Mechanics of Slope Walking in the Cat: Quantification of Muscle Load, Length Change, and Ankle Extensor EMG Patterns

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Gregor, Robert J., D. Webb Smith, and Boris I. Prilutsky. Mechanics of slope walking in the cat: quantification of muscle load, length change, and ankle extensor EMG patterns. *J Neurophysiol* 95: 1397–1409, 2006. First published October 5, 2005; doi:10.1152/jn.01300.2004. Unexpected changes in flexor–extensor muscle activation synergies during slope walking in the cat have been explained previously by *1*) a reorganization of circuitry in the central pattern generator or *2*) altered muscle and cutaneous afferent inputs to motoneurons that modulate their activity. The aim of this study was to quantify muscle length changes, muscle loads, and ground reaction forces during downslope, level, and upslope walking in the cat. These mechanical variables are related to feedback from muscle length and force, and paw pad cutaneous afferents, and differences in these variables between the slope walking conditions could provide additional insight into possible mechanisms of the muscle control. Kinematics, ground reaction forces, and EMG were recorded while cats walked on a walkway in three conditions: downslope (−26.6 deg), level (0 deg), and upslope (26.6 deg). The resultant joint moments were calculated using inverse dynamics analysis; length and velocity of major hindlimb muscle-tendon units (MTUs) were calculated using a geometric model and calculated joint angles. It was found that during stance in downslope walking, the MTU stretch of ankle and knee extensors and MTU peak stretch velocities of ankle extensors were significantly greater than those in level or upslope conditions, whereas forces applied to the paw pad and peaks of ankle and hip extensor moments were significantly smaller. The opposite was true for upslope walking. It was suggested that these differences between upslope and downslope walking might affect motion-dependent feedback, resulting in muscle activity changes recorded here or reported in the literature.

INTRODUCTION

There is general consensus in the literature that a central pattern generator (CPG) located in the spinal cord is capable of producing a basic rhythmic pattern of alternating flexor (swing-related) and extensor (stance-related) muscle activity during locomotion (Brown 1914; Grillner 1981; Orlovsky et al. 1999; Rossignol 1996). The structure and function of this generator, however, have been the subject of extensive debate considering that, although the CPG can generate locomotor activity patterns in muscle nerves independently (as in fictive locomotion), movement-related input from muscle, skin, and joint afferents can strongly influence the magnitude, timing, and pattern of muscle activity and the duration of stance and swing phases during locomotion (Bouyer and Rossignol 2003; McCrea 1998; Pearson et al. 1998).

Recent results reported by Smith and colleagues (1998b) on muscle activity patterns during downslope walking demonstrated—surprisingly—that activity of the one-joint hip extensors (i.e., the anterior biceps femoris and anterior semimembranosus), although typical for locomotion on level ground, was not present during the stance phase of gait, whereas the one-joint hip flexor (i.e., the iliopsoas) was active instead. These observations could not be explained by existing models of the CPG and subsequently led Smith et al. (1998b; their Fig. 12) to propose modifications to the "unit burst" model of the CPG (Grillner 1981) to account for these new findings. Although this explanation accounts for the modifications in muscle synergies between up- and downslope walking, it has difficulty explaining differences in the magnitude and timing of EMG activity of major hind limb muscles between these slope conditions (Pearson 2000). As suggested by Pearson (2000) modifications of sensory input arising from changes in mechanical settings, such as limb posture and orientation and external load during slope walking, could also affect the intensity and timing of muscle activity either bypassing the CPG or/and through modification of its networks.

Indeed during slope walking one might expect a redistribution of ground reaction forces between the fore- and hindlimbs because of the changes reported in body orientation with respect to gravitational force (Smith et al. 1998a,b). For example, during downslope walking, the hindlimbs appear to be loaded less when compared with level or upslope walking and thus cutaneous output from the plantar surface of the paw and muscle force-dependent activation of group Ib afferents from hindlimb extensor muscles might be reduced. This redistribution of load between forelimbs and hindlimbs also might subsequently modify the activity of extensors and flexors (Bouyer and Rossignol 2003; Conway et al. 1987; Gorassini et al. 1994; Gossard et al. 1994; Guertin et al. 1995; McCrea et al. 1995; Pearson and Collins 1993). It is further expected that muscle length–dependent feedback signals from groups Ia and II afferents are enhanced in downslope walking and reduced in upslope walking compared with level locomotion (Abelew et al. 2000; Gregor et al. 2001), which could also affect the activity of hindlimb muscles (e.g., Eccles et al. 1957, 1958).

Although the differences in the mechanical conditions between slope and level walking and their potential effects on shaping muscle activity patterns appear important and have been presented sporadically in the literature (Abelew et al. 2000; Carlson-Kuhta et al. 1998; Gregor et al. 1999, 2001; Kaya et al. 2003; Pierotti et al. 1989; Smith et al. 1998b), muscle length, ground reaction

forces, and loads on the muscles have not been quantified for slope walking. This information can help determine the extent to which afferent signals might be modified in this type of locomotion and help explain the dramatic changes previously reported in the flexor/extensor synergy.

The aim of this study was to quantify differences in muscle length changes, ground reaction forces, and muscle loads between level, downslope, and upslope walking in the cat.

METHODS

Procedures

Five adult cats (*felis domesticus*) were selected on the basis of size (average 3.8 kg) and response to food reward. All cats were cared for in accordance with the American Physiological Society Animal Care Guidelines. Before data collection, both hindlimbs were shaved and marked with nontoxic reflective markers placed on the iliac crest, greater trochanter, approximate knee joint center, lateral malleolus, base of the fifth phalanx, and the distal end of the fifth digit.

