) Nonspiking pathways in a joint-control loop of the stick insect *Carausius morosus*. J Exp Biol 151:133–160

Chandler JM, Duncan PW, Studenski SA (1990) Balance performance on the postural stress test: Comparison of young adults, healthy elderly, and fallers. Phys Ther 70:410–415

Chasserat C, Clarac F (1983) Quantitative analysis of walking in a decapod crustacean, the rock lobster *Jasus lalandii* II. Spatial and temporal regulation of stepping in driven walking. J Exp Biol 107:219–243

Cohen H, Keshner EA (1988) Current concepts of the vestibular system reviewed: 2. Visual/vestibular interaction and spatial orientation. Am J Occupat Ther 43:331–337

Debrodt B, Bässler U (1990) Responses of flexor motor neurones to stimulation of the femoral chordotonal organ of the phasmid, *Extatosoma tiaratum*. Zool Jb Physiol 94:101–119

Dietz V, Quintern J, Berger W (1984) Corrective reactions to stumbling in man: functional significance of spinal and transcortical reflexes. Neurosci Letters 44:131–135

Dietz V, Quintern J, Berger W (1986) Stumbling reactions in man: release of a ballistic movement pattern. Brain Res 362:355–357

Dietz V, Quintern J, Sillem J (1987) Stumbling reactions in man: significance of proprioceptive and pre-programmed mechanisms. J Physiol 386:149–163

Do MC, Breniere Y, Brenguier P (1982) A biomechanical study of balance recovery during the fall forward. J Biomechanics 15:933–939

Duncan PW, Studenski S, Chandler J, Bloomfeld R, LaPointe LK (1990) Electromyographic analysis of postural adjustments in two methods of balance testing. Phys Ther 70:88–96

Field LH, Burrows M (1982) Reflex effects of the femoral chordotonal organ upon leg motor neurones of the locust. J Exp Biol 101:265–285

Forman RR, Zill SN (1984) Leg position learning by an insect. II. Motor strategies underlying learned leg extension. J Neurobiol 15:221–237

Forssberg H (1979) Stumbling corrective reaction: a phase dependent compensatory reaction during locomotion. J Neurophysiol 42:936–953

Heitler WJ (1974) The locust jump: specializations of the metathoracic femoral-tibial joint. J Comp Physiol 89:93–104

Heitler WJ, Burrows M (1977a) The locust jump. I. The motor programme. J Exp Biol 66:203–219

Heitler WJ, Burrows M (1977b) The locust jump. II. Neural circuits of the motor programme. J Exp Biol 66:221–241

Hoyle G (1978) Intrinsic rhythm and basic tonus in insect skeletal muscle. J Exp Biol 73:173–203

Hoyle G (1983) Muscles and their neural control. John Wiley and Sons, New York

Keshner EA, Cohen H (1988) Current concepts of the vestibular system reviewed: 1. The role of the vestibulospinal system in postural control. Am J Occupat Ther 43:320–330

Keshner EA, Woollacott MH, Debu B (1988) Neck, trunk and limb responses during postural perturbations in humans. Exp Brain Res 71:455–466

Macpherson JM (1988) Strategies that simplify the control of quadrupedal stance. I. Forces on the ground. J Neurophysiol 60:204–217

Markl H (1971) Proprioceptive gravity perception in Hymenoptera. In: Gordon SA, Cohen MJ (eds) Gravity and the organism. University of Chicago Press, Chicago, pp 185–194

Matheson T (1990) Responses and locations of neurones in the locust metathoracic femoral chordotonal organ. J Comp Physiol A 166:915–927

Matheson T, Field LH (1990) Innervation of the metathoracic femoral chordotonal organ of *Locusta migratoria*. Cell Tissue Res 259:551–560

Nashner LM (1976) Adapting reflexes controlling the human posture. Exp Brain Res 26:59–72

Nashner LM (1977) Fixed patterns of rapid postural responses among leg muscles during stance. Exp Brain Res 30:13–24

Nashner LM, McCollum G (1985) The organization of human postural movements: a formal basis and experimental synthesis. Behav Brain Sci 8:135–172

Nashner LM, Woollacott M, Tuma G (1979) Organization of rapid responses to postural and locomotor-like perturbations of standing man. Exp Brain Res 36:464–476

Neil DM (1975) The mechanism of statocyst operation in the mysid shrimp, *Praunus flexuosus*. J Exp Biol 62:505–518

O'Shea M, Evans PD (1979) Potentiation of neuromuscular transmission by an octopaminergic neurone in the locust. J Exp Biol 79:169–190

Pflüger HJ (1980) The function of hair sensilla on the locust's leg: the role of tibial hairs. J Exp Biol 87:163–175

Phillips CE (1980) An arthropod muscle innervated by nine excitatory motor neurons. J Exp Biol 88:249–258

Piek T, Van Marle J, Mantel P, Lind A (1979) Peripheral control of basic tonus and myogenic rhythm in the extensor tibiae of *Schistocerca gregaria*. Comp Biochem Physiol 64A:565–569

Usherwood PNR, Runion HI, Campbell JI (1968) Structure and physiology of a chordotonal organ in the locust leg. J Exp Biol 48:305–323

Wendler G (1971) Gravity orientation in insects: the role of different mechanoreceptors. In: Gordon SA, Cohen MJ (eds) Gravity and the organism. University of Chicago Press, Chicago, pp 195–201

Wilson DM, Larimer JL (1968) The catch property of ordinary muscle. Proc Natl Acad Sci USA 61:909–916

Wolfson LI, Whipple R, Amerman P, Kleinberg A (1986) Stressing the postural response: A quantitative method for testing balance. J Am Ger Soc 34:845–850

Yox DP, DiCaprio RA, Fourtner CP (1982) Resting tension and posture in arthropods. J Exp Biol 96:421–423

Zill SN (1985a) Plasticity and proprioception in insects. I. Responses and cellular properties of the locust metathoracic femoral chordotonal organ. J Exp Biol 116:435–461

Zill SN (1985b) Plasticity and proprioception in insects. II. Modes of reflex action of the locust metathoracic femoral chordotonal organ. J Exp Biol 116:463–480

Zill SN, Frazier SF (1990a) Responses of locusts in a paradigm which tests postural load compensatory reactions. Brain Res 535:1–8

Zill SN, Frazier SF (1990b) Range fractionation in responses of spiking interneurons that detect joint movement in locusts. Neurosci Abstr 16, Part 1, p 117

Zill SN, Jepson-Innes KA (1988) Evolutionary adaptation of a reflex system: sensory hysteresis counters muscle "catch" tension. J Comp Physiol A 164:43–48

Zill SN, Jepson-Innes KA (1990) Functions of a proprioceptive sense organ in freely moving insects: characteristics of reflexes elicited by stimulation of the locust metathoracic femoral chordotonal organ. Brain Res 523:211–218