

MECHANOSENSORY ENCODING OF FORCES IN WALKING UPHILL AND DOWNHILL: FORCE FEEDBACK CAN STABILIZE LEG MOVEMENTS IN STICK INSECTS

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ABSTRACT: Force feedback could be valuable in adapting walking to diverse terrains but the effects of changes in substrate inclination on discharges of sensory receptors that encode forces have rarely been examined. In insects, force feedback is provided by campaniform sensilla, mechanoreceptors that monitor forces as cuticular strains. We neurographically recorded responses of stick insect tibial campaniform sensilla to 'naturalistic' forces (joint torques) that occur at the hind leg femur-tibia (FT) joint in uphill, downhill and level walking. The FT joint torques, obtained in a previous study that used inverse dynamics to analyze data from freely moving stick insects, are quite variable during level walking (including changes in sign) but are larger in magnitude and more consistent when traversing sloped surfaces. Similar to vertebrates, insects used predominantly extension torque in propulsion on uphill slopes and flexion torques to brake forward motion when going downhill. Sensory discharges to joint torques reflected the torque direction but, unexpectedly, often occurred as multiple bursts that encoded the rate of change of positive forces (dF/dt) even when force levels were high. All discharges also showed hysteresis (history dependence) as firing substantially decreased or ceased during transient force decrements. These findings have been tested in simulation in a mathematical model of the sensilla (Szczecinski et al. 2021) which accurately reproduced the biological data. Our results suggest the hypothesis that sensory feedback from the femoro-tibial joint indicating force dynamics (dF/dt) can be used to counter the instability in traversing sloped surfaces in animals and, potentially, in walking machines.

250 words

NEW AND NOTEWORTHY

Discharges of sensory receptors (campaniform sensilla) in the hindlegs of stick insects can differentially signal forces that occur in walking uphill versus walking downhill. Unexpectedly, sensory firing most closely reflects the rate of change of force (dF/dt) even when the force levels are high. These signals have been replicated in a mathematical model of the receptors and could be used to stabilize leg movements both in the animal and in a walking robot.

INTRODUCTION

Walking on sloped surfaces, the natural habitat for most terrestrial animals, requires adaptation of muscle activities to changes in the effects of gravity. The adaptive changes in motor activities in walking on slopes were first precisely and elegantly characterized in cats (Smith et al. 1998; Carlson-Kuhta et al. 1998; Gregor et al. 2006; comparable studies in humans: Gottschall and Nichols 2011; DeWolf et al. 2019, 2020). In walking on uphill slopes, activities of extensor muscles at a number of leg joints are enhanced to push the animals upward and forward. In traversing downhill slopes, the effects 'reverse' and flexor muscle activities are increased and operate in an eccentric mode to brake forward motion during flexor muscle lengthening.

Previous studies have also suggested that receptors monitoring forces in the legs contribute to these adaptations, potentially in diverse ways. Recordings of muscle activities at the ankle in humans walking on a treadmill that could be tilted, showed the extensor muscle activities late in the stance phase of the step cycle were modulated by afferents that detected forces, potentially by a mechanism of positive feedback (Grey et al. 2007). Modeling and experimental studies in cats walking on pegs in sloped

walkways also suggested that Golgi tendon organs (which detect muscle forces and loads) were the primary source of sensory feedback affecting motor outputs at the ankle joint (Hatz et al. 2012). However, studies that have examined multiple joints and intermuscular effects of force receptors have suggested that inhibitory feedback at some leg joints may also play a role in regulating whole limb mechanics (Lyle and Nichols 2018). Thus, force feedback can have excitatory and inhibitory components that 'coexist in various combinations based on motor task' (Nichols 2018).

Studies in stick insects walking on sloped surfaces have shown remarkably similar motor adaptations to those found in vertebrates (Cruse, 1976a,b; Dallmann et al. 2019; review Büschges and Gruhn, 2020). Stick insects can ascend or descend non-horizontal substrates without major changes in the angular movements of most leg joints (Dallmann et al. 2019). In contrast, measurements from force plates and recordings of activities in hindleg muscles in freely moving stick insects have shown extensive, joint-specific adaptations in walking on sloped surfaces: at the knee (femoro-tibial joint) animals generate extensor forces that push the center of mass forward in uphill walking but exert braking (flexor) forces when traversing downhill slopes (Dallmann et al. 2019). Comparable changes are seen in muscles at the junction of the leg and body (protractors-retractors) but activities at the intermediate coxo-trochanteral joint, which maintains body height above the substrate, were similar on all substrate slopes. The basic similarities in motor strategies in diverse animals most likely reflect solutions to the common biomechanical problems of adapting legged locomotion to changes in the effects of the gravitational vector.

Few studies have directly examined activities of sense organs that could detect these changes in forces in sloped walking in freely moving animals. Recordings of tendon organ afferents in cats walking freely on horizontal surfaces indicate that they signal 'a dynamic, non-linear function of whole muscle force over a range encompassing movements involving very low to very high force levels' (Appenteng and Prochazka, 1984; Roll et al. 1989). Modeling studies suggest that force levels can be calculated in the central nervous system by summing the ensemble discharge of tendon organs (Mileusenic and Loeb 2009), but this has not been confirmed by data from walking animals. In contrast, earlier studies suggest that the dynamic sensitivities of Golgi tendon organs should predominate during walking in some muscles (Jami 1992) and calculation of force levels would require the temporal integration of sensory signals over time in the central nervous system.

In insects, forces generated by and acting upon the legs are monitored by campaniform sensilla (Dickerson et al. 2021). Activities of tibial campaniform sensilla recorded in freely moving cockroaches show considerable dynamic sensitivities, although forces were not directly measured in those studies (Zill and Moran 1981; Noah et al. 2004). Responses of tibial sensilla in the middle legs of stick insects were studied using forces that replicated joint torques of freely moving animals walking on level surfaces and suggested that receptors strongly encode force dynamics (Ridgel et al. 2001; Zill et al. 2021). However, it was not clear how the receptors would discharge to higher levels of forces necessary in traversing sloped surfaces.

In the present experiments, we have extended the previous studies to examine sensory encoding of joint torques in walking up and downhill. We examined the

encoding of mean torque values and also individual steps, which reflected changes in forces that can occur due to variations in gait in freely moving animals. These studies suggest that sensory discharges of tibial receptors do not simply encode the force level but more closely reflect variations and force dynamics. These signals could be used to compensate for load variations and aid in generating the smooth and continuous joint movements seen in both level and sloped walking.

We have also previously developed a mathematical model that captured the response properties of campaniform sensilla (Szczecinski et al. 2021). In the present study, we tested the model using the waveforms of joint torques in walking on level and sloped substrates and were able to reproduce the discharges of the sensilla without additional tuning of parameter values. These findings support use of the model campaniform sensillum in future studies of sensorimotor control of walking machines.

METHODS

Experiments were performed on the hind legs of adult, female Indian stick insects (*Carausius morosus*, N =14) obtained from a commercial supplier (Backwater Reptiles, USA).

Sensory recordings

The techniques used to record activities of stick insect tibial campaniform sensilla (Figs. 1A-C) are described in previous publications (Zill et al. 2013, 2021). In the present study, animals were first restrained on a platform and nerves to the left hind leg severed in the thorax, effectively eliminating all afferent and efferent connections to the central nervous system (CNS). The femur of the hind leg was placed against a small resin block so that the plane of movement of the femoro-tibial joint was in a horizontal

plane (Fig. 1D,E). Movements at the femoro-tibial joint were eliminated using a pin and a small amount of cyanoacrylate adhesive at the joint. The tarsus was amputated in the distal tibia. For sensory recordings, two 50 micron silver wires (Goodfellow Ltd, AG005825) were inserted through holes made with an insect pin and positioned along the main leg nerve. The insulating layer surrounding the wires was removed over the portion inserted into the leg. Neural activities were monitored during positioning of the wires to achieve proximity to the nerve (nervus cruris) in the femur. The wires were fixed to the cuticle with cyanoacrylate. Sensory activities were recorded using a custom-built amplifier (Michael Duebber, University of Cologne) and stored digitally using a Spike2 interface (Cambridge Electronic Design (CED), Cambridge, UK).

Mechanical stimuli

Forces were generated through the Spike 2 interface using conventional ramp and hold functions and waveform of joint torques. The torque waveforms were obtained from a previous study that recorded ground reaction forces of single legs via force plates and three-dimensional kinematics of leg movements via a marker-based motion capture system in freely moving stick insects that walked on level and sloped substrate (Fig. 1D; Dallmann et al. 2019; Zill et al. 2021). Torques about the femoro-tibial leg joint were determined by inverse dynamics using a three-dimensional rigid link model. It is important to note that we mimicked joint torques by applying forces on the distal end of the tibia in these tests. However, these sensory responses were consistent with discharges obtained by direct application of forces to the apodeme (tendon) of the tibial flexor muscle (Zill et al. 2011).

In the present study, the torque values (in the stance phase) were normalized in duration to 800 ms and imported into Spike 2 sequencer files, then played and re-recorded with low pass filtering to eliminate voltage steps. The final output voltages were applied to the tibia using a motor (position controlled, Michael Dübbert, University of Cologne) that displaced a probe containing strain gauges (Fig. 1E), producing bending forces on the leg. The torque waveforms of single steps were applied repetitively (mean 0.5 repetitions per second $\pm$ 0.004 SD). In this paper, a single repetition of the torque waveform is referred to as a 'step' or test. Sensory discharge frequencies were stable and showed no long-term adaptation throughout a series of tests.

Subgroup identification

Units could be identified by the size of their extracellularly recorded amplitude and time of occurrence within the stimulus. In the present experiments, bending forces were applied to the distal tibia during placement of the recording wires with the goal of maximizing the recorded amplitude of the smallest 6B sensilla. We utilized ablation of the subgroups to confirm unit identification (Fig. 2A): after ablation of the caps of 6B sensilla, subsequent retesting to torque waveforms showed that discharges of 6A sensilla were retained due to their proximal location in the tibia (see text below for details). Subsequent ablation of 6A receptors eliminated those components of responses.

Morphology

Scanning electron micrographs were taken of the isolated tibiae of the hind legs of newly molted animals using a Hitachi S450 microscope (Fig. 1 C; techniques described

in Zill et al. 2011). Light micrographs of caps of campaniform sensilla were obtained from whole mounts of cuticle of the proximal tibia (Harris et al. 2020).

Data storage and analysis

Data on firing rates and forces were analyzed using Spike 2 scripts. The rate of change of force was calculated in Excel. Statistical tests were performed and plotted in Sigma plot (Systat software) and SPSS (IBM).

RESULTS

1- Structure and response characteristics of hindleg tibial sensilla in stick insects

The tibial campaniform sensilla of the stick insect hindleg occur as two spatially separated subgroups (Groups 6A and 6B) on dorsal surface of the proximal end of the tibia (Fig. 1A-C), similar to the homologous receptors in the middle leg (Zill et al. 2013). Group 6A is located approximately 0.5 mm and Group 6B 1.5 mm distal to the femoro-tibial joint (as measured from the joint condyles). The cuticular caps of the Group 6B sensilla are diverse in structure (Fig. 1C): there are consistently 3 sensilla (occasionally 2 sensilla) with caps that appear round (or slightly rectangular), located close to the proximal ends of the surrounding cuticular collars (Fig. 1Ci) and a variable number of other receptors with oval shaped caps in the surrounding (150 microns) cuticle (Fig 1Cii). Group 6A consists of two receptors with ovate caps whose cap long axes are approximately parallel to the tibial long axis although the posterior sensillum appears tilted ~ 20-40 degrees (Fig 1Ciii). The spatial separation of the subgroups greatly facilitated their identification in extracellular recordings as the caps of the 6B receptors could be ablated (en masse) without affecting firing of 6A receptors. Similar structure

and numbers of the tibial sensilla have also been recently reported for the Madagascar stick insect, *Sipyloidea sipyilus* (Strauß 2020).

The subgroups of sensilla were differentially activated in tests using bending forces applied to the tibia using ramp and hold functions (Fig. 2) (Zill et al. 2011; Gebehart et al. 2021). Extracellular recordings consistently (N = 12) showed discharges of sensilla of large amplitude during the ramp increases in force in the direction of joint extension that adapted completely (or fired at a low level, <10 Hz) during the hold phase (Fig. 2A left). Receptors with smaller spike amplitude fired tonically throughout the hold phases. Ablation of cuticular caps confirmed that these discharges (both larger and smaller spike size) were derived from 6B sensilla (Fig. 2A right). Activities of all 6B receptors completely ceased when forces began to decrease and firing of 6A sensilla occurred when forces declined substantially or approached zero. Tests in which forces were applied to different levels of the hold phase showed that the tonic discharges (sampled late in the hold phase) reflected the force magnitude over a broad range (Fig. 2B) but the frequency of sensory discharge depended upon the rate of adaptation, which was prolonged at high force levels (data not shown). Force application at different rates of rise and decline (Fig. 2C) indicated that the large sensilla can effectively encode the rate of force increase (Fig. 2D) and decrease (Fig. 2E) but the discharge frequencies depended upon the force amplitude. These complex features of responses of campaniform sensilla belie their characterization as simple force detectors but are reproduced in the mathematical model of the receptors (see below).

2- Forces and joint movements in the hindleg during level and sloped walking -

The responses of tibial campaniform sensilla were characterized to forces applied to the tibia that were derived (as a subset) from the data of Dallman et al., 2019. That study measured leg movements and ground reaction forces and utilized inverse dynamics to calculate joint torques in freely moving stick insects walking on horizontal and sloped surfaces. In the present study, we utilized both the mean femoro-tibial joint torque as well as selected individual steps. As in our previous study, steps were selected that had average torque values that substantially deviated from the mean (methods of Zill et al. 2021). We also analyzed the kinematic and kinetic parameters of the selected steps and compared them with all steps in the original data set (Dallmann et al. 2019). Figure 3 shows plots of the forces (femoro-tibial (FT) joint torques) and joint movements for the step waveforms used as mechanical stimuli in the present study. The direction and time course of torques at the FT joint in the selected steps generally depended upon the substrate slope (Fig 3A, B): in walking on horizontal surfaces, the torques varied considerably in individual steps (and could change in sign/direction) and the calculated mean torque was quite small in magnitude. In contrast, the mean FT torques were much greater in walking on slopes to oppose the action of the gravitational vector: strong extensor torques were generated in walking uphill that would provide propulsion, while large flexor torques were produced to brake forward motion in traversing downhill slopes.

The FT joint torques of individual steps could show substantial variations from the mean (Figure 3C) during the 'stance' phase in all substrate inclinations. Torque values were most variable in walking on a level substrate with periods of net extensor or flexor forces (Fig. 3C left). Hindleg torques were more consistent in sign in walking on slopes

(Fig. 3C middle, right) but many steps had substantial inflections and fluctuations that could reflect adjustments of motor output to forces produced by the placement and lift of the other legs. In contrast, measurements of the FT joint angles in these steps showed much less variability in individual steps, although the ranges of movement varied somewhat (Fig 3Di). Examination of the torque and joint angle values in individual steps showed that, for some steps, small inflections of the values of joint angles could be accompanied by large variations in joint torque (Fig 3Dii). Figure 3Diii is a plot of the net torque values (average value in stance) versus the range of joint angles in the steps taken on horizontal and sloped surfaces. This plot shows that in sloped walking flexor torques tended to occur in ranges of joint extension and extension torques in ranges of joint flexion (Dallmann et al. 2019). The joint torques could therefore provide support and stability by acting to oppose the effects of body weight on the legs (see Discussion).

3- Sensory discharges to joint torques differ in uphill vs downhill walking and reflect, but do not simply encode, the force magnitude

Recordings of activities of tibial sensilla to imposed forces that mimicked walking on slopes showed that the responses of subgroups of sensilla were consistent with the direction of applied force (Fig. 4, all forces shown as positive values). Flexor torques, which were predominant in walking on level surfaces (Fig. 4A,B) and larger in downhill walking (Fig. 4C), activated 6B sensilla during force increases and could elicit firing of 6A receptors when forces decreased. Extensor torques (consistently occurring in uphill walking) produced the opposite pattern of activation: firing of 6A sensilla to force increases and discharges of 6B receptors to force decrements (Fig. 4D).