Each cat was trained to walk within a Plexiglas-enclosed walkway with ground contact kinetics [ground reaction force (GRF)], center of pressure components, and joint position data collected for all level and slope walking trials according to the procedures outlined by Fowler et al. (1993). The entire walkway surface (2.5 × 0.4 m) was covered with a thin, nonslip mat (the mat over each force platform in the center of the walkway was isolated from the remainder of the walkway) and a trial was considered acceptable if the cat walked with an uninterrupted gait at constant speed through the walkway, and the hindlimb under study made contact with either one of the two force platforms (Bertec) independent of the surrounding surface. Confirmation of these acceptable conditions was made using one of two motion capture systems (Peak Performance Technology and Vicon) that recorded coordinates of the body markers at 120 field/s. Force and center of pressure data were sampled at 360 Hz. Food and affection were used to encourage each cat to walk on a level surface (0%) and two different slope conditions, i.e., ±50% (±26.6 deg).

Three of the five cats were surgically implanted with EMG electrodes. EMG fine-wire electrodes (Teflon-insulated multistrand, 100 μm diameter, Cooner Wire, Chatsworth, CA) were passed subcutaneously from a head-mounted multipin connector and implanted chronically in soleus (SO), lateral gastrocnemius (LG), medial gastrocnemius (MG), and/or plantaris (P) muscles. One cat had electrodes implanted in the SO and MG muscles in the left hindlimb; a second cat had electrodes implanted in the SO and LG muscles, bilaterally; and a third cat had electrodes implanted in the SO, MG, LG, and P in the right hindlimb. Each channel of EMG was sampled at a rate of 3,000 Hz and processed in a bandwidth between 30 and 1,000 Hz (3 dB). EMG signals were synchronized to the force plate and motion capture data with a common pulse.

Data analyses

HINDLIMB KINEMATICS.   A trial consisted of four to five step cycles but only the step cycle in which the cat hindlimb independently contacted the force plate was used in both the kinematic and inverse dynamics analyses (see following text). A total of 96 step cycles, one from each of 96 trials, was used in these analyses. The first paw liftoff (PO) was defined kinematically from motion capture data, whereas paw contact (PC) and the second paw liftoff were identified for each trial using the GRF components. These time points were subsequently used to define a complete step cycle and its swing and stance phases. Cycle periods were measured from successive paw liftoffs; stance phase duration was measured from PC to PO and expressed as a percentage of the step cycle. Because walking speed affects the magnitude and profile of gait, kinematic and kinetic pattern analyses were limited, a priori, to trials in which

the stance duration, which is related to speed (e.g., Goslow et al. 1973), was between 450 and 600 ms.

Hindlimb kinematics for the five-segment two-dimensional (2D) model, including the pelvis, thigh, leg, tarsals, and digits, were calculated from the segment endpoint markers mentioned above. Digitized coordinates were smoothed using a fourth-order, zero-lag Butterworth filter with the cutoff frequency based on 98.5% of the signal power. Knee joint position was extrapolated from the hip and ankle coordinates using thigh and shank segment lengths (Fowler et al. 1993; Goslow et al. 1973) obtained in postmortem measurements. (The recorded knee marker coordinates were not used for the kinematic analysis but used only for constructing initial stick figures to verify completeness of the recordings.) Linear and angular velocities and accelerations were calculated for each segment using the method of finite differences.

DETERMINATION OF MUSCLE-TENDON UNIT LENGTH AND VELOCITY. Muscle-tendon unit (MTU) lengths were calculated for nine muscles in the cat hindlimb for each of the 96 step cycles described earlier following the model presented by Goslow et al. (1973). In this geometric model, each muscle is represented as a straight line connecting the points of muscle attachment to the bone. The mean distances from the joint centers to the corresponding muscle origins and insertions were obtained by Goslow et al. (1973) in 28 cats (their Table 2) and used in this study. After calculating MTU lengths, MTU velocities were computed using the method of finite differences. The amount of MTU lengthening during the yield phase of stance (from PC to the peak stretch) as well as the peaks of MTU stretch velocities were obtained for further statistical analysis. The muscles included in this analysis were the SO, MG, LG/P, iliopsoas (IP), rectus femoris (RF), vastus lateralis (VL), semimembranosus anterior (SMA), biceps femoris posterior (BFP), and the semitendinosus (ST). The behavior of the anterior biceps femoris (ABF) muscle, one-joint hip extensor, was discussed extensively by Smith et al. (1998b) but the ABF muscle is not presented in the model proposed by Goslow et al. (1973) used in our analysis of muscle stretch. The Goslow model includes another one-joint hip extensor, SMA. Thus we estimated MTU stretch of one-joint hip extensors using the SMA muscle assuming the location of the SMA and ABF with respect to the hip joint in the sagittal plane was similar.

EXTERNAL FORCES APPLIED TO THE HINDLIMB.   Recorded ground reaction forces were smoothed using a fourth-order, zero-lag Butterworth filter with a cutoff frequency of 25 Hz. The normal (orthogonal to the walkway surface) and anterior–posterior (parallel to the walkway surface) components of the ground reaction force vector recorded during each trial were used to calculate the magnitude of the resultant force vector during the stance phase. The peaks of the resultant vector and the normal component and the negative and positive peaks of the anterior–posterior component were selected for further statistical analysis.