The sensory discharges were not, however, simply related to the force magnitude, even at high levels of force application. In many steps (Fig. 4 A-D), firing of large sensilla occurred as a series of bursts and regularly ceased or decreased to very low levels after the maximum force was attained. Discharges of small sensilla could be more sustained and generally reflected the force magnitude (but saturated at high force levels). In addition, small amplitude sensilla also showed strong hysteresis: firing showed graded increase during force increments but sensory discharge was completely inhibited when small force decreases occurred during sustained force application, even though the overall force magnitude was high.

4 - Discharges of tibial campaniform sensilla are correlated with dF/dt in level and sloped walking and show hysteresis, even at large force amplitudes

Figure 5 shows histogram plots of the sensory discharge rates (mean $\pm$ SD) of tibial sensilla to all imposed joint torques in tests of walking on level surfaces, as well as the force magnitude (upper trace) and the rate of change of force (line in second trace). Forces at the FT joint generally occurred as flexor torques that were smaller in magnitude than in slope walking. Both the large and small amplitude 6B sensilla discharged in multiple bursts within a step that did not reflect the force level but closely followed the positive values in the rate of change of force ($+dF/dt$) (see Figs. 5 iii-v). All afferent activities also showed hysteresis in that firing ceased (6B large receptors) or sharply declined (6B small receptors) when the rate of change decreased (particularly apparent in Figs. 5ii, iii). This could produce a rapid series of discharges within single 'steps', even when the overall level of force was increasing (Fig. 5 ii). Activities of 6A sensilla, which discharge to force decreases in ramp and hold tests, only occurred when

force levels declined rapidly or to low levels in tests using torque wave form. These activities were generally at low frequencies, as was observed in tibial sensilla of middle legs (Harris et al. 2022). Tests of extensor torques in level walking (Fig. 5 v) produced activation of 6A sensilla but firing was also limited to the rising phases of force fluctuations and closely followed the changes in the force rate.

Torque values could reach much higher levels in walking on slopes (Fig. 6) and, in tests of downhill walking, could attain twice the values that occurred on level surfaces (compare Fig. 5iii and Fig. 6A iv,v). In these tests, the subgroups of tibial sensilla were activated according to the force direction, as 6B sensilla firing predominated on downhill slopes and 6A signaled positive torques in uphill walking. In downhill walking (Fig 6A), discharges of 6B receptors were more prolonged, particularly in plots including small 6B receptors (Fig. 6A ii, iii, v). Firing frequencies of small 6B sensilla were modulated but not separated in many discrete short bursts as seen in level walking, in part because the fluctuations in forces were less prominent. However, despite the large force magnitude, the sensory discharges were not sustained during these tests but were largely restricted to the rising phases of force. Also, activities in large and small amplitude sensilla showed high sensitivity to variations in the rate of change of force (dF/dt) (Figs. 6A ii, iii) even when these variations produced small changes in force magnitude (rising phase of force in Figs. 6A iv, v). In addition, afferent firing showed strong hysteresis and often decreased during transient periods in which the rate of change declined, even at high force levels. Discharges of 6A receptors again occurred during large force decreases and firing was often limited to the period of decline of force at the end of the 'stance' phase.

Discharges of 6A receptors during uphill walking and 6B receptors in downhill walking (Fig. 6) had many of the same characteristics as responses to level surfaces and were largely restricted to the rising phase of the extensor torque (Fig. 6B ii, iv). However, the discharge frequencies were extensively modulated and followed the rate of change of force (Fig. 6Biv) even when the apparent magnitude of changes in force level were small. In these tests, 6B discharges were restricted to the periods of force decrease, but again showed a high sensitivity to the rate of force decrement and discharges could be initiated by rapid decreases even when the force levels were relatively large.

5 - Tibial campaniform sensilla show the same sensitivity to the rate of change of force (dF/dt) in walking on all substrate inclinations

Dynamic sensitivities of campaniform to joint torques on different substrate slope are compared in the plots in Figure 7. Figures 7 A-C show plots of the sensillum firing frequencies at different positive rates of change of force (derived and pooled from all steps in the data sets in Figs. 5 and 6) for 6B sensilla in level (Fig. 7A) and downhill (Fig. 7B) and 6A receptors in uphill walking (Fig. 7C). Although there is some spread in the values of firing frequencies as they depended both on the force level and rate of change, there were general correlations (regression coefficients R^2 : A = 0.78, B = 0.69, C = 0.71) that reflect a strong dependence of sensory firing frequency on the rate of force increase. This dependence is also apparent when the data are averaged over ranges of dF/dt (Figs. 7D, E).

6 - A mathematical model of campaniform sensilla reproduces sensory activities in level and sloped walking

We have developed a mathematical model of campaniform sensilla that can successfully reproduce, in software, many characteristics of the sensory transform (input/output) of campaniform sensilla (Szczecinski et al. 2021). In this model, the biological parameters (response gain, adaptation) are not explicitly determined variables but instead emerge by tuning. For campaniform sensilla, we tuned the model parameters to reproduce the response time-courses from tests of responses to the mean joint torques.

The model was applied using the force (torque values) from the mean steps in walking on level and sloped surfaces, as well as steps that substantially deviate from the mean (methods of Zill et al. 2021). Figures 8 and 9 show simulations of the sensory discharges on a level surface (Fig. 8) and on substrates that slope (Fig. 9). The model discharges show many of the same characteristics as the biological sensilla in that 1) 6B receptors can indicate the torque direction as they are active during force increases in level and downhill walking while 6A sensilla fire when walking uphill; 2) sensilla of opposite subgroups fire during periods of force decrease; 3) sensory activity reflects the rate of force development (dF/dt) on all substrates. However, the model was less accurate in simulating sensory discharges to force decreases (Fig. 9 A-E). For example, the mean discharge of 6B sensilla to force decreases in uphill walking was 9.07 ($\pm$ 2.31 SD) action potentials per second while the simulation predicted firing at a higher level (76.2 $\pm$ 7.04 spikes per second) (data in Fig 9B).

The model responses share many features with the experimental recordings, despite only being tuned to replicate the response to one stimulus. The other 14 fits are completely “feedforward”, i.e., parameter values are not tweaked to better fit those data.

There was a mean absolute error of 10% or less in almost all cases despite no retuning of parameter values, which suggests that the model is capturing fundamental response properties of the tibial sensilla. We observed that tuning the model to each individual trial would improve the fit to that trial (data not shown). This is not surprising, because each cohort of animal subjects would have different properties, e.g., tibia length, cuticle hardness (time from last molt). However, we believe that a model that can reproduce responses of many different animals to widely varying stimuli is most useful for understanding how the nervous system processes force feedback.

DISCUSSION

Walking on slopes represents a discrete adaptation of behavior in stick insects, as leg movements remain relatively constant while different muscle synergies and levels of activation are generated in countering forces when going uphill vs downhill (Dallmann, et al. 2019). The present experiments have, for the first time, directly tested responses of force receptors in restrained preparations to joint torques that occur at the femoro-tibial joints in walking of freely moving animals on sloped surfaces. The major findings of this study are that 1) the subgroups of tibial sensilla are selectively activated in uphill or downhill walking and 2) the receptors do not simply encode the force magnitude but consistently provide signals about the rate of change (dF/dt) of joint torques. In the following we will discuss the structure and response properties of the receptors and how the signals about the direction and rate of change of force (dF/dt) (termed 'yank', Lin et al. 2019; Blum et al. 2020) could aid in adapting walking to achieve stable and relatively constant movements when variations in forces occur due to gait or substrate inclination.

These findings will also be compared to the results of comparable studies in other animals, including vertebrates.

1- Morphology and response properties of hindleg tibial campaniform sensilla -

a. Morphology - The tibial campaniform sensilla of the hindlegs are arranged as two spatially separated subgroups (as in the middle legs, Zill et al. 2011; Harris et al. 2020). The Group 6A receptors have oval shaped cuticular caps, typical of stick insect campaniform sensilla (Hofmann and Bässler, 1982, 1986) while Group 6B is more complex and has 3 large sensilla with round cuticular caps in asymmetrical collars and a variable number of other smaller sensilla with oval caps close to (within ~1.5 mm) the larger receptors. This more dispersed and diverse arrangement is similar to the findings in recent studies of Madagascar stick insects (Strauß 2020) and fruit flies (Dinges et al. 2021, 2022) and further studies are planned to quantify these variations. Variability in the number of campaniform sensilla in groups was documented in the original study of Pringle in the American cockroach (Pringle 1938) who reported different numbers of receptors in the right and left legs of the same animal. In the present study, potential differences in afferent responses associated with these smaller receptors was not specifically examined as they often produced very small potentials in extracellular recordings and their caps were difficult to visualize in a dissecting microscope. Identification of units as 6B receptors was based upon ablation of the entire region of the cuticle and 6A receptors were identified by subsequent more proximal ablations. It is important to note that this variability in morphology may be of limited functional consequence as campaniform sensilla apparently act post-synaptically in the CNS as populations of receptors (Zill et al. 2012; Gebehart et al. 2021).

b. Response properties - Recordings of the tibial sensilla to application of forces as ramp and hold functions showed the same pattern of activities as seen in the middle legs (Zill et al. 2011; Gebehart and Büschges 2021): 6B receptors fired during the rising and hold phases while 6A receptors discharged in a separate burst when forces declined (stick insect Haberkorn et al. 2021; similar results cockroaches Ridgel et al. 2000; Noah et al. 2001). Recordings of Group 6B similarly showed two classes of sizes of recorded potentials that corresponded to larger more phasic units and smaller tonic units (Zill et al 2013). Small sensilla provided much of the sustained discharge during the hold phase and could reflect the force level, although there was individual variability in sensitivity, potentially due to the extent of cuticular sclerotization (Fig. 2B). The discharge of the larger units during the ramp rise reflected the rate of change of force (to faster ramps) although the slope of increase also depended upon the stimulus amplitude (Fig. 2E). While the overall discharges of the 6B sensilla reflected force increases over the broad range of force magnitudes that occur in the hind legs, the interactive effects of stimulus amplitude, hysteresis and rate sensitivity complicates their classification as simple tonic or phasic receptors and afferent encoding was only captured by mathematical modeling (see below).

2- Different subgroups of receptors are activated by joint torques in uphill vs downhill walking

All tests showed that different subgroups of tibial campaniform sensilla are activated by joint torques mimicking those occurring in uphill or downhill walking. The discharges of 6A and 6B sensilla to the mean positive torques in walking on different slopes are compared as a summary in Figure 10. 6A sensilla were activated to the extensor

torques that generated propulsive forces when going uphill (Fig 10A) and 6B receptors discharged to flexion torques that produced braking forces in walking downhill (Fig 10B). The pattern of alternating discharge of the subgroups of tibial sensilla is elicited in both cockroaches and stick insect to forces imposed as ramp and hold functions (Ridgel et al. 2001; Fig. 3, Gebehart and Büschges 2021; Harris et al 2022) and is similar to the activities recorded in walking in freely moving or semi-restrained animals (Noah et al. 2000; Zill et al. 2013). Thus, the tibial sensilla are effectively acting as proprioceptors in monitoring the torques generated by the animal to adapt to the inclination of the walking surface as well as forces that result from load transfer in gait.

The maximal firing frequencies were obtained in most tests on both uphill and downhill slopes during the initial rise in forces (mimicking the start of stance) which elicited firing of both the larger and smaller Group 6B sensilla in level and downhill walking and multiple units of 6A sensilla in going uphill. After the initial increase, the firing frequencies either decreased to a much lower level (Fig 10A) or discharges ceased entirely. These findings reflect the finding that the joint torques occurring at the femoro-tibial joint in walking are largely dynamic in walking of freely moving animals: there is no prolonged hold phase (Harris et al. 2022; Zyhowski et al. 2023). Many torque measurements in walking of vertebrates also never attain a constant level at distal leg joints (Winter et al. 1978; Yang et al 1990; Gregor et al. 2006).

3- Sensory Discharges in individual steps that deviate from the mean: sensilla encode positive values of dF/dt but show strong hysteresis

We have found that, in naturally occurring steps which deviated from the mean, sensilla fired in repeated short bursts rather than prolonged discharges, even though

the torque magnitude remained large. These bursts were reflective of the 1) afferent sensitivities to relatively small variations in the rate of force increases and 2) hysteresis following relatively small decrements in the force rate which could produce large decelerations or complete interruption of the sensory discharges. These characteristics were also seen in discharges of the small campaniform sensilla, which are tonically active to low levels of force. Small sensilla showed more prolonged activity than the large 6B receptors (Fig 10B) but the receptor discharges were inhibited or strongly modulated by small decreases in the force rate. As in our previous study, discharges of sensilla of the opposite subgroup (for example, 6A firing in level and downhill walking) generally did not occur to small force decreases but were at higher threshold (Harris et al. 2022) although this varied with cuticular properties (stiffness and viscoelasticity, data not shown). All campaniform sensilla at the FT are, therefore, generating a fine grained reflection of the rate of force (torque) increase even in sloped walking when large forces are generated to overcome the effects of gravity.

Our previous study of activities of tibial CS in the middle legs in walking on a level substrate also found a high sensitivity to dF/dt (Zill et al. 2021). All sensilla directionally encoded the dynamics of force increases and showed hysteresis to transient force decreases. Smaller receptors exhibited more tonic firing. However, the forces applied to the middle legs were of modest amplitude and it was of interest to see if the same sensitivities were found when higher forces are generated necessary for sloped walking. The findings of the present study support the idea that dynamic sensitivity in force feedback can modulate ongoing muscle activities to stabilize distal joints even when large forces are generated at proximal joints.

The highly phasic responses that we observed from large tibial receptors parallel the responses observed in other force-detection sensory systems. Sensory discharges that strongly reflect the rate of change of force but do not directly encode the force level were obtained in early studies of bipolar neurons associated with the insertion of the opener muscle in the distal leg segments of crabs (Tryba and Hartman 1997), similar to the large spike tibial campaniform sensilla of stick insects. A number of studies have also documented sensitivities to the rate of change (dF/dt) in vertebrates, in which forces are monitored and controlled as muscle tensions (Jami, 1992; Wessberg and Vallbo 1995; Nichols, 2018; Lin et al. 2019; Sahrom et al. 2020; Gordon et al. 2020) as well as invertebrate species in which forces are detected by cuticular mechanoreceptors or sense organs associated with muscle insertions (Tryba and Hartman 1997; Majeed et al. 2013; Tuthill and Wilson 2016). Although it is not currently known precisely what role dF/dt plays in the control of posture and/or locomotion, its ubiquity across a variety of legged animals suggests that it can play an important role in dynamically adapting motor output to the environment (Ting et al. 2009; Lin et al. 2019; see also Taylor and Krapp 2007).

4- Hysteresis in force detection by campaniform sensilla

The presence of strong hysteresis in sensory discharges in sloped walking was unexpected. In tests applying forces as ramp and hold waveforms, the effect of the large magnitude of the forces predominated and both the discharges to ramp and hold and mean torque waveforms showed reduced adaptation during the period of force application. However, the steps with torque variations demonstrated that relatively small but rapid decreases could strongly reduce or completely inhibit sensory discharges,

even in the small tonic receptors (see Fig. 6A iv, v; Fig 6B iv, v). As in our previous study, discharges to force decreases in sensilla of the opposite subgroup (ex. 6A in level and downhill walking) generally did not occur to small force decreases but were elicited by more rapid decreases or by complete unloading at the end of 'stance' (Harris et al. 2022).

The source of hysteresis in sensory discharges is unknown although it has been demonstrated in other groups of campaniform sensilla (trochanteral sensilla, Hofmann and Bässler 1986; Zill et al. 1999, 2012), in receptors that encode kinematic variables (Segundo and Diaz Martinez 1985; Matheson 1990; Büschges 1994; Mamiya et al. 2018) and is present in sensory processing in the insect nervous system (Siegler 1981; Gebehart et al. 2021). Hysteresis is also seen in discharges of receptors (Ross et al. 2016) and in sensory encoding in the CNS in vertebrates (Mountcastle et al. 1963). Golgi tendon organs can also show hysteresis (Houk and Simon 1967) and discharges are completely inhibited by rapid force decreases although very slow decreases produce modulation of firing frequencies (Appenteng and Prochazka 1984; Scott 2005). Hysteresis may be adaptive and act to reduce residual tensions in leg muscles (Zill and Jepson-Innes 1988; Tuthill and Wilson 2016) and compensate for variations in muscle properties (Nichols and Houk 1976).

5 - Functions: force sensing at the FT joint can aid in countering instabilities

The biomechanical challenge for nervous system control of walking on slopes is to raise or lower the body center-of-mass while maintaining balance. Our working hypothesis is that the campaniform sensilla at the femoro-tibial joint in the hindlegs can aid in meeting this challenge by providing signals that monitor fluctuations in forces and

that the CNS can use this information to adjust motor outputs to maintain stability while generating smooth and uninterrupted joint movements. The tests of uphill and downhill walking showed that even though the forces are producing discharges in different subgroups of sensilla, the sensilla are strongly reflecting the same variable ($+dF/dt$) on all substrates (Fig. 7E). The tibial sensilla do not directly convey the magnitude of the Newtonian force or reflect the body weight (as, for example a bathroom weighing scale). Previous studies have provided evidence that the much more numerous CS in groups on the trochanter and proximal femur (CTr joint and TrF joints) provide signals that can strongly affect magnitude and time course of muscle activities that support body load in standing, in the stance phase of walking on a level surface (Hofmann and Bässler 1986; Zill et al. 1999; Pearson 2008) or in climbing an obstacle (Watson et al. 2002). In contrast, the tibial campaniform sensilla can modulate the muscle activities (set by the CPG and sustained by feedback from proximal joints) to tune motor outputs to variations in load. The distribution of forces and torques occurring at different joints have been shown to vary in other motor behaviors such as walking on inverted surfaces or climbing vertical substrates (Cruse 1976b) and so there may be flexibility in the force distribution and relative contributions of the CTr and FT groups of sensilla to force outputs in the system (see also Günzel et al. 2022). In addition, further understanding of muscle properties would aid in understanding how the patterns of neural activities are transformed to muscle tensions and movements (Sponberg et al. 2023).

Analysis of the relationship between the FT joint torque and ground reaction forces also provides preliminary support for the potential function of tibial CS as corrective or 'error' detecting signals. Figure 11 shows plots of the values of the FT joint torques vs

the ground reaction forces during the 'stance phase' for all steps in walking on level and inclined surfaces. While the plots in walking on a level surface show inconstant relationships, there is a strong correlation of the magnitude of the FT joint torque with ground reaction forces to support body load and counter the effects of gravity in the walking direction (F_x). In addition, in walking downhill, the FT torques are very strongly correlated with lateral forces (F_y) that could maintain postural stability when the legs act to pull the tarsus in toward the body (Dallmann et al. 2019), as in distributed inward grip (Wile et al. 2008). In walking downhill, the hindlegs are exerting large braking forces, and joint flexor muscles are active even when the joint angle is extending. The effects of gait (lifting of other legs and redistribution of support) could contribute to the large lateral forces in downhill walking and to a high correlation of the FT joint torque with F_y . This idea is supported by experiments that showed that perturbations of the substrate oriented perpendicular to the body long axis in freely standing cockroaches produce vigorous activation of hindleg tibial campaniform sensilla (Ridgel et al. 2001) and motor neurons to leg muscles (ibid. Fig 3B). Further studies that carefully examine movements of multiple legs and ground reaction forces are needed to study the potential effects of gait in producing instability to lateral forces.

6 - Comparison with slope walking in vertebrates: most insects do not have a vestibular system to maintain postural stability

There are both common features and significant differences in neuromuscular control of walking on slopes in vertebrates and invertebrates. The similarities result from biomechanics and the need to generate additional propulsion in going uphill and braking forces when walking downhill. For example, myographic recordings of muscles at the

hip and ankle joints in freely moving cats and humans consistently show enhancement of activities of hip extensor muscles in walking uphill (Carlson-Kuhta et al. 1998; Lay et al. 2006; Pickle et al. 2016), as is seen at the coxo-trochanteral joint in insects (Dallmann et al. 2019). Early experiments in humans using perturbations (unloading) imposed on the ankle joint suggested that inputs from receptors that monitor forces (Golgi tendon organs) strongly contribute to these changes (Houk and Simon 1967; Horcholle-Bossavit et al. 1990; Grey et al. 2007) although the potential role of sensory signals of force dynamics (Jami 1992) were not directly evaluated. These effects of force feedback are similar to the functions postulated for the trochanteral campaniform sensilla and coxo-trochanteral muscles in insects (Zill et al. 2012).

A significant difference is that, while the movements of intrinsic leg joints in insects are relatively constant in all substrate orientations, joint movements in vertebrates differ significantly on sloped compared to level substrates (Smith et al. 1998), particularly at the knee joint (Klishko et al. 2021). Recent studies concluded that control of sloped walking in vertebrates utilizes integration of inputs from both receptors that monitor forces and sensory inputs (muscle spindles) that encode joint position and movement (Gregor et al. 2006; Daley and Biewener 2011; Frigon et al. 2021). In addition, some of the specific adaptations in walking on slopes in vertebrates may also be related to problems of maintaining postural stability on fewer legs than in insects. Recent analysis of downhill walking in cats suggests that these adaptations result from supraspinal inputs, potentially mediated by the vestibular system, which monitors the effects of gravity and acceleration in vertebrates but is absent in most insects (Klishko et al. 2021). However, the activities of sensory receptors that monitor forces have not, as yet,

been studied in vertebrates in walking on slopes (Flanders, 2011) to allow comparison with the results obtained from stick insects.

7- Are signals of dynamic decreases in force preserved in the stick insect central nervous system?

The present study has shown that when forces are applied using waveforms of joint torques of freely walking animals, signals from the tibial campaniform sensilla strongly reflect the force dynamics (dF/dt). It is still unclear how or whether the signals of transient force decreases are encoded in the nervous system. In a previous study we demonstrated that transient increases in forces resisting muscle contraction, signaled in part by the trochanteral campaniform sensilla, can produce increases in activities of motor neurons of stance phase muscles in stick insects (Zill et al. 2012), but the effects of force decreases were not systematically examined. Campaniform sensilla can potentially have direct effects on motor neurons but have been shown to affect activities in a number of non-spiking interneurons in stick insects (Gebehart and Büschges 2021; Gebehart et al. 2021, 2022). These interneurons can act as low-pass filters but tests using forces applied as ramp and hold functions show that interneurons can reflect both phasic and sustained components of force application, as signaled by campaniform sensilla but signaling of the rate of change of force were not systematically studied (Gebehart et al. 2021). Previous studies have suggested that multimodal proprioceptive feedback can function as 'error signals', as suggested by the present study, but the requisite elements that can differentiate unexpected loads from self-generated forces have not been identified in insects (Flanders, 2011) . Further studies are necessary to

understand how force dynamics can be preserved in motor outputs during 'active' behaviors, such as walking (Bidaye et al. 2018).

8- Discussion of Mathematical Model

These tests show that the model we have developed, although tuned with limited data sets, can describe a variety of additional responses with these same parameter values, suggesting that the model replicates the underlying dynamics of CS afferents without over fitting to the data, although further tuning of the model might improve predictions of discharges to decreasing forces. These findings also demonstrate that similar parameters are encoded in walking uphill and downhill, supporting the hypothesis that insects do not use different motor programs in sloped walking (Dallmann, et al. 2019) but utilize the same local mechanisms of motor control on all substrates.

9- Limitations of this study

The waveforms of joint torques of the hindleg FT joint that were used as mechanical stimuli in this study were derived by inverse dynamics from a previous study of sloped walking of free moving animals (Dallmann et al. 2019; also Dallmann et al. 2016, 2017; Zill et al. 2021). The method of inverse dynamics makes the assumptions that limbs are composed of rigid segments and leg joints are frictionless (Simpson et al. 2015; Zajac and Gordon 1989). In the study of Dallmann (2019), the joint torques at the most proximal leg joint (body-coxa) were closely correlated with recordings of muscle activities, supporting the validity of the method. It is also important to note that, in the present study, many of the characteristics of afferent discharges, such the sensitivities to small force decreases, were evident in the discharges of sense organs to all waveforms, despite the variations of their detailed dynamics or amplitude. In addition,

the waveforms were applied to the leg without control for the effects of visco-elasticity of the cuticle. However, we found that in using the dynamic waveforms applied in the present study, the resultant forces closely (within 10%) followed the the shape of the torque waveforms and the effects of visco-elasticity, such as stress relaxation, were minimal.

10- Conclusions and future work

This study has recorded the activities of sense organs that monitor forces and shown that feedback during walking can provide specific information that could aid in countering instabilities in traversing slopes. The findings also suggest that force feedback and information about force dynamics are not monotonic but may be related to the specific functions of individual leg joints. Succeeding experiments will examine responses of the trochanteral and femoral campaniform sensilla (the largest groups of receptors) to torque waveforms to test whether the dynamic sensitivities and hysteresis are similar to those found in the tibial sensilla in the present study. These characteristics of force detection may also be beneficial in the control of legs of walking machines in locomotion on sloped surfaces.

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922 **FIGURE LEGENDS**

923 **Figure 1 - Structure of Campaniform Sensilla of Stick Insect Hindleg Tibia and**
 924 **Experimental Preparation.** A. Campaniform sensilla monitor forces through a dendrite
 925 that inserts to a cuticular cap embedded in the exoskeleton. B. Scanning electron
 926 micrograph of hindleg proximal tibia - The tibial sensilla are arranged in two spatially
 927 separated subgroups (Groups 6A, 6B). C. Structure of cuticular caps. i. The tibial
 928 Group 6B typically has three sensilla with round cuticular caps, similar to the

arrangement in middle legs. ii. Group 6B also contains a variable number of other sensilla that have oval shaped caps. iii. Group 6A has two sensilla (one shown) with oval caps orient close to parallel with the long axis of the tibia. D. Joint forces (torques) in freely moving stick insects were derived from experiments using a small force plate inserted in a walkway that could be tilted (previous study by Dallmann et al. 2019). E. Sensory responses of the tibial campaniform sensilla were recorded in the femur while forces were imposed on the tibia, including ramp and hold waveforms and waveforms of joint torques from freely moving animals.

Figure 2 - Response properties of tibial campaniform sensilla of the stick insect

hindleg. A. (left) - Bending forces applied to the distal tibial in the direction of joint extension (movement resisted) elicited vigorous discharges of 6B sensilla during the rising and hold phases and 6A receptors during the ramp decline; (right) ablation of 6B receptors (right) selectively eliminated the discharges during the ramp rise and hold. B. Plot of mean firing frequency of all 6B sensilla during the hold phase to bending forces applied to the distal tibia at different amplitudes in four animals. Discharges reflect the force magnitude but vary with stiffness of cuticle. C. Response to forces applied at different rates of rise and decline. D. and E Plots of mean firing during the ramp rising phase show that 6B large sensilla encode the rate of change of force increase (D) and 6A receptors the rate of force decrease (E) over a range of force amplitudes.

Figure 3 - Torques and movements of the femoro-tibial joint. A and B. The mean forces (torques) at the femoro-tibial joint of selected steps used in this study (derived from data set of Dallmann et al. 2019) vary according to substrate orientation: forces are variable on a level substrate but provide propulsion (extensor torque) in walking uphill

952 and a strong braking force (flexor torque) on downhill slopes. C. Joint torques of
953 individual steps in walking. The torques of individual steps used in this study showed
954 variability and inflections in walking on level (left), uphill (middle) and downhill (right)
955 substrates. D. Joint movements. i. The mean FT joint angle is consistently extended
956 over a relatively constant range during the stance phase of walking on all surfaces. ii.
957 Plot of FT joint torque and joint angle in a single, sample step. Many individual steps
958 showed substantial variability in joint torques but relatively constant joint movement. iii.
959 Plot of the mean joint angles in which torques occurred for steps used in this study.
960 Flexor torques tended to occur in ranges of joint extension while extensor torques were
961 found in ranges of flexion, although torques in walking on horizontal substrates were
962 variable.

963 **Figure 4 - Recordings of Sensory discharges to Joint Torque Waveforms.** A, B. -
964 Walking on level surface. 6B sensilla fired in bursts that reflected fluctuations in both
965 the mean forces (A) and larger forces that occurred during individual steps (B). 6B
966 sensilla discharge during periods of force increase while 6A receptors fired when force
967 decrements declined to low levels. C. Downhill walking - 6B sensilla fired more
968 intensely during the larger braking forces but discharges were inhibited when forces
969 fluctuated and briefly decreased even at high sustained levels. D. Uphill walking - 6A
970 receptors discharged to forces exerted in propulsion while 6B receptors discharged
971 when force decreases approached zero. E. Controls - Identification of units derived
972 from subgroups 6B and 6A were based upon action potential size and confirmed by
973 selective ablations of cuticular caps of subgroups. Discharge to force increases (left

level walking step) was selectively eliminated by ablation of Group 6B (right) while firing of Group 6A receptors persisted after the ablation.

Figure 5 - Sensory encoding of joint torques in walking on a level substrate. Plots of pooled data from tests of sensory responses to joint torque waveforms. i. Walking on a level substrate - Force levels were relatively small in calculated mean joint torques (i) but larger in individual steps (ii-v, see scale). In tests with net flexor torques (i-iv) 6B sensilla fire to torque increases. The discharge frequency of large 6B sensilla (histogram second trace) and all 6B sensilla (histogram third trace) occur as bursts that do not follow the force level but instead reflect variations in the rate of change of force (dF/dt line overlaid on second trace). In steps with net extensor torques, the 6A sensilla more closely follow the rate of force increases, while 6B receptors discharge to force decrements.

Figure 6 - Sensory encoding of joint torques in walking on sloped substrates.

A. Downhill walking - Firing of 6B sensilla reflects the rate of change of force (dF/dt overlay line in second trace) and is inhibited by a transient force decrease in a single step (right). B. Uphill walking - 6A receptors fired to force increases when walking uphill. The discharge of the calculated mean torque (left) shows considerable adaptation, while the firing in an individual step is completely inhibited by a transient force decrease.

Figure 7 - Encoding of rate of change of force (dF/dt), A.-B. Plots of firing frequencies of large 6B sensilla at different rates of change of force (dF/dt) derived from data in Figs. 4, 5) in walking on level surfaces (A) and uphill C. Similar plot of firing of 6A receptors in uphill walking. D. Pooled, averaged data on mean firing of all 6B sensilla vs. dF/dt . E. Summary plot of firing of 6B large receptors vs rate of change of

force on substrate orientations. Large 6B sensilla encode the rate of change of force in all substrate orientations. (Animals N = 5, tests: Level n = 852, Downhill n = 1035, Uphill n = 997)

Figure 8 - Simulation of sensory discharges in walking on a level surface Walking on a level substrate - The model produced the same pattern of discharge of 6B receptors to force increases in both the smaller mean torque (A) and larger torques of individual steps that varied from the mean (B-E). Similar patterns of firing of 6A receptors to force decreases were also seen in simulation to force decreases.

Figure 9 - Simulation of sensory encoding of joint torques in walking on sloped substrates. A. Downhill walking - The model generated firing of 6B sensilla in downhill walking that reflected the rate of change of force. The inhibition that occurred to transient force decrease was also reproduced in some but not all steps. B. in a single step (right). B. Uphill walking - In simulation, 6A receptors fired to force increases when walking uphill. The discharge of the calculated mean torque (left) shows considerable adaptation, while the firing in an individual step is completely inhibited by a transient force decreases.