CALCULATION OF JOINT MOMENTS.   Joint moments of force represent the quantitative measure of the net action of the agonist and antagonist muscles at a joint assuming that the moment contributions of other tissues (such as ligaments and joint capsules) are negligible. Given relatively small coactivation between the major hindlimb antagonists in level and slope walking (Carlson-Kuhta et al. 1998; Smith et al. 1998b), flexor and extensor joint moments can be used to characterize loading of the flexor and extensor muscles.

Joint moments for the hip, knee, and ankle were calculated using Newtonian equations of motion and the methods of inverse dynamics. Conventions used for the hip, knee, and ankle joints were those reported by Fowler et al. (1993). The hindlimb was modeled as a five-segment (pelvis, thigh, shank, tarsals, and digits) planar, rigid body system. Segment mass, center of mass location, and the moment of inertia for each segment were calculated using regression equations derived by Hoy and Zernicke (1985). Extensor moments were as-

SO

LG

MG

P
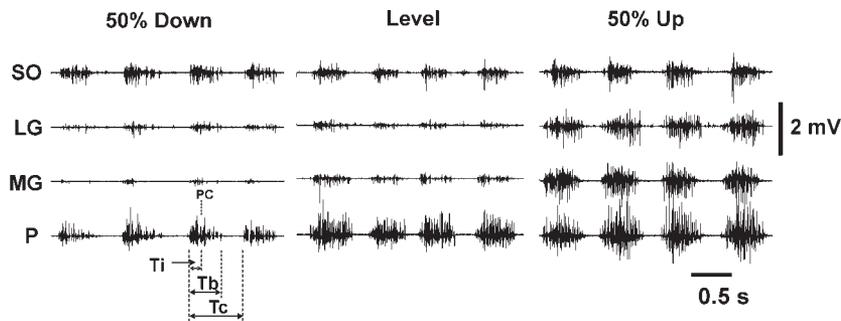
FIG. 1. Raw electromyogram (EMG) patterns for the soleus (SO), lateral gastrocnemius (LG), medial gastrocnemius (MG), and plantaris (P) during downslope, level, and upslope overground walking. Ti, the precontact activation time, is the time between EMG onset and paw contact (PC); Tb, the burst duration, is the time from burst onset to cessation; and Tc, the muscle burst cycle, is the time from burst onset to subsequent burst onset. These data are exemplar data for one cat.

signed positive values at each joint and their positive and negative peaks in the stance phase were measured.

EMG MAGNITUDE. Peak and mean EMG (burst integral/burst duration) were calculated and averaged across four to five step cycles in a total of 34 trials for all walking conditions of the three cats with implanted EMG electrodes. These 34 trials were selected from the original 96 trials that had a stance duration between 450 and 600 ms as determined from the ground reaction forces and used in the kinetic analysis. Mean and peak EMGs were studied because the mean represents the general level of recruitment in response to changes in environmental demands, whereas the peak is related to peak force during the individual step cycle. The effect of slope intensity on the mean EMG for each of the four muscles was tested for significance by first normalizing the mean EMG to the maximum value observed across all conditions within each cat (usually upslope walking) and then grouping the data for each muscle across cats. Peak EMG values were obtained from band-pass–filtered full-wave rectified signals and also compared for each muscle between all conditions across all cats.

Additionally, timing of the EMG bursts was analyzed for the steps in which the ground reaction forces were recorded in the three implanted cats (34 trials in total). The following timing parameters of the EMG burst were measured (see Fig. 1): EMG time onset with respect to PC [precontact activation time (Ti)], EMG burst duration [time of onset before PC to offset during stance (Tb)], and the muscle burst cycle [time between EMG onset and the onset of the next subsequent burst (Tc)]. These EMG timing parameters and the parameters of burst magnitude were used to investigate the effects of slope in a statistical analysis.

STATISTICAL ANALYSIS. To investigate the effects of slope conditions on characteristics of MTU length changes, ground reaction forces, joint moments, and EMG magnitude and timing in selected muscles, several t-tests were performed. Each of the above variables was tested for differences between level, upslope, and downslope conditions. The values of the variables obtained in every step cycle of each hindlimb and cat were used together in this analysis. In the preceding statistical tests the significance level was set at 0.05.

RESULTS

Step cycle kinematics

Although a relatively narrow range of stance durations was used, a priori, in the selection of a given trial for analysis to reduce the effects of locomotor speed, very small but significant differences in the average speed of progression [defined as the average speed of the iliac crest marker (I in Fig. 2) over the step cycle] were observed between slope conditions (see Table 1). The percentage of time devoted to stance (61.6–67.6%) and swing (32.3–38.4%), however, remained within the definition provided by Hildebrand (1976) of slow to moderate walking for all three conditions (see Table 1).