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FIGURES AND LEGENDS

Figure 1 - Structure of Campaniform Sensilla of Stick Insect Hindleg Tibia and Experimental Preparation

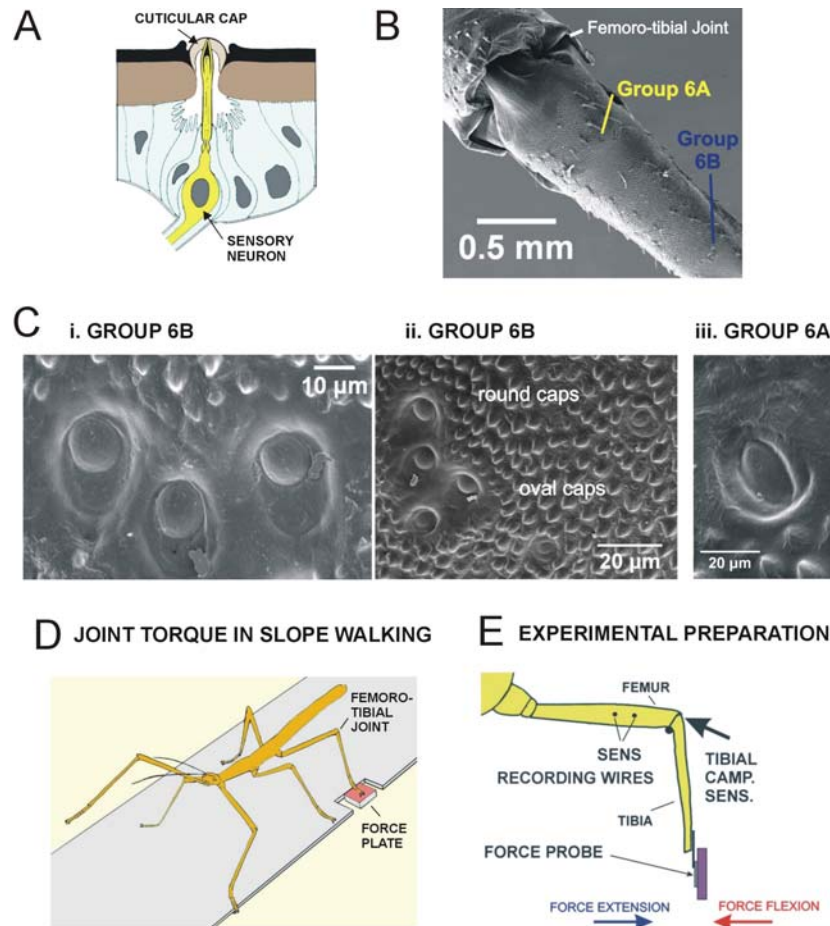


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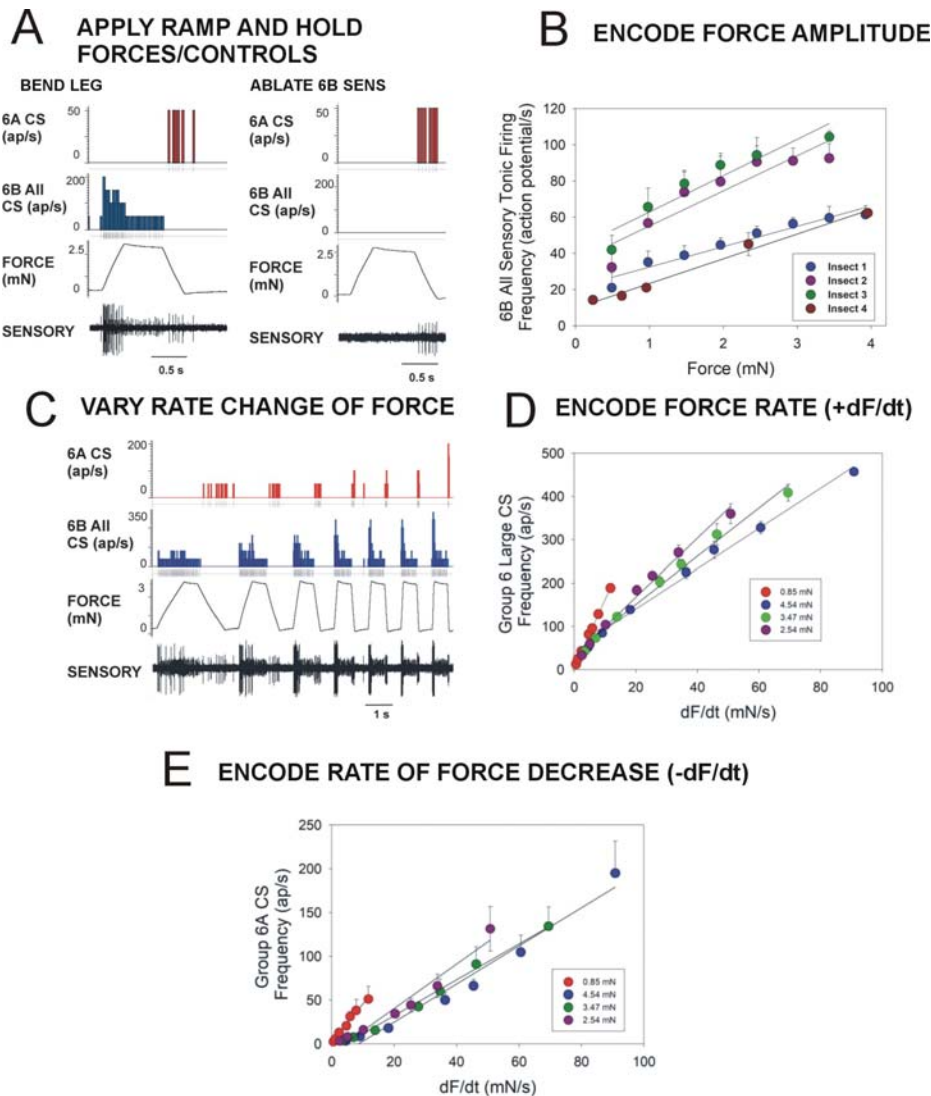


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Figure 3 - Torques and movements of the femoro-tibial joint

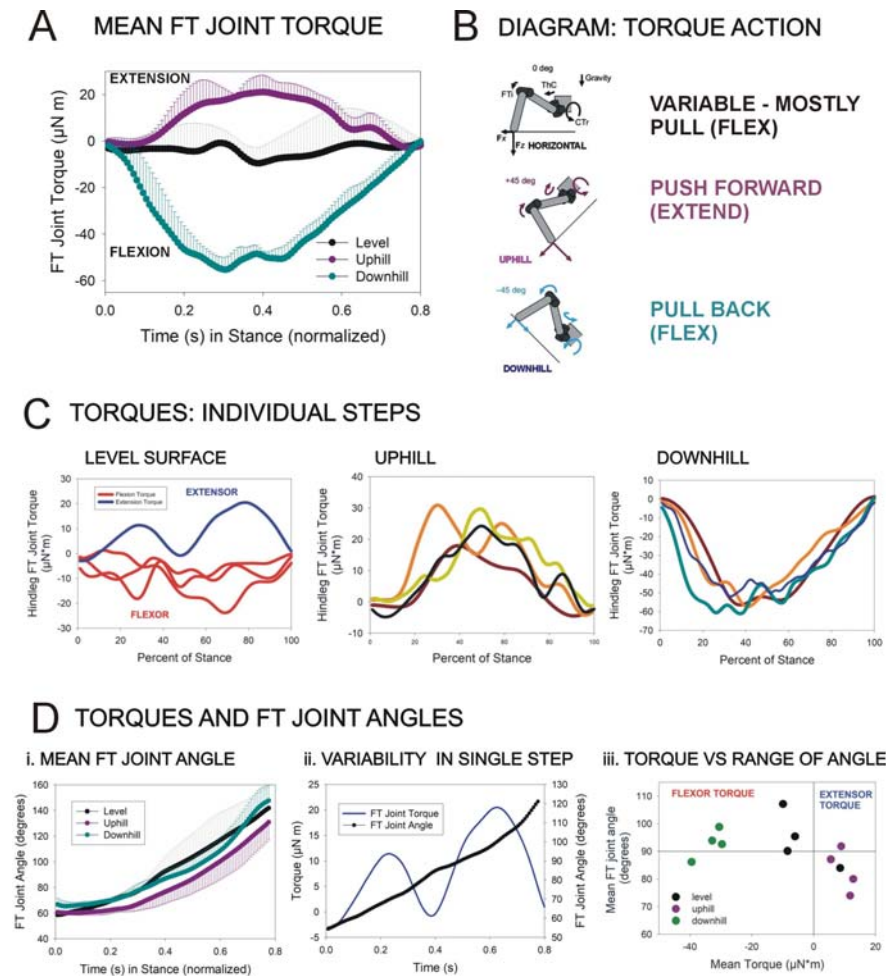


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Figure 4 - Recordings of Sensory discharges to application of forces using joint torque waveforms

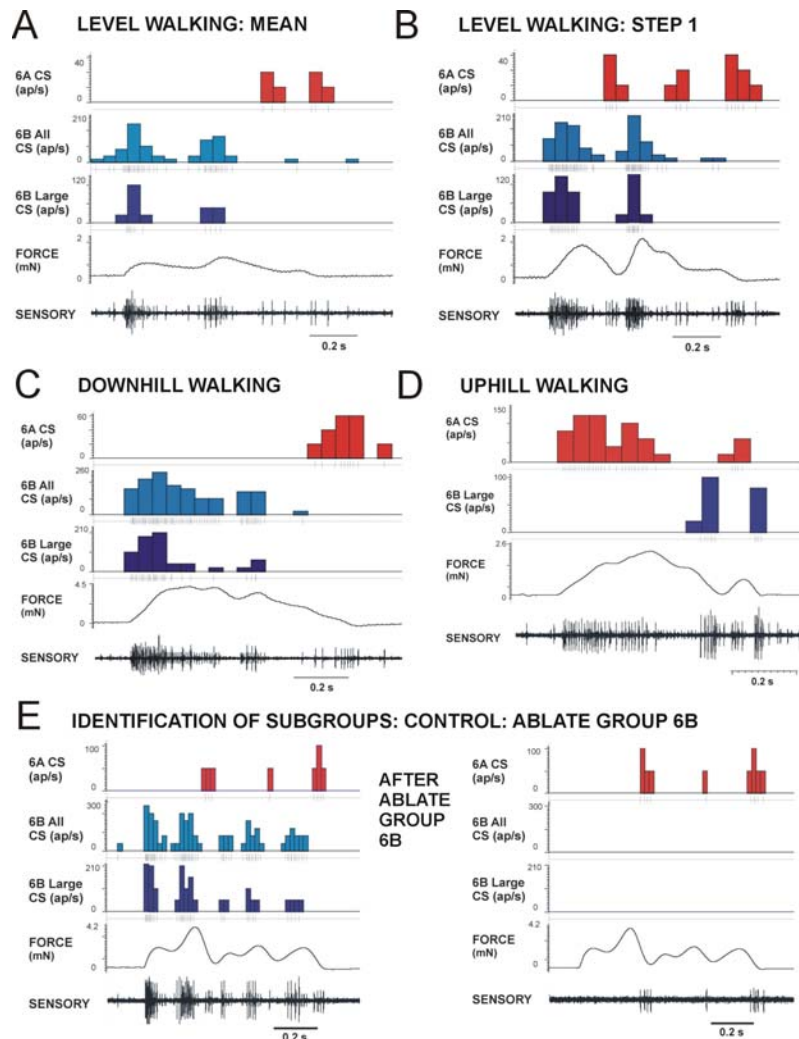
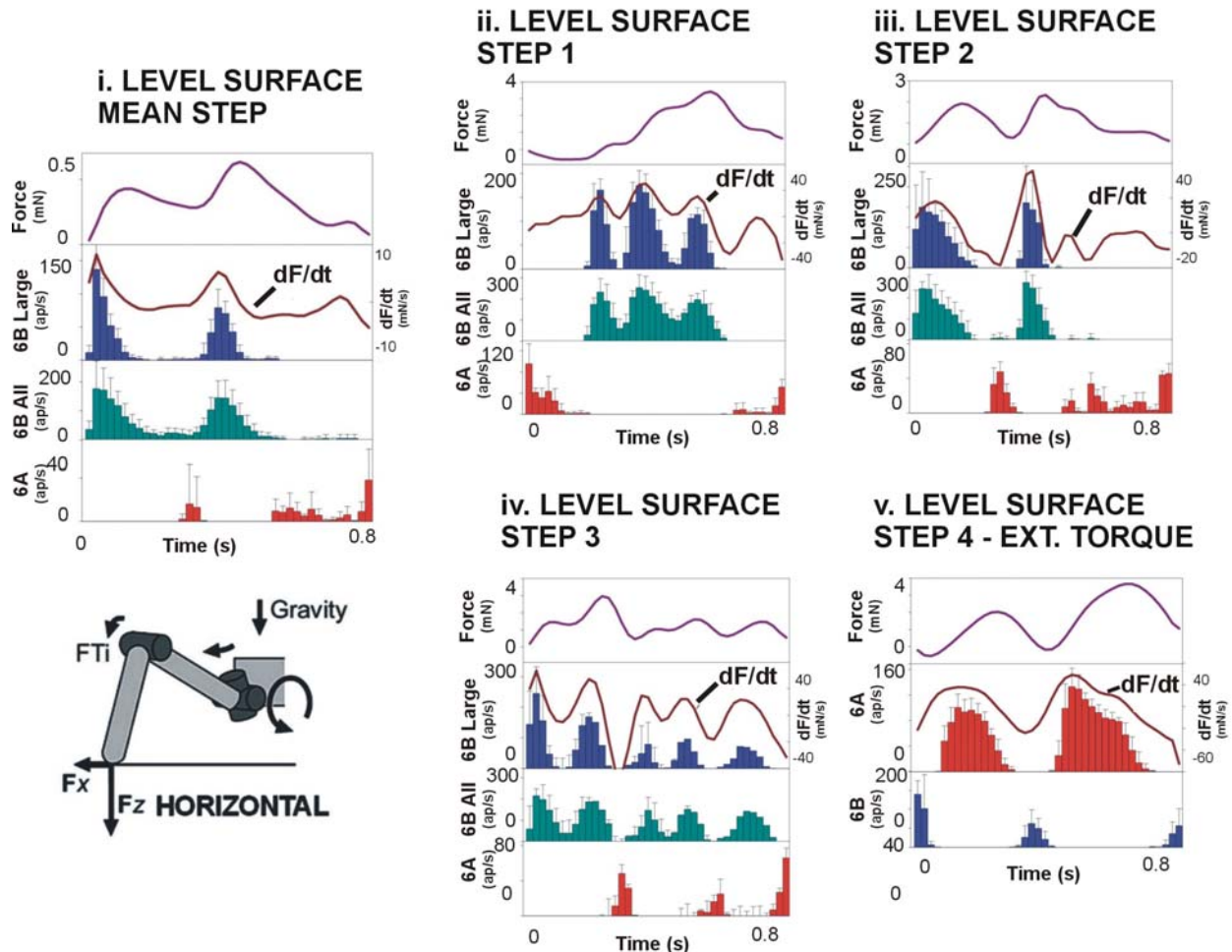


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SENSORY DISCHARGES: WALKING ON A LEVEL SUBSTRATE



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Figure 6 - Sensory encoding of joint torques in walking on sloped substrates