Following conventions established by Carlson-Kuhta et al. (1998) and Smith et al. (1998b) (Fig. 2, see their Fig. 3), three measures were used to describe hindlimb orientation at paw contact (PC) and paw liftoff (PO) for the three slope conditions. Hip height (Hh) during stance, anterior placement of the paw at contact (Da), and posterior placement of the paw at
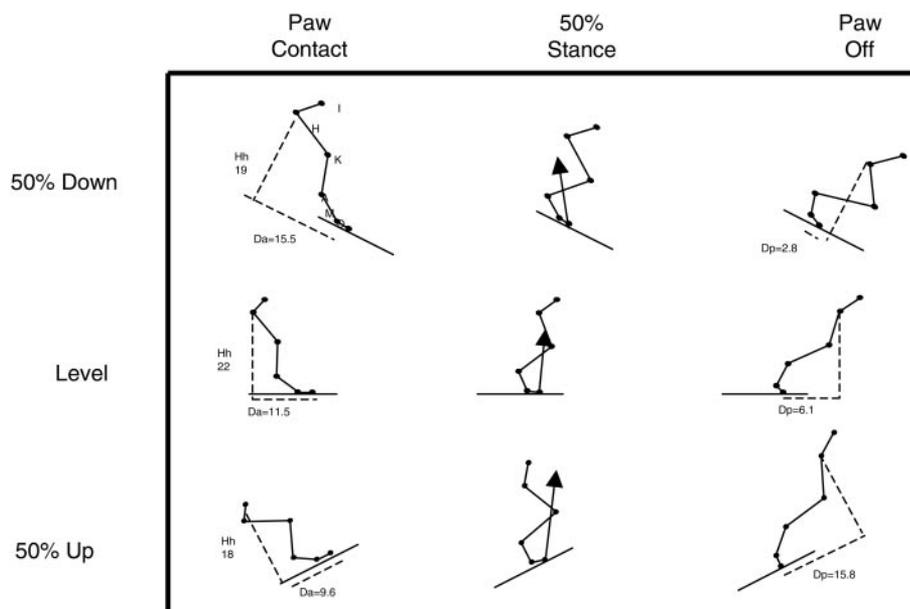
FIG. 2. Position of the hindlimb at PC, 50% stance, and paw off (PO) during downslope, level, and upslope overground walking. Letters I, H, K, A, and M denote marker positions on the iliac crest and the hip, knee, ankle, and metatarsophalangeal (MTP) joints, respectively. Hh is the line denoting the shortest distance from the hip to the walkway; Da and Dp correspond to the distance between Hh line and the digit marker at PC and PO, respectively, parallel to the walkway surface; the resultant ground reaction force vector (the arrow at 50% stance) is positioned with respect to the hindlimb at midstance. Data are exemplar data for one cat.

TABLE 1. *Average parameters of hindlimb orientation and cycle duration*

Kinematics	Downslope	Level	Upslope
Da, m	*†0.17 ± 0.01	†0.11 ± 0.02	0.09 ± 0.01
Dp, m	*†0.05 ± 0.03	†0.13 ± 0.03	0.18 ± 0.01
Hh, m	*†0.21 ± 0.01	†0.23 ± 0.02	0.20 ± 0.01
Speed, m/s	*†0.48 ± 0.09	0.54 ± 0.07	0.55 ± 0.05
% Stance	*†64.4 ± 2.0	†61.6 ± 2.9	67.6 ± 3.0
% Swing	*†35.6 ± 2.0	†38.4 ± 2.9	32.3 ± 3.0

Values are ±SD. *Denotes a value significantly different ($P < 0.05$) from the value calculated for level walking. †Denotes a value significantly different ($P < 0.05$) from the value calculated for upslope walking. Hindlimb orientation parameters Da, Dp, and Hh are defined in Fig. 2.

liftoff (Dp) were measured for all step cycles used in the kinetic analyses. In general, Da decreased significantly and Dp increased significantly ($P < 0.05$) as slope intensity progressed from downslope to level to upslope walking (Table 1). Changes in hip height were very small across the three conditions, although the differences were significant ($P < 0.05$; Table 1).
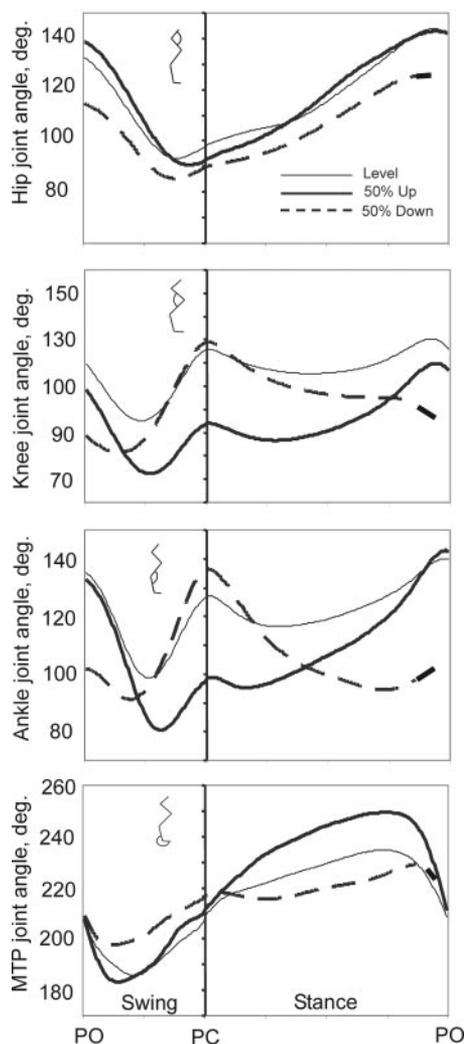
FIG. 3. Average angles for the hip, the knee, the ankle, and the MTP joints as a function of a normalized cycle time (in arbitrary units) during downslope, level, and upslope overground walking. PC, paw contact; PO, paw off. Hindlimb stick figures on each panel show joint angle definitions.