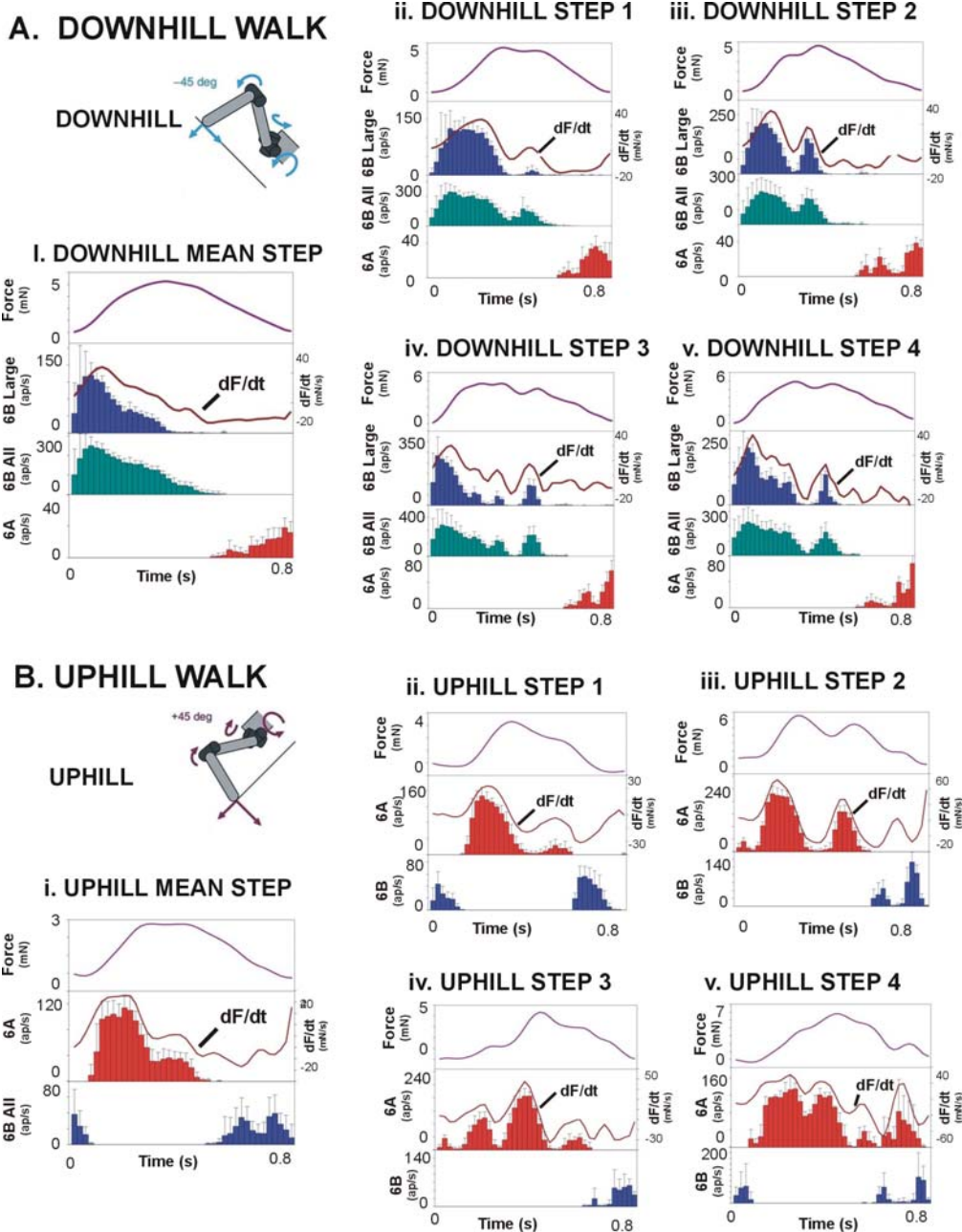
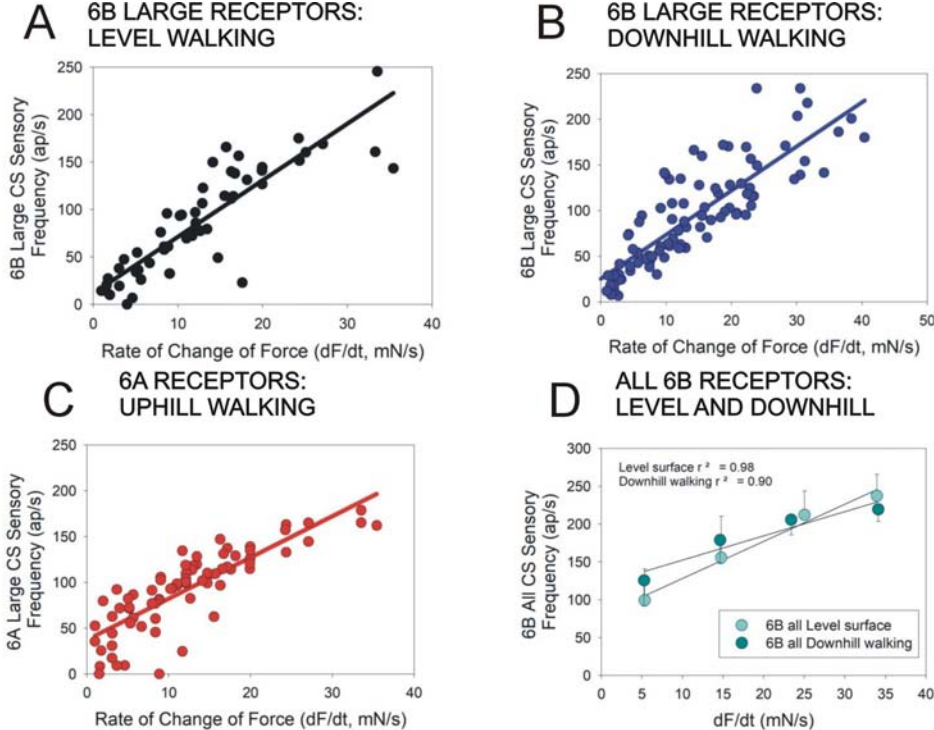


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Figure 7 - Sensory discharges encoding of the rate of change of force (dF/dt) on all substrates



E SUMMARY: LARGE SENSILLA CONSISTENTLY ENCODE RATE OF CHANGE OF FORCE IN ALL TESTS

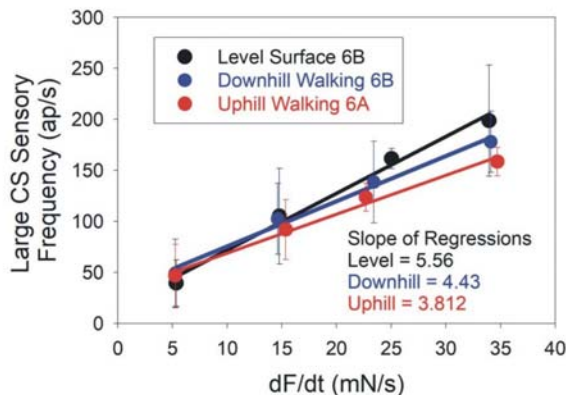


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Figure 8 - Simulation of sensory discharges in walking on a level surface

MODEL SENSORY DISCHARGE: LEVEL SUBSTRATE

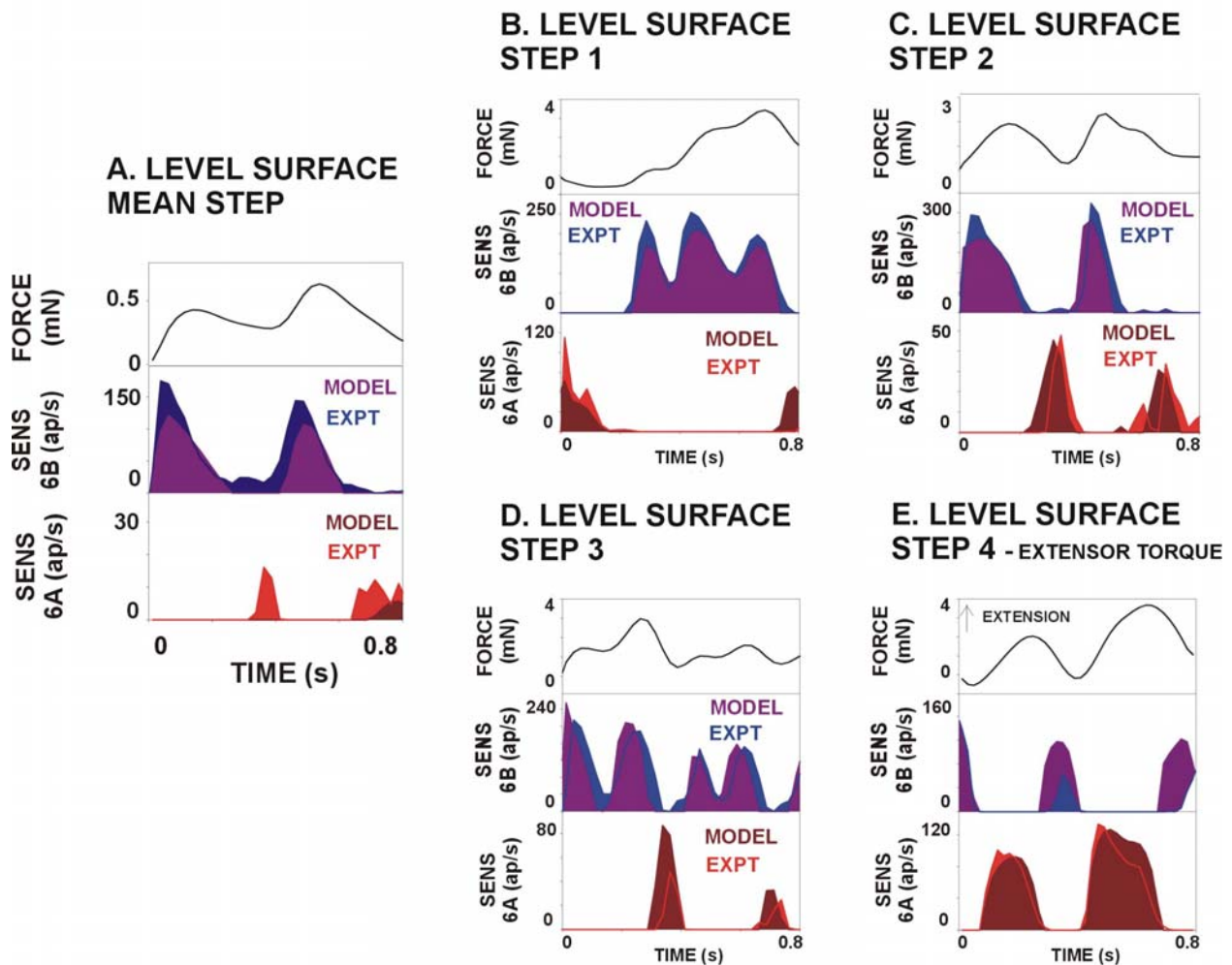


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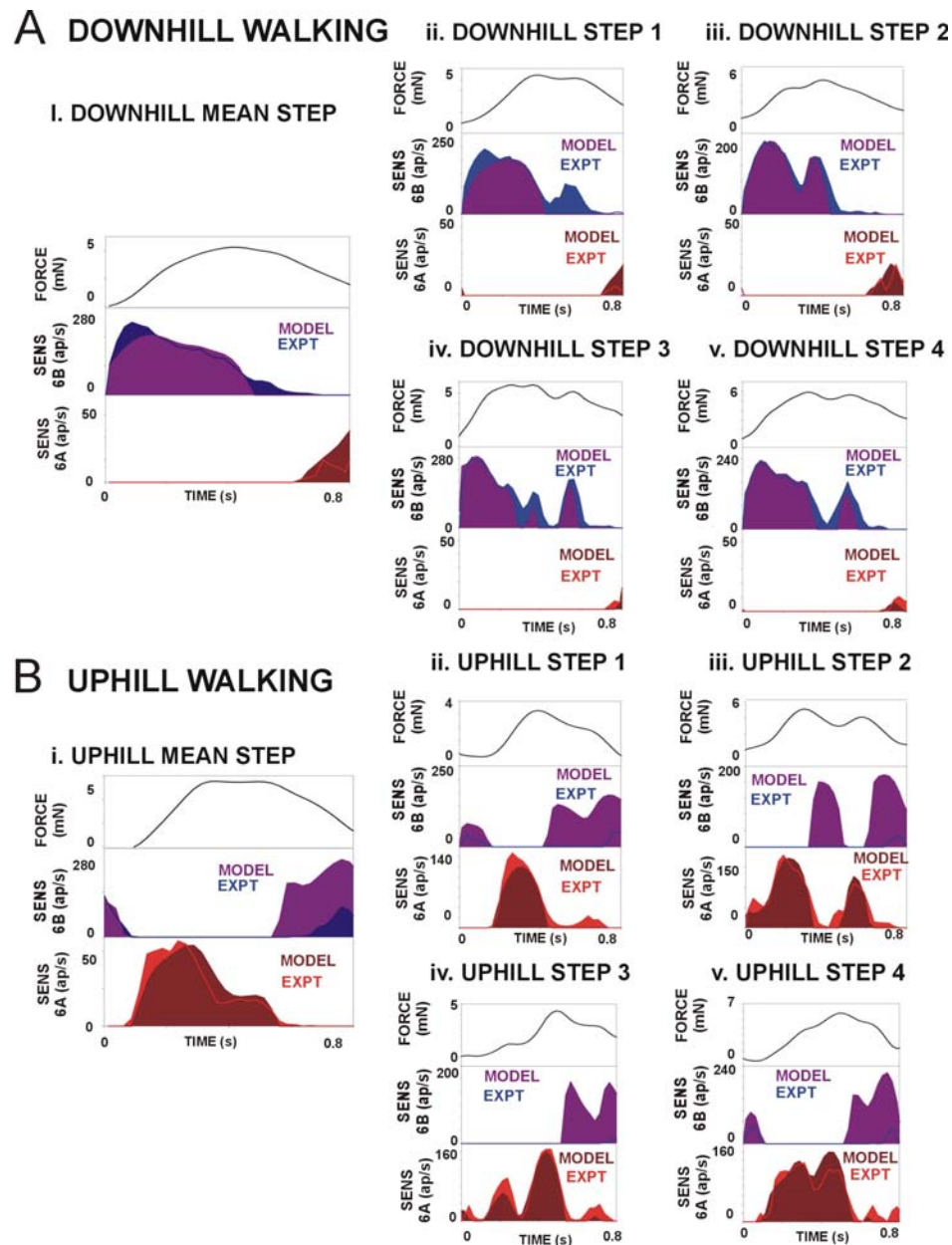
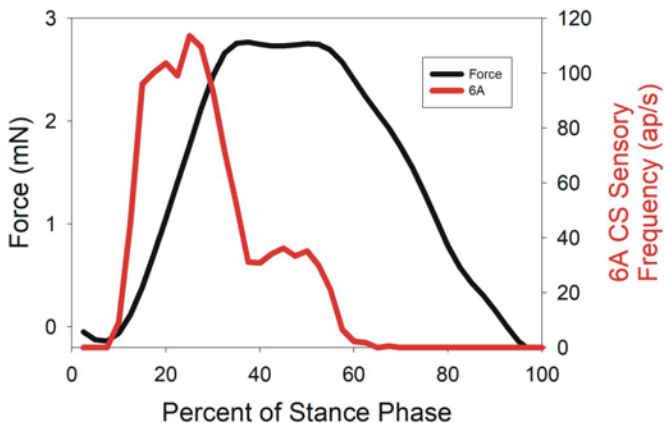


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A UPHILL WALKING



B DOWNHILL WALKING

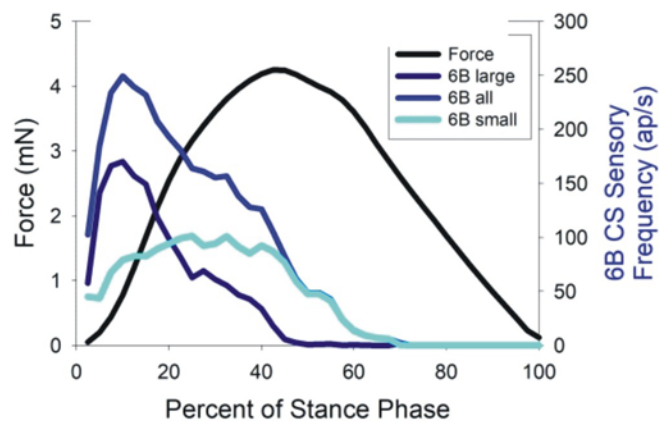


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Figure 11 - FT Joint Torques and Ground Reaction forces in walking on level and sloped surfaces