Angles for the hip, knee, ankle, and metatarsophalangeal (MTP) joints were calculated, time normalized, and averaged within and then across cats for each grade (Fig. 3). During all three slope conditions the hip generally flexed during swing and extended during stance. The primary difference between the downslope and upslope conditions was a more flexed range of motion during downslope walking and a more extended range of motion during both level and upslope walking. Patterns for both the knee and ankle joints during stance, however, although generally similar during swing (i.e., flexion and then extension) were very different across the three slope conditions. During stance, the signature displacement at the knee and ankle joints was generally flexion during downslope and extension during upslope walking. Knee and ankle patterns during level walking showed the well-described yield phase in early stance: i.e., flexion, followed by extension during propulsion in late stance. Finally, the MTP joint, similar to the three more proximal joints, flexed and extended during swing with the lowest range of motion during downslope walking. In stance, the MTP extended and then flexed with the smallest range of motion during downslope walking. Observed differences across slope conditions were consistent with the animals' general need to control its descent in downslope walking and propel its center of mass during level and more profoundly during upslope walking.

For comparison to the data presented by Carlson-Kuhta et al. (1998) and Smith et al. (1998b) the angle of peak flexion during swing (their F–E₁ angle), peak extension during stance (their Peak E angle), and the angle at paw contact (their PC angle) were highlighted (Table 2; see their Table 2). For the data reported here, few significant differences were observed between slope conditions for these three variables at the MTP joint, although slope had a significant effect in the majority of comparisons for the hip, knee, and ankle joints at these three points in the step cycle (Table 2).

Muscle-tendon unit length and velocity changes during the step cycle

Length change patterns for nine muscles in the cat hindlimb calculated for each experimental condition are represented by exemplar data from one cat and presented in Fig. 4A. A total of 96 step cycles were analyzed, i.e., the same step cycles used in the kinematic and kinetic analyses during the three slope

TABLE 2. *Average (SD) joint angle kinematic parameters*

Angle, deg	Joint	Downslope	Level	Upslope
Peak flexion angle (Swing)	Hip	83 ± 11	†91 ± 8	85 ± 7
	Knee	*83 ± 10	†98 ± 9	75 ± 11
	Ankle	*†89 ± 7	†102 ± 9	82 ± 6
	MTP	192 ± 15	190 ± 20	179 ± 10
Peak extension angle (Stance)	Hip	*†124 ± 7	†146 ± 7	140 ± 5
	Knee	†137 ± 12	†139 ± 18	115 ± 19
	Ankle	*140 ± 6	147 ± 9	144 ± 4
	MTP	*225 ± 10	245 ± 20	248 ± 6
Avoid @ paw contact	Hip	91 ± 10	†97 ± 9	88 ± 7
	Knee	†132 ± 17	†132 ± 17	95 ± 6
	Ankle	†133 ± 18	†130 ± 9	100 ± 6
	MTP	214 ± 8	214 ± 14	213 ± 5

Values are ±SD. *Denotes a value significantly different ($P < 0.05$) from the value calculated for level walking. †Denotes a value significantly different ($P < 0.05$) from the value calculated for upslope walking.
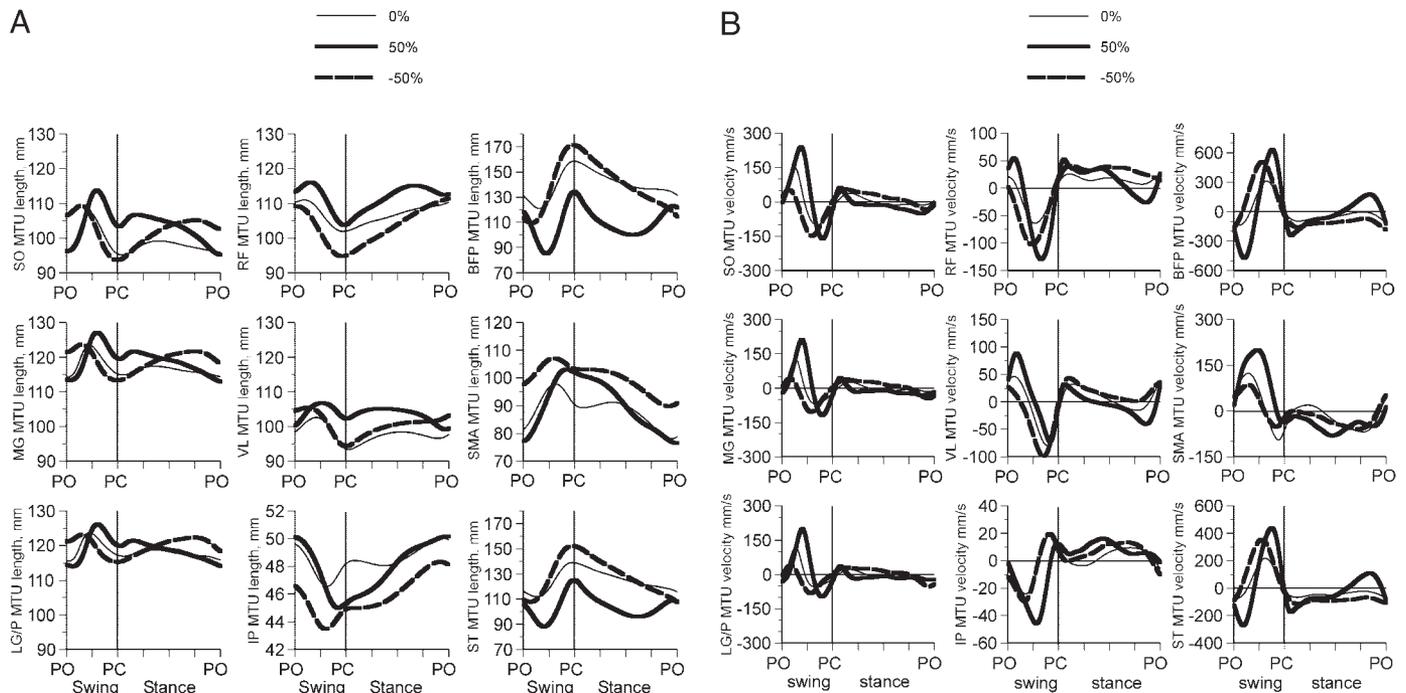
FIG. 4. *A*: length of hindlimb muscle-tendon units (MTUs) as a function of normalized cycle time (in arbitrary units) during representative trials of level (0%), upslope (+50%), and downslope (−50%) overground walking. PO, paw off; PC, paw contact. *B*: velocity of the MTUs as a function of normalized cycle time for the same 3 conditions as in *A*. MTUs presented are SO (soleus), MG (medial gastrocnemius), LG/P (lateral gastrocnemius/plantaris), IP (iliopsoas), RF (rectus femoris), VL (vastus lateralis), SMA (semimembranosus anterior), BFP (biceps femoris posterior), and the ST (semitendinosus). Positive velocity values correspond to MTU stretch, negative to shortening. These data are exemplar data for one cat.

conditions. Thirty-two trials were analyzed for level walking, 29 for the 50% downslope condition, and 35 for the 50% upslope condition.

Clearly the MTU length patterns for the three separate experimental conditions are different for each of the nine muscles (Fig. 4*A*). The statistical analysis revealed significant differences in the magnitudes of the MTU length change during stance between the slope conditions for all ankle and knee extensors selected for analysis (see Table 3). In five muscles (i.e., the SO, MG, LG/P, VL, and RF) the muscle-tendon units experienced a much greater magnitude of stretch during stance in downslope walking compared with that of both level and upslope walking ($P < 0.05$).

Interestingly, the iliopsoas (IP) muscle, a primary one-joint hip flexor, showed no significant difference in stretch magnitude between downslope and level walking; however, it had

slightly larger ($P < 0.05$) stretch in the upslope condition (Table 3; Fig. 4*A*). The one-joint hip extensor, anterior semimembranosus (SMA), similar in function to the anterior biceps femoris, and the two-joint hip extensors and knee flexors biceps femoris posterior (BFP) and semitendinosus (ST) mostly shortened during stance (Table 3).

Peaks of MTU stretch velocities of the ankle extensors during the yield phase of stance were consistent, in general, with those of MTU stretch (exemplar data in Fig. 4, *A* and *B*; Table 4). In particular, the peaks of MTU stretch velocities of the ankle extensors were larger in downslope walking [$P < 0.05$, range from 69 mm/s (SD 11) to 49 mm/s (SD 9) for SO, MG, LG/P] than in level [38 mm/s (SD 14) to 28 mm/s (SD 10)] or in upslope walking [32 mm/s (SD 17) to 23 mm/s (SD 15)]. However, there was no significant difference in the peaks of MTU stretch velocity of the knee extensors between the

TABLE 3. *Average stretch magnitudes (in mm) in nine hindlimb muscles during stance*

Muscle	Downslope	Level	Upslope
SO	*†12.1 ± 1.8	†3.1 ± 1.3	1.3 ± 0.9
MG	*†9.9 ± 1.8	†2.3 ± 1.0	1.0 ± 0.7
LG/P	*†8.8 ± 1.9	†2.0 ± 0.8	0.9 ± 0.6
IP	†4.1 ± 0.9	†4.4 ± 0.9	5.1 ± 0.7
RF	*†15.7 ± 1.4	†10.2 ± 1.6	9.4 ± 1.3
VL	*†6.5 ± 1.2	†2.1 ± 1.0	1.1 ± 0.5
SMA	0.1 ± 0.2	—	—
BFP	0.2 ± 0.1	0.8 ± 0.9	2.5 ± 4.3
ST	*0.1 ± 0.1	0.9 ± 0.4	—

Values are ±SD. *Denotes a value significantly different ($P < 0.05$) from the value calculated for level walking. †Denotes a value significantly different ($P < 0.05$) from the value calculated for upslope walking.

TABLE 4. *Average stretch velocity magnitudes (in mm/s) in nine hindlimb muscles during stance*

Muscle	Downslope	Level	Upslope
SO	*†69 ± 11	38 ± 14	32 ± 17
MG	*†55 ± 10	29 ± 13	26 ± 16
LG/P	*†49 ± 9	28 ± 10	23 ± 15
IP	15 ± 3	16 ± 4	16 ± 2
RF	41 ± 10	41 ± 12	41 ± 6
VL	†36 ± 9	37 ± 22	28 ± 15
SMA	†47 ± 21	—	—
BFP	*†26 ± 20	†49 ± 28	129 ± 22
ST	†19 ± 13	†27 ± 19	—

Values are ±SD. *Denotes a value significantly different ($P < 0.05$) from the value calculated for level walking. †Denotes a value significantly different ($P < 0.05$) from the value calculated for upslope walking.

three walking conditions (exception: significantly larger stretch velocity in VA between down- and upslope conditions). There were no differences in IP stretch velocity found between the three slope conditions (Table 4).