FT JOINT TORQUES VS GROUND REACTION FORCES

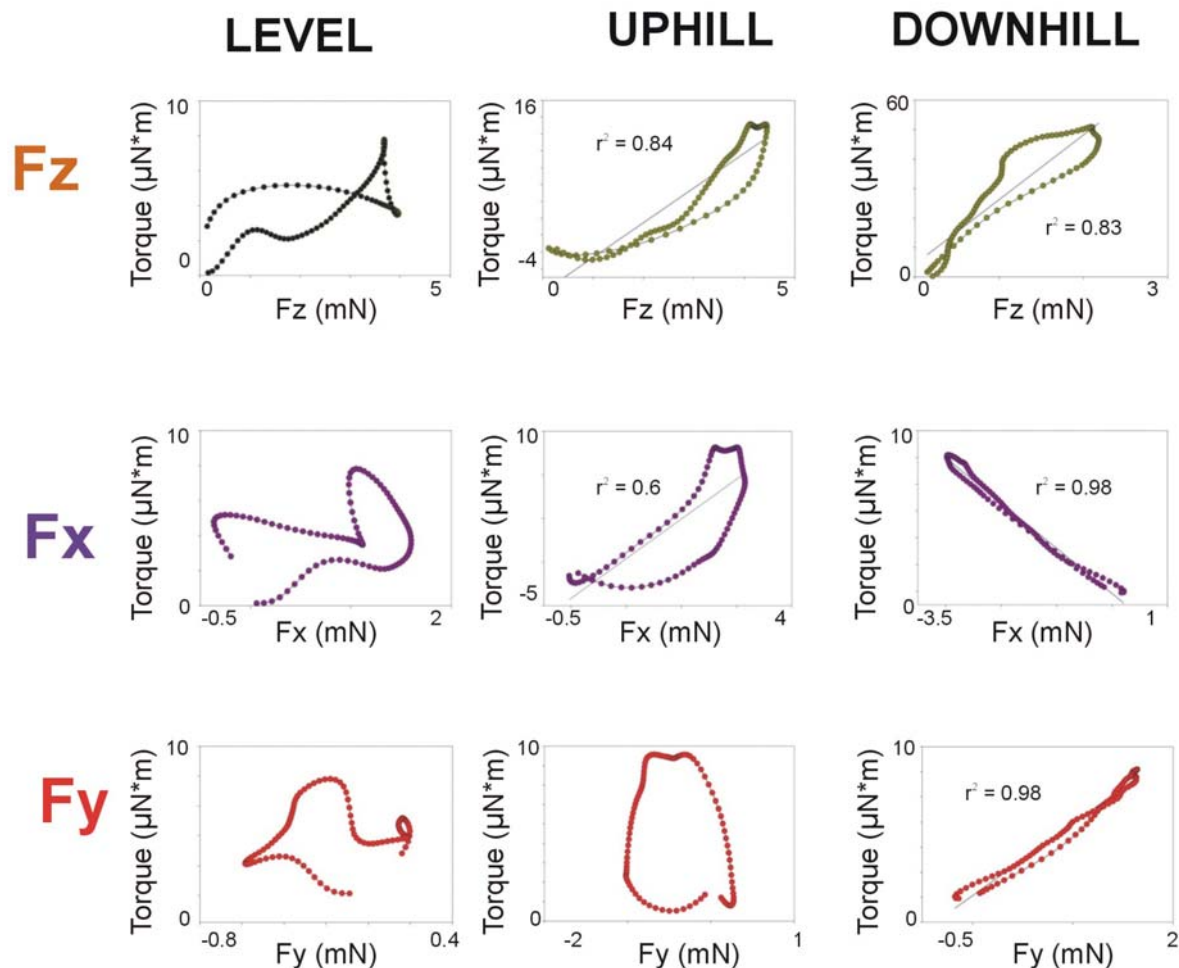
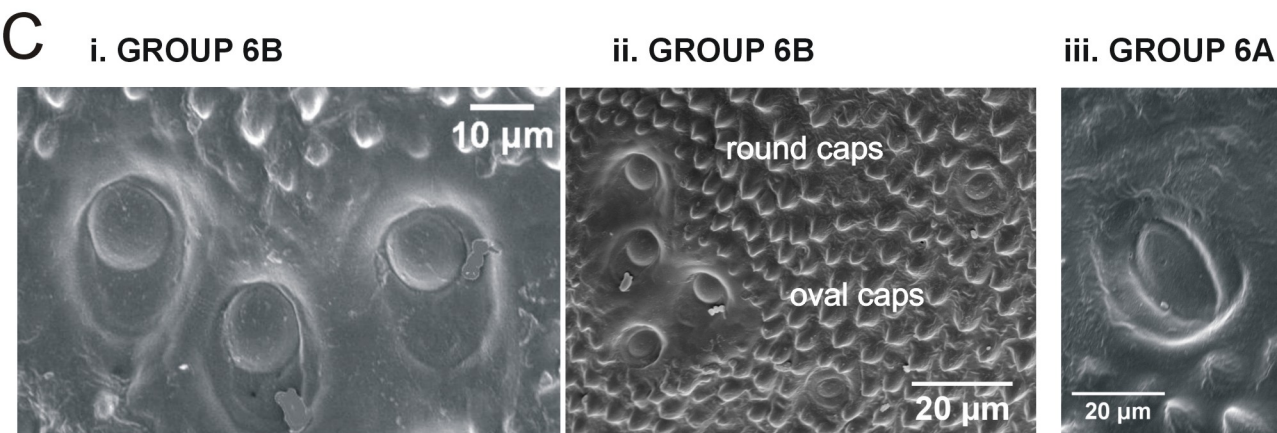
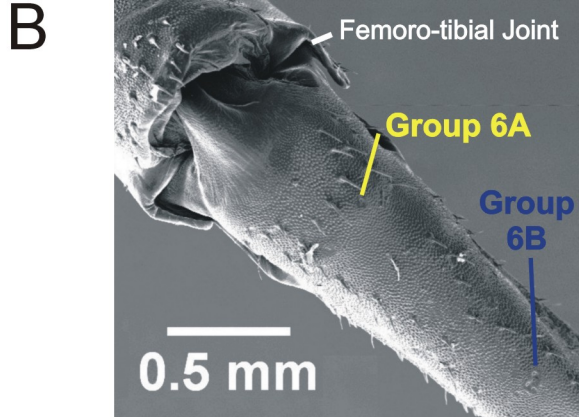
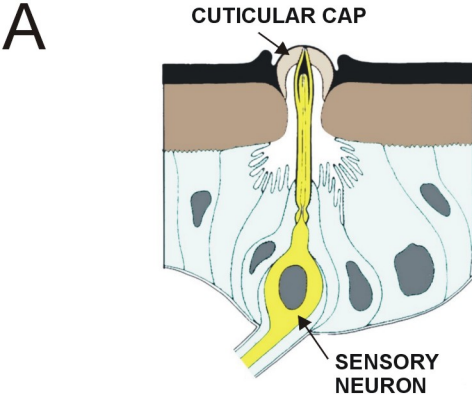
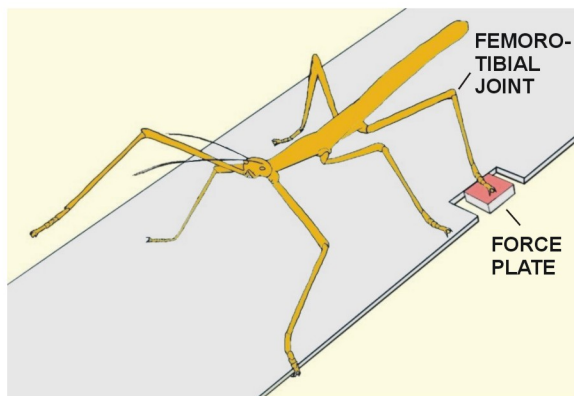


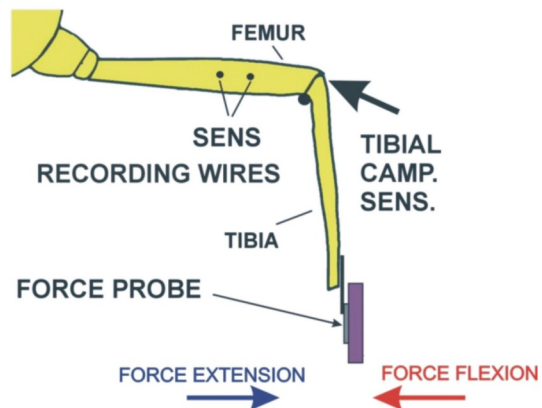
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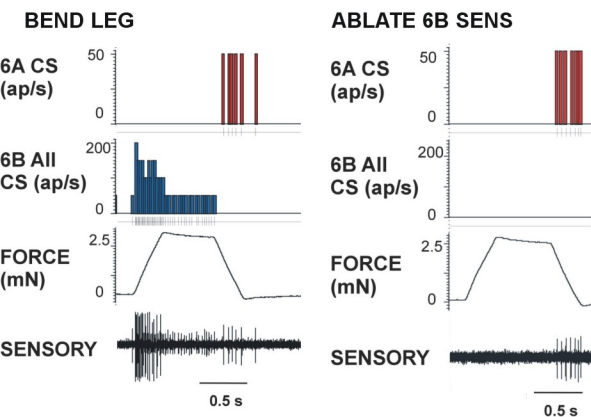
D JOINT TORQUE IN SLOPE WALKING



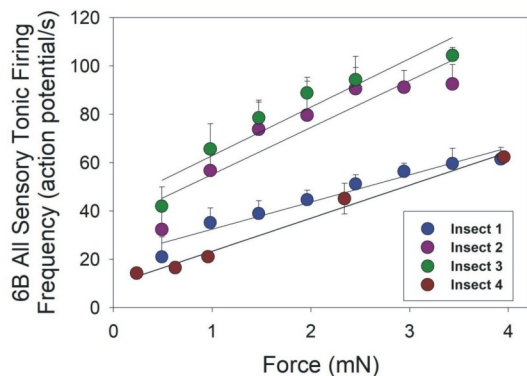
E EXPERIMENTAL PREPARATION



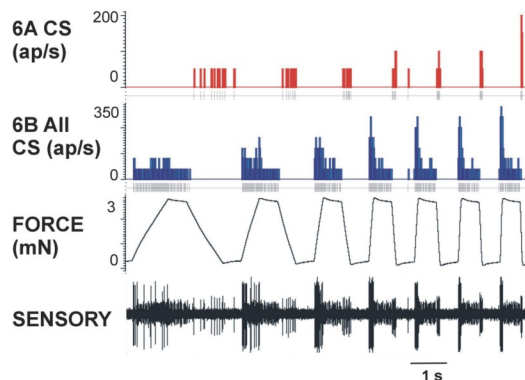
A APPLY RAMP AND HOLD FORCES/CONTROLS



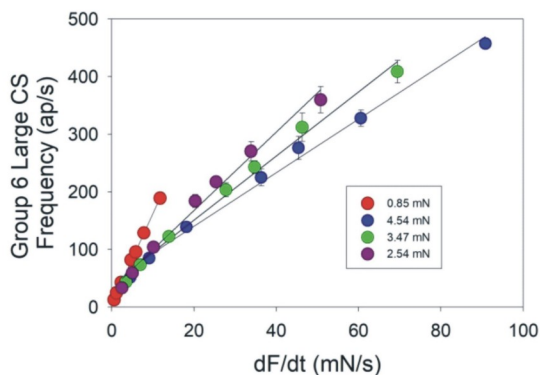
B ENCODE FORCE AMPLITUDE



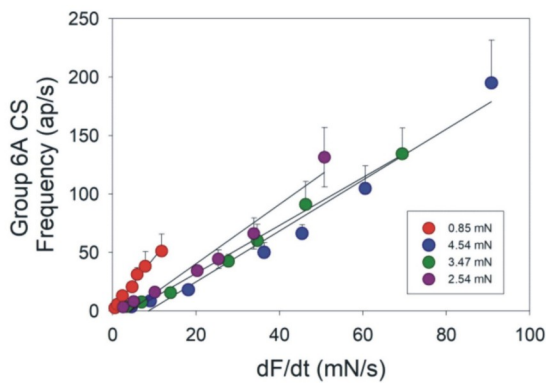
C VARY RATE CHANGE OF FORCE



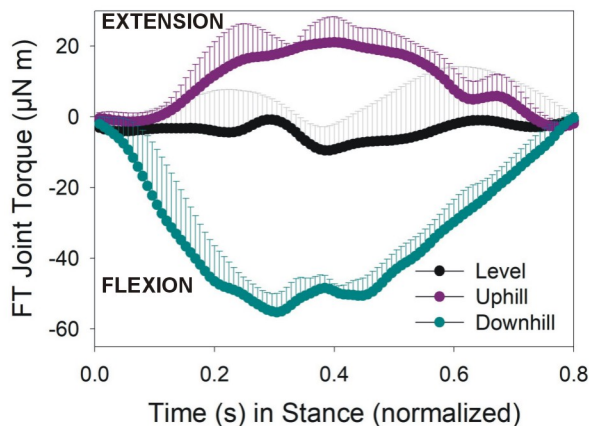
D ENCODE FORCE RATE (+dF/dt)



E ENCODE RATE OF FORCE DECREASE (-dF/dt)



A MEAN FT JOINT TORQUE



B DIAGRAM: TORQUE ACTION

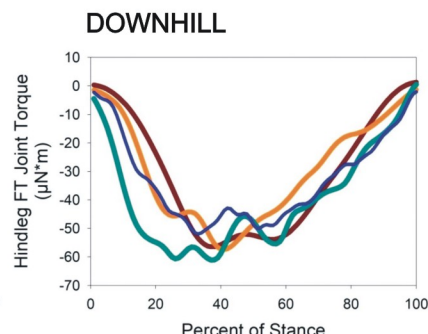
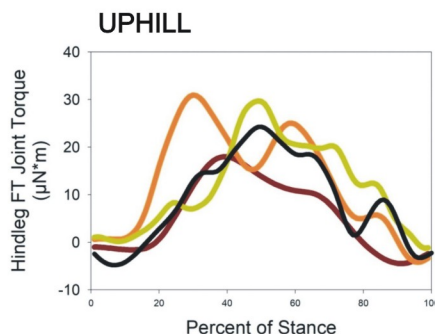
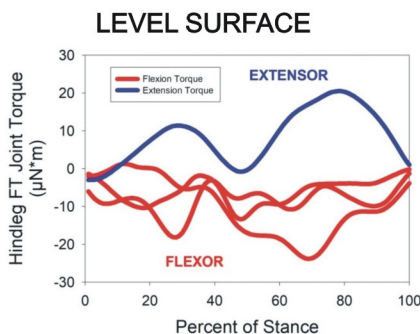


VARIABLE - MOSTLY PULL (FLEX)

PUSH FORWARD (EXTEND)

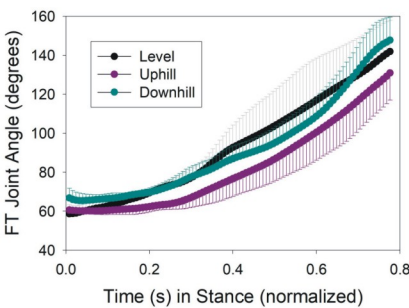
PULL BACK (FLEX)