Ground reaction forces during slope walking

Average ground reaction force components for all 96 trials used in the joint moment calculation (Fx and Fz), together with the magnitude of the average resultant force (Fr), are presented for all three conditions in Fig. 5 with the results of a statistical analysis on peak values presented in Table 5. Clearly, the orientation and magnitude of the load on the hindlimb are different during the three walking conditions (see exemplar data for midstance in Fig. 2). Compared with level walking, upslope walking required a more anteriorly directed force vector (Fr) during stance, i.e., a significantly larger anterior shear force (+Fx, $P < 0.05$) and a significantly higher normal force (Fz), orthogonal to the surface of the walkway ($P < 0.05$; Fig. 5; Table 5). In contrast, downslope walking required a more posteriorly directed force vector during the entire stance period compared with level walking, i.e., a significantly larger posterior shear force during the initial braking phase ($P < 0.05$) and a significantly lower normal force ($P < 0.05$; Fig. 5; Table 5). Peak resultant ground reaction forces, representing the peak resultant load on the hindlimb, were also significantly higher ($P < 0.05$) for upslope compared with those of both the level and downslope walking conditions (Fig. 5; Table 5).

Joint moments during the step cycle

Changes in muscular load as a function of slope (50% upslope, 50% downslope, and level walking at 0% slope) are described using joint moment calculations. Although the MTP joint is significant to any discussion of muscle activity intrinsic to the tarsals and digits (Trank and Smith 1996), we have concentrated on the three more proximal joints in the kinetic analysis because these joints are most important to limb propulsion during locomotion. In the absence of ground reaction forces during swing, peak moment magnitudes were substantially lower than those during stance (Fig. 6). During stance, changes in slope had an appreciable effect on both the pattern and magnitude of the moments at each of the three major joints: hip, knee, and ankle. A total of 96 separate step cycles were analyzed for kinematic and kinetic analyses, the same number and distribution across conditions as reported for the muscle length changes.

ANKLE MOMENTS.   At PC, an extensor moment increased precipitously in all conditions for all cats (Fig. 6). The peak extensor moment occurred in early stance for all conditions and was significantly higher ($P < 0.05$) in upslope walking than during level walking, significantly higher during level than during downslope walking, and significantly smaller during downslope than during upslope walking ($P < 0.05$; Table 6). Peak ankle flexor moments at the end of stance were close to zero, and in a few cases were negative, indicating a dorsiflexor moment.

KNEE MOMENTS.   In all conditions a knee flexor moment occurred in early stance and was followed by a knee extensor
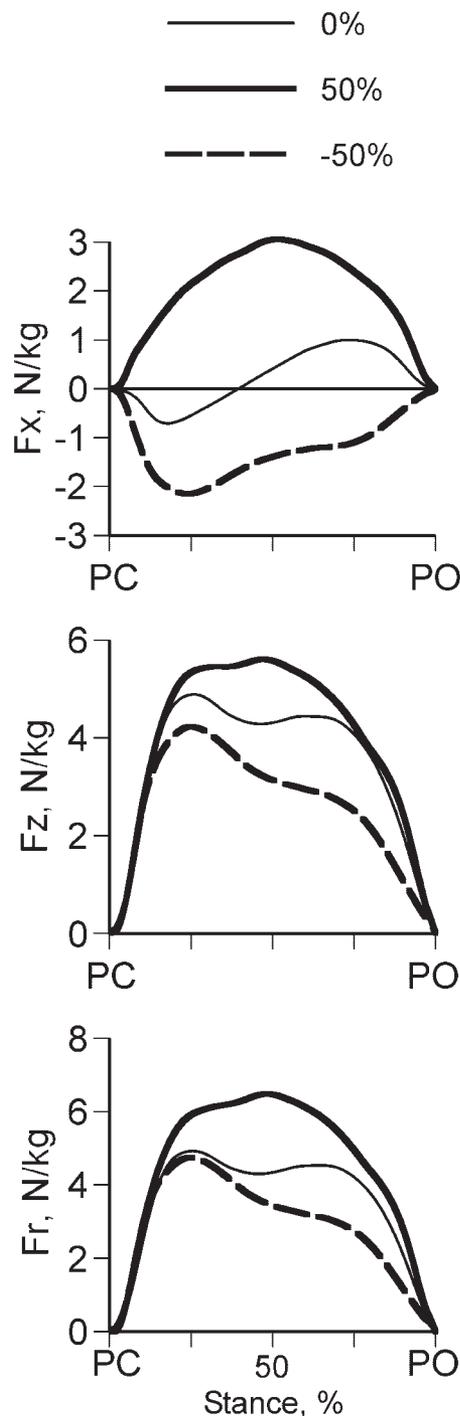
FIG. 5.   Averaged ground reaction forces as a function of normalized stance time (in arbitrary units) during level (0%), upslope (+50%), and downslope (−50%) overground walking. PC, paw contact; PO, paw off. Fx, anterior/posterior shear force along the walkway surface; Fz, force component perpendicular to the walkway surface; Fr, resultant force.

moment for the remainder of the stance (Fig. 6). The magnitude of the peak flexor moment increased as the slope increased with the lowest values observed during the downslope and level conditions. The peak flexor moment observed for the upslope condition was significantly greater than that of either of the two other conditions (Table 6; $P < 0.05$). Peak knee extensor moments were always observed in late stance and, in

TABLE 5. *Average peak ground reaction forces (in N/kg) during stance*

Force Component	Downslope	Level	Upslope
Fx	*−2.3 ± 0.6	−0.8 ± 0.4 †1.2 ± 0.4	3.2 ± 0.8
Fz	*†4.6 ± 1.1	†5.3 ± 1.2	6.0 ± 1.3
Fr	†5.1 ± 1.3	†5.4 ± 1.2	6.8 ± 1.7

Values are ±SD. *Denotes a value significantly different ($P < 0.05$) from the value calculated for level walking. †Denotes a value significantly different ($P < 0.05$) from the value calculated for upslope walking. Fx, Fz, and Fr are the anterior–posterior, normal, and resultant ground reaction force.

contrast to the knee flexor moment, they were not significantly different between downslope and upslope walking (Table 6). However, the peak knee extensor moment during level walking was significantly smaller ($P < 0.05$) than both the downslope and upslope values. Additionally, the average duration of the flexor moment in early stance was related to slope intensity; i.e., the zero crossing from flexor to extensor was significantly later in stance during the upslope walking compared with that of either the level or the downslope conditions ($P < 0.05$, Fig. 6).