C TORQUES: INDIVIDUAL STEPS

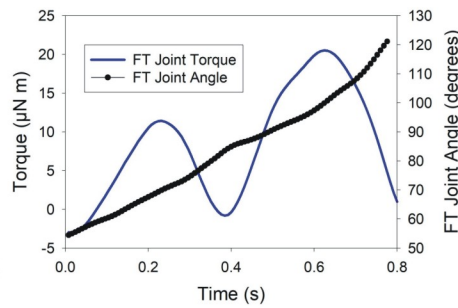


D TORQUES AND FT JOINT ANGLES

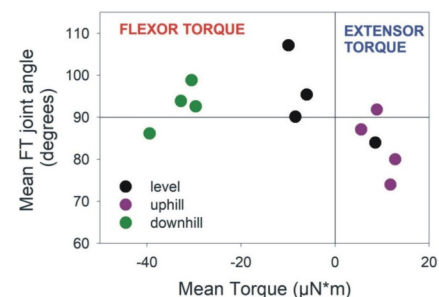
i. MEAN FT JOINT ANGLE

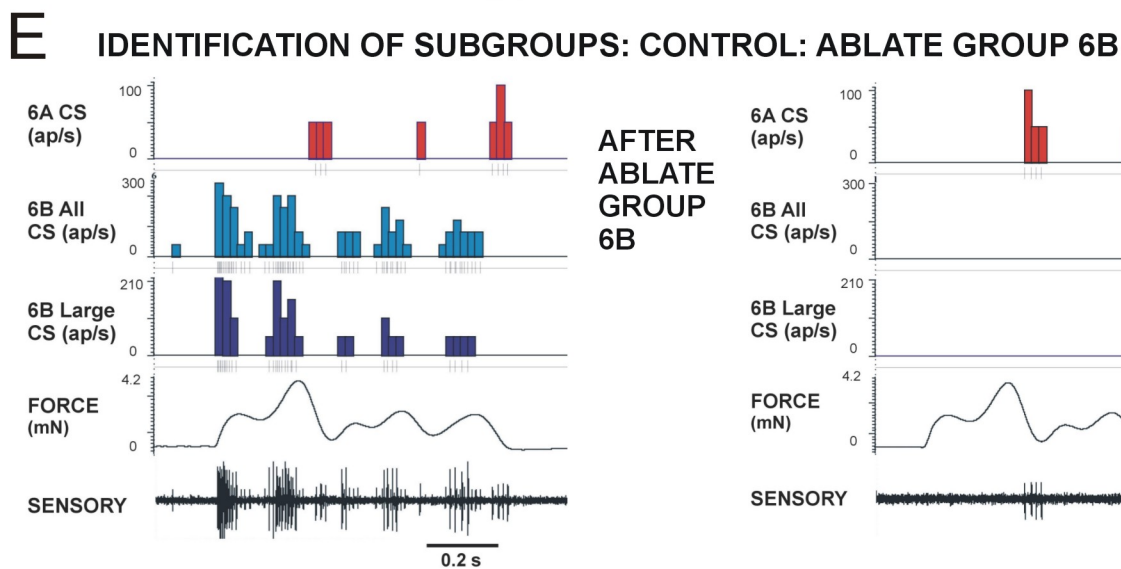
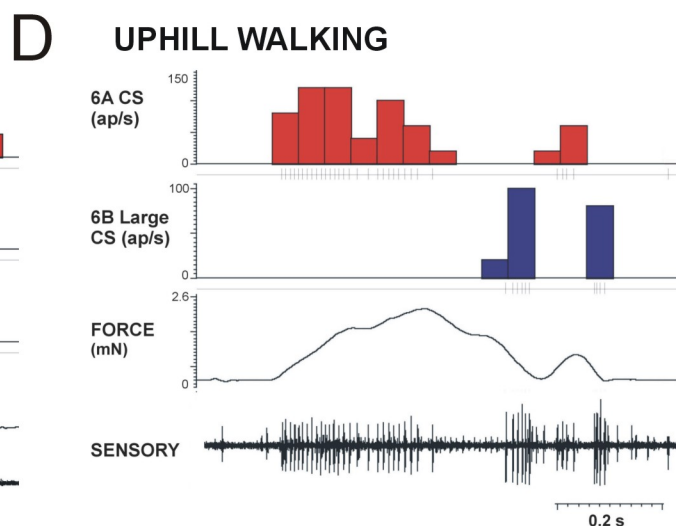
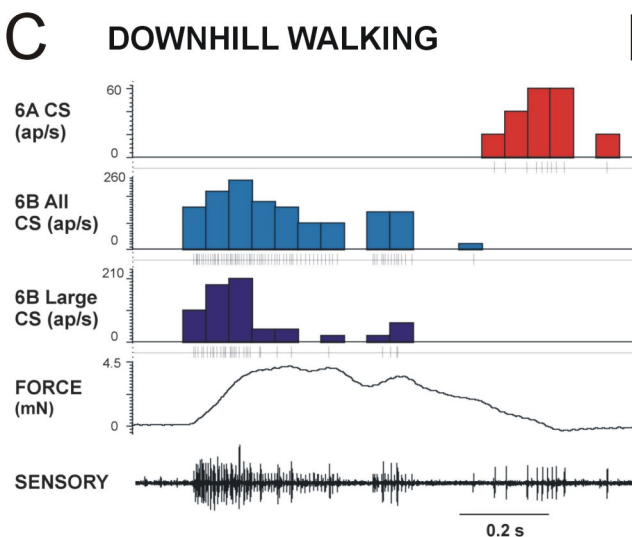
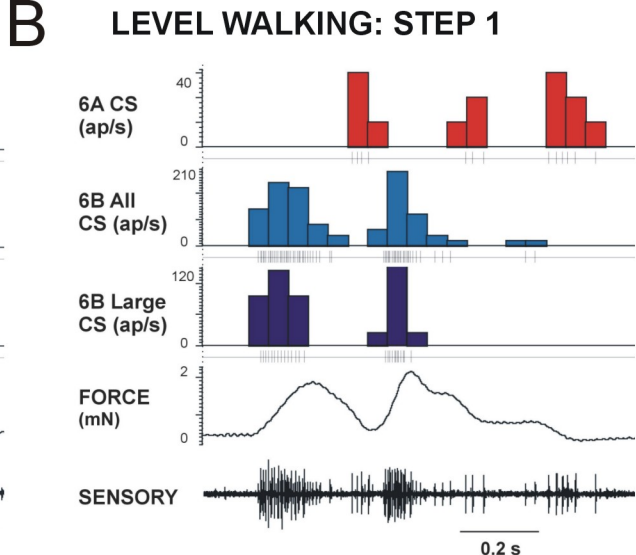
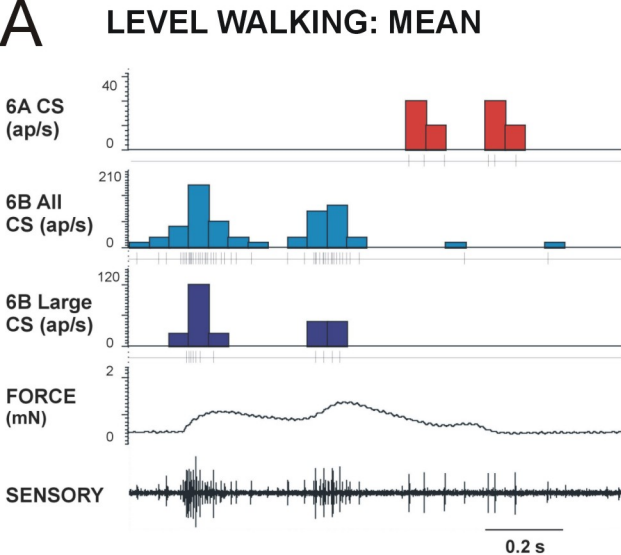


ii. VARIABILITY IN SINGLE STEP



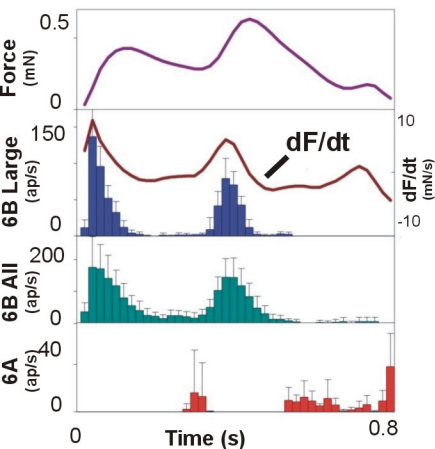
iii. TORQUE VS RANGE OF ANGLE



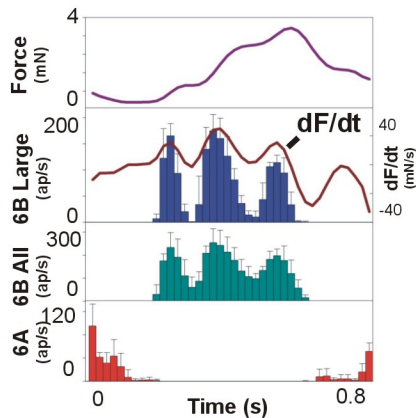


SENSORY DISCHARGES: WALKING ON A LEVEL SUBSTRATE

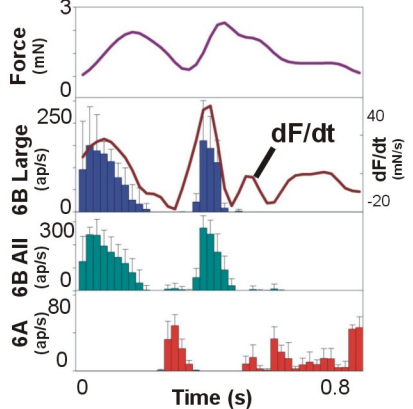
i. LEVEL SURFACE MEAN STEP



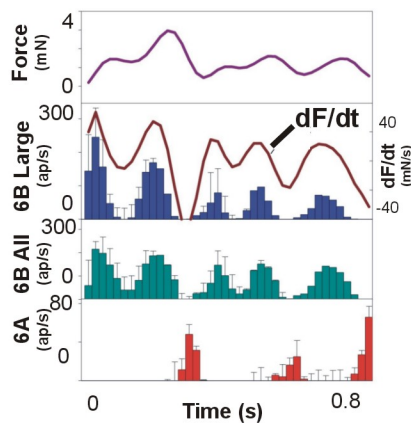
ii. LEVEL SURFACE STEP 1



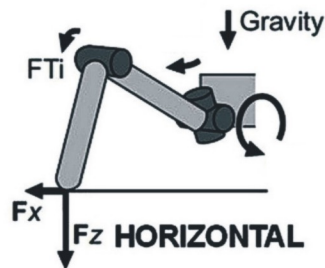
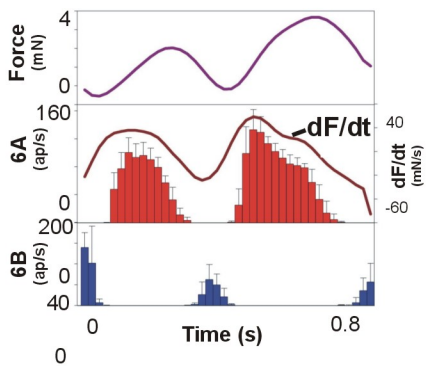
iii. LEVEL SURFACE STEP 2



iv. LEVEL SURFACE STEP 3



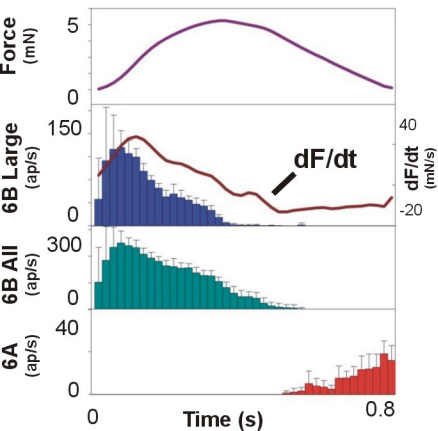
v. LEVEL SURFACE STEP 4 - EXT. TORQUE



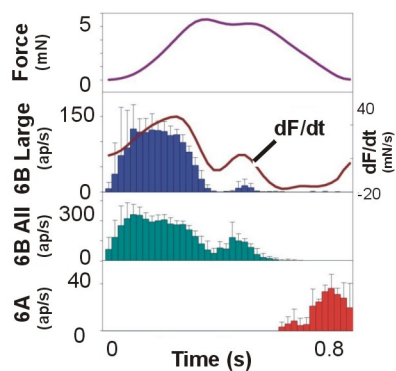
A. DOWNHILL WALK



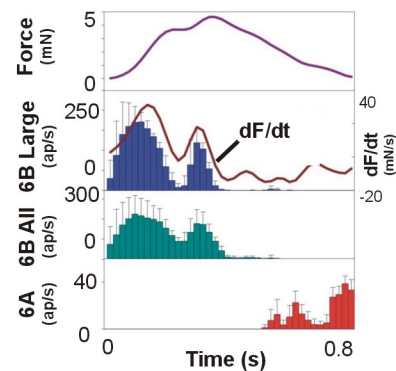
I. DOWNHILL MEAN STEP



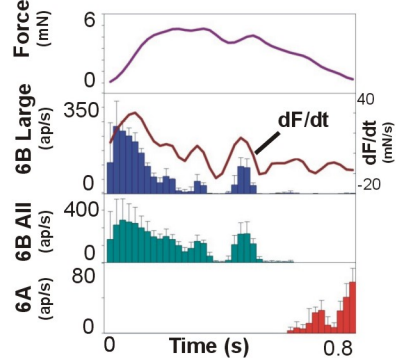
ii. DOWNHILL STEP 1



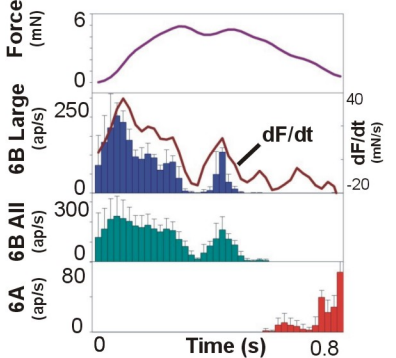
iii. DOWNHILL STEP 2



iv. DOWNHILL STEP 3



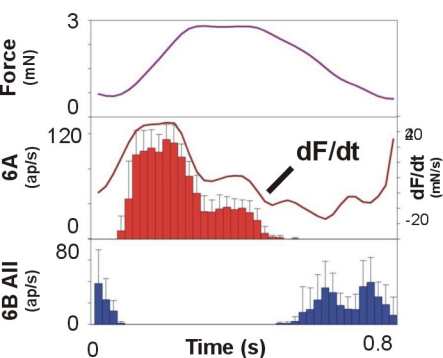
v. DOWNHILL STEP 4



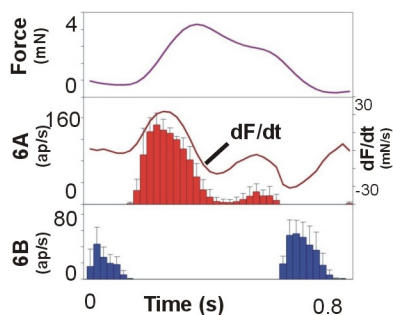
B. UPHILL WALK



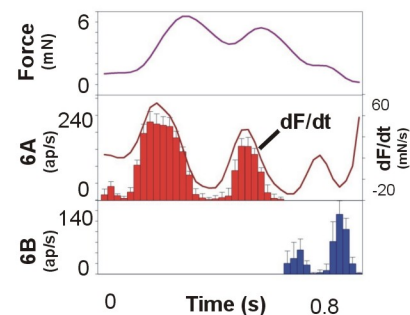
i. UPHILL MEAN STEP



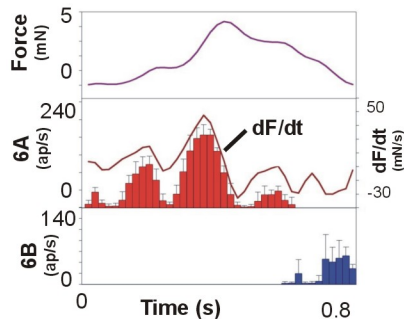
ii. UPHILL STEP 1



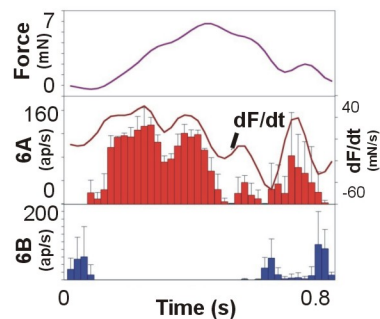
iii. UPHILL STEP 2



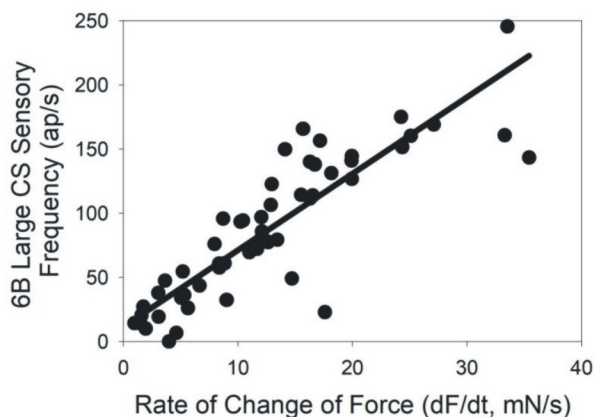
iv. UPHILL STEP 3



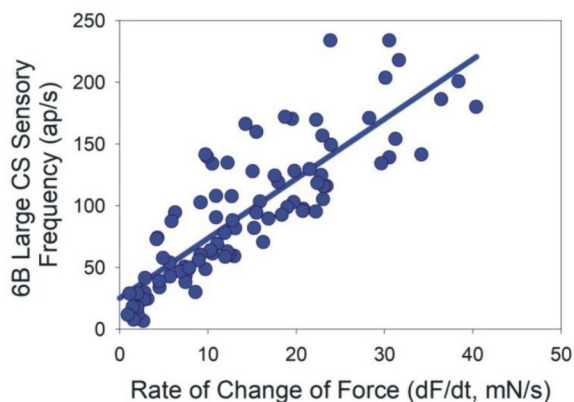
v. UPHILL STEP 4



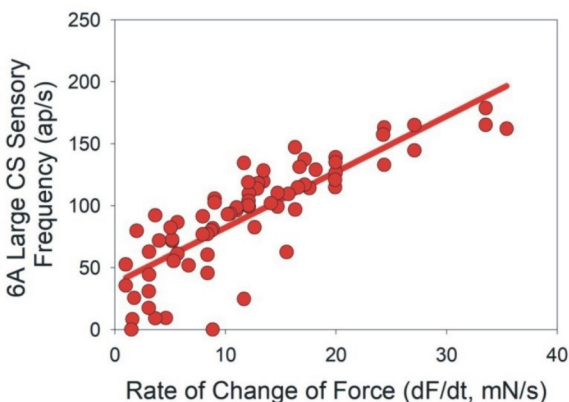
A 6B LARGE RECEPTORS:
LEVEL WALKING



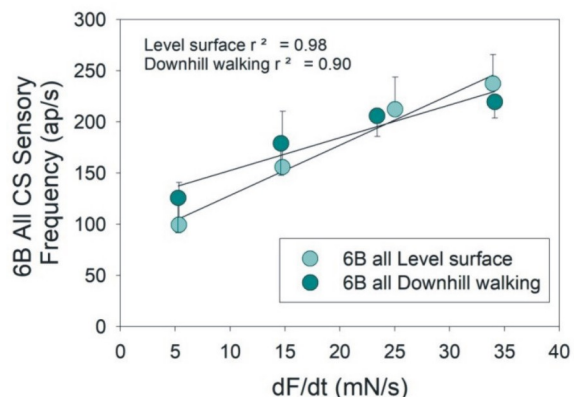
B 6B LARGE RECEPTORS:
DOWNHILL WALKING



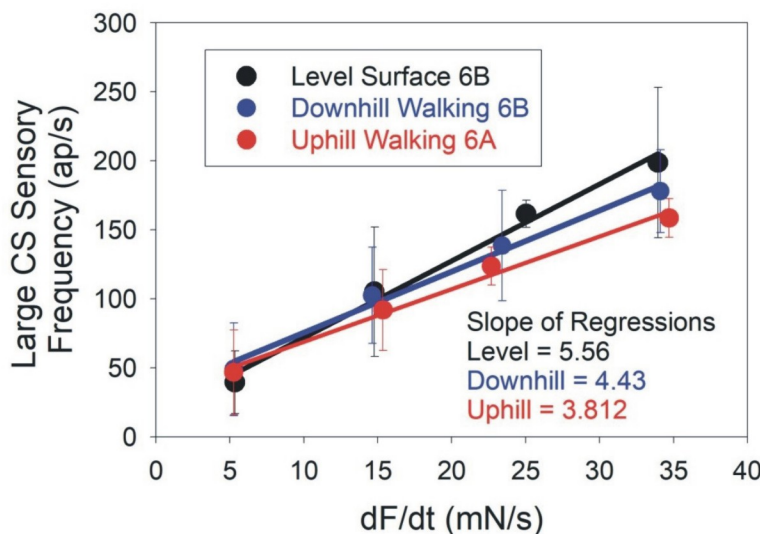
C 6A RECEPTORS:
UPHILL WALKING



D ALL 6B RECEPTORS:
LEVEL AND DOWNHILL

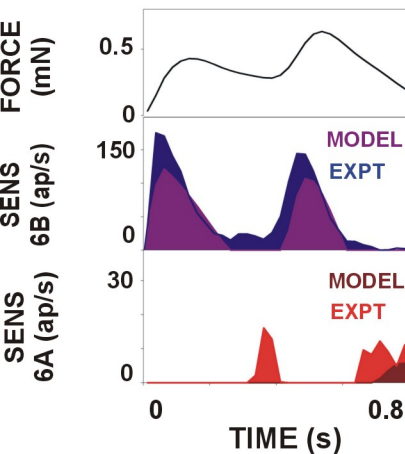


E SUMMARY: LARGE SENSILLA CONSISTENTLY
ENCODE RATE OF CHANGE OF FORCE IN ALL TESTS

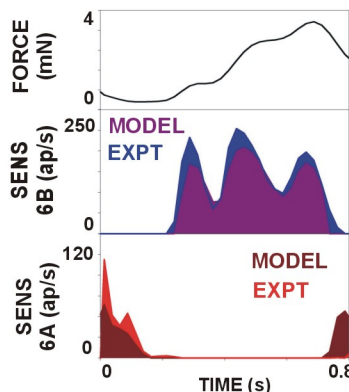


MODEL SENSORY DISCHARGE: LEVEL SUBSTRATE

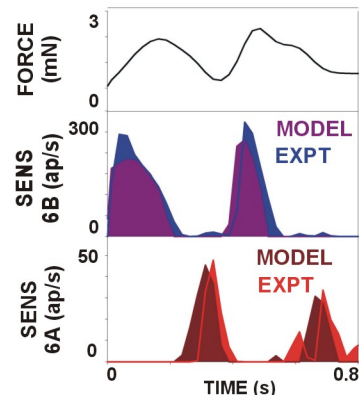
A. LEVEL SURFACE MEAN STEP



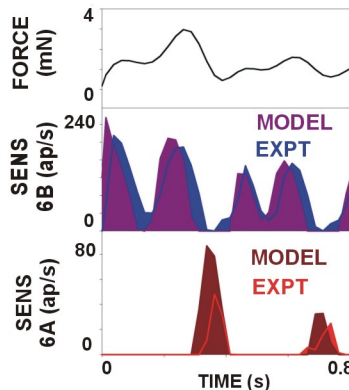
B. LEVEL SURFACE STEP 1



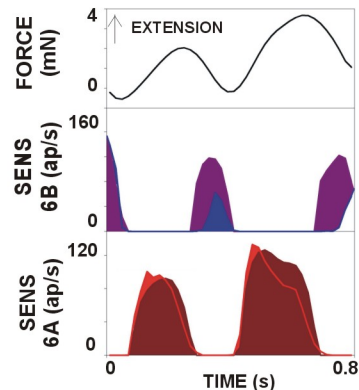
C. LEVEL SURFACE STEP 2



D. LEVEL SURFACE STEP 3

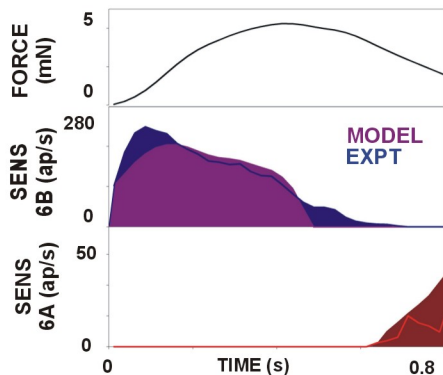


E. LEVEL SURFACE STEP 4 - EXTENSOR TORQUE

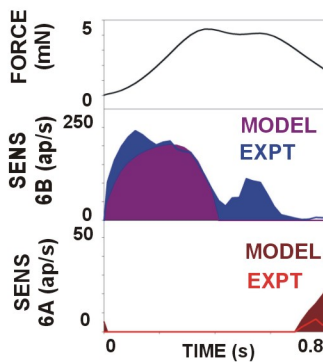


A DOWNHILL WALKING

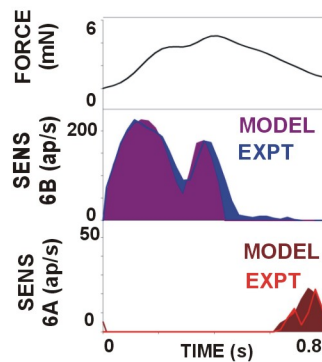
I. DOWNHILL MEAN STEP



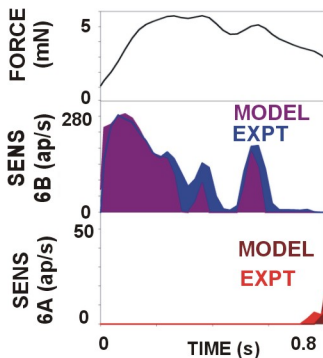
ii. DOWNHILL STEP 1



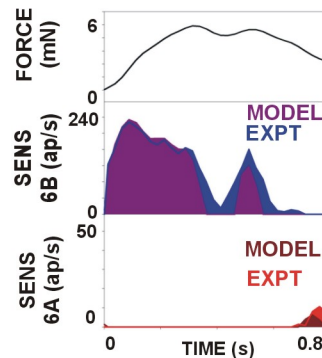
iii. DOWNHILL STEP 2



iv. DOWNHILL STEP 3

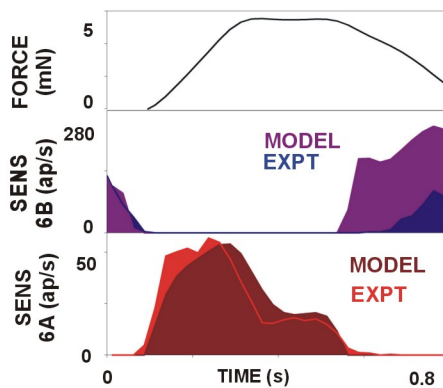


v. DOWNHILL STEP 4

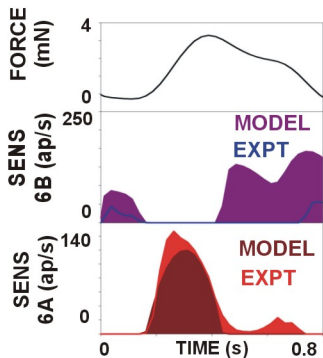


B UPHILL WALKING

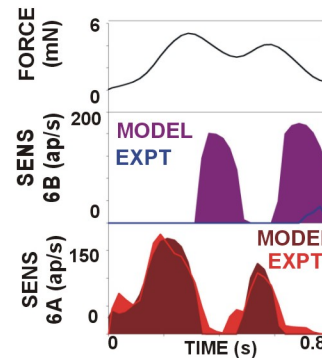
i. UPHILL MEAN STEP



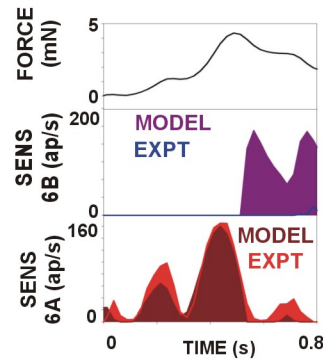
ii. UPHILL STEP 1



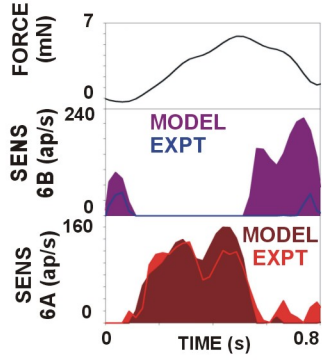
iii. UPHILL STEP 2



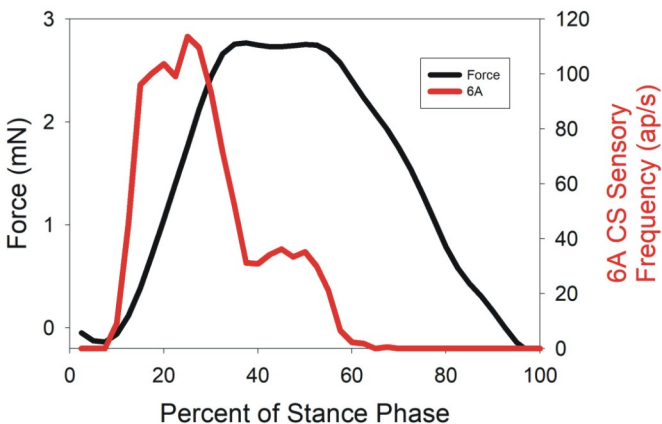
iv. UPHILL STEP 3



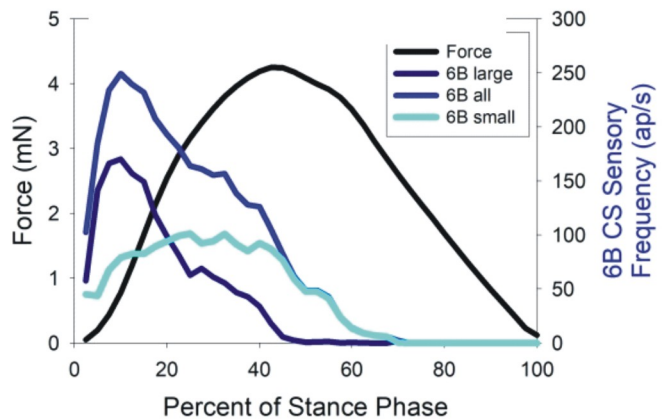
v. UPHILL STEP 4



A UPHILL WALKING



B DOWNHILL WALKING



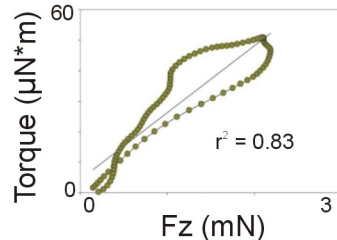
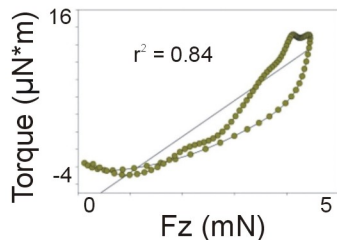
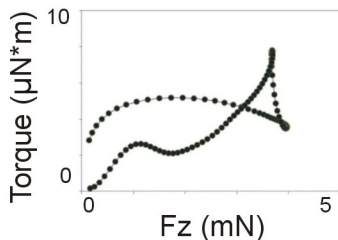
FT JOINT TORQUES VS REACTION FORCES

LEVEL

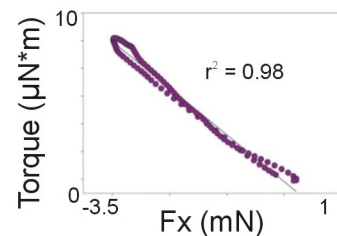
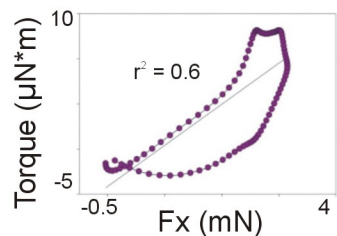
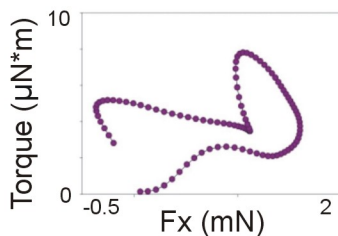
UPHILL

DOWNHILL

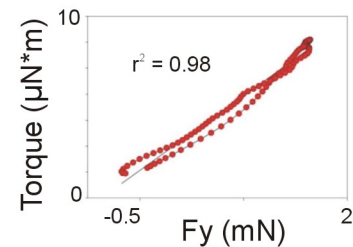
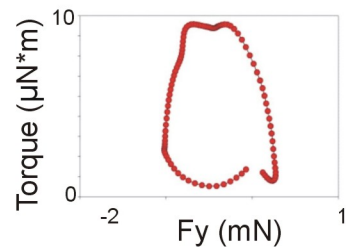
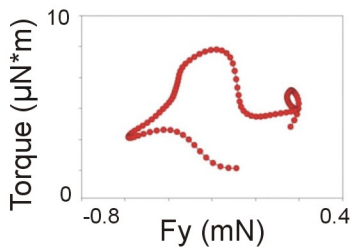
F_z



F_x

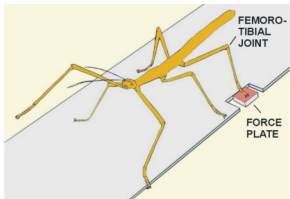


F_y

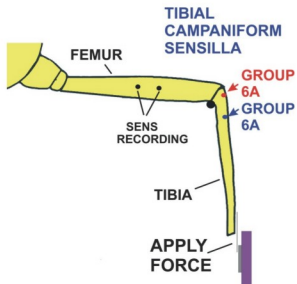


MECHANOSENSORY ENCODING OF FORCES IN WALKING UPHILL AND DOWNHILL: FORCE FEEDBACK CAN STABILIZE LEG MOVEMENTS IN STICK INSECTS

MEASURE FORCES AND JOINT TORQUES IN WALKING ON SLOPED SURFACES

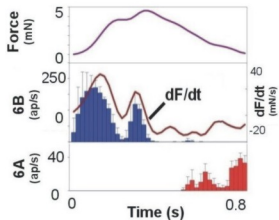


RECORD SENSORY DISCHARGES TO JOINT TORQUES IN WALKING DOWNHILL AND UPHILL

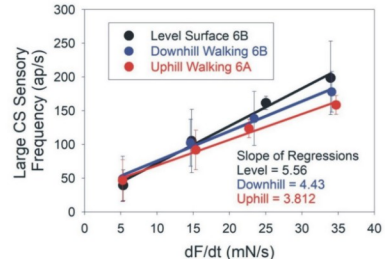


DIFFERENT RECEPTORS ARE ACTIVATED IN UPHILL AND DOWNHILL WALKING

GROUP 6B RECEPTORS FIRE IN WALKING DOWNHILL



SENSORY DISCHARGES SIGNAL THE RATE OF CHANGE OF FORCE (dF/dt) NOT THE FORCE LEVEL ON ALL SLOPES



CONCLUSIONS:

- 1) DIFFERENT GROUPS OF RECEPTORS ARE ACTIVATED IN WALKING UPHILL OR DOWNHILL
- 2) ALL RECEPTORS SIGNAL THE RATE OF CHANGE OF FORCE (dF/dt) EVEN AT HIGH LEVELS OF FORCE
- 3) THESE SIGNALS COULD AID IN STABILIZING LEG MOVEMENTS IN WALKING ON SLOPES