HIP MOMENTS. At paw contact and during early stance an extensor moment occurred during all slope conditions (Fig. 6). Peak magnitudes changed significantly with slope ($P < 0.05$) with peak values during level walking significantly greater than during downslope walking and peak values during upslope walking significantly greater than during level walking (Table 6; $P < 0.05$). On average, the change from an extensor moment to a flexor moment occurred at 25% of stance during downslope walking, at 60% of stance during level walking, and at 75% of stance during upslope walking (Fig. 6). The percentage of stance at which the hip extensor moment changed sign was significantly different ($P < 0.05$) between the downslope, level, and upslope conditions. Additionally, the hip flexor moment during late stance was significantly greater during downslope walking than that during both level and upslope walking (Table 6; $P < 0.05$). Finally, peak flexor moments for upslope walking were significantly greater than the peak flexor moments during level walking (Table 6; $P < 0.05$).

Ankle extensor EMG during slope walking

EMG MAGNITUDE. The effect of slope on normalized peak and mean EMG is illustrated in Fig. 7. The SO peak and mean EMG increased significantly ($P < 0.05$) during upslope walking compared with those during both level and downslope walking. Moreover, the SO peak and mean EMG during the downslope walking were significantly larger than those observed during level walking (Fig. 7).

Peak and mean EMG in the ankle extensors and knee flexors—the MG, LG, and P—also increased significantly ($P < 0.05$) during upslope walking compared with that during level and downslope walking (Fig. 7). The peak and mean EMG of the MG and P decreased significantly ($P < 0.05$) during downslope walking compared with that during walking on a level surface (Fig. 7), whereas peak and mean EMG for the LG showed no significant difference between level and downslope walking.

EMG TIMING. Precontact activation time (Ti; Fig. 1), commonly referred to as the E1 burst duration, was found to be slope dependent in all muscles studied (Fig. 8; $P < 0.05$) with Ti significantly longer in all four muscles ($P < 0.05$) during downslope walking compared with that during both level and upslope walking. The duration of Ti in the MG and LG muscles, however, was not significantly different in the upslope compared with that in the level walking condition (Fig. 8).
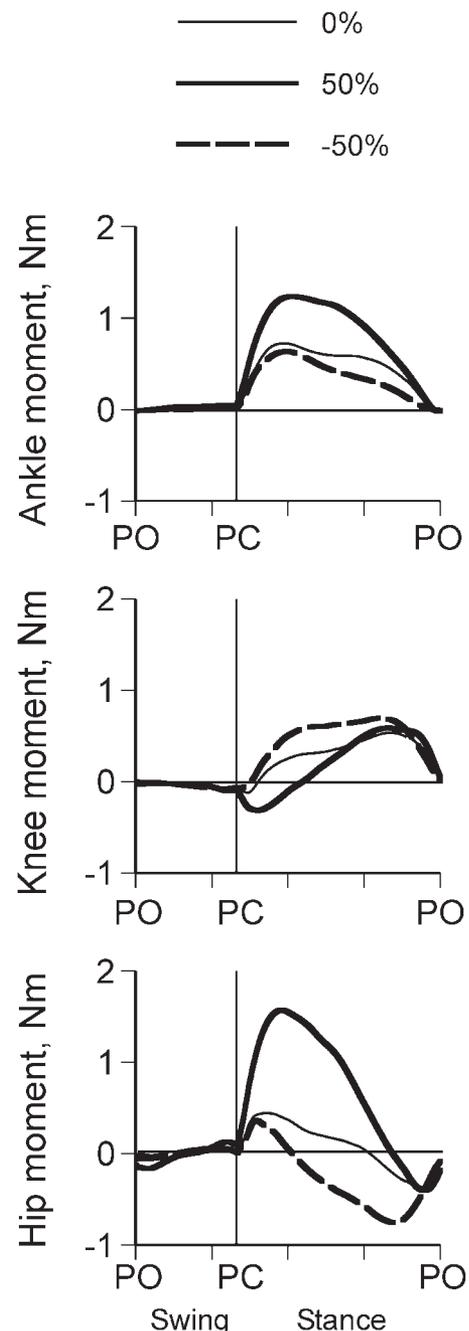
FIG. 6. Averaged joint moment patterns for hip, knee, and ankle joints as a function of normalized cycle time (in arbitrary units) during level (0%), upslope (+50%), and downslope (−50%) overground walking. PO, paw off; PC, paw contact. Positive values correspond to extensor moments, negative to flexor moments.

TABLE 6. *Average peak joint moments (in Nm) during stance*

Joint	Downslope	Level	Upslope
Ankle	*†0.52 ± 0.18	†0.75 ± 0.12	1.24 ± 0.2
Knee	*†−0.08 ± 0.03	†−0.12 ± 0.07	−0.28 ± 0.2
	*0.71 ± 0.11	†0.58 ± 0.23	0.70 ± 0.19
Hip	*†−0.80 ± 0.15	†−0.37 ± 0.12	−0.48 ± 0.13
	*†0.24 ± 0.18	†0.41 ± 0.2	1.39 ± 0.4

Values are ±SE. *Denotes a value significantly different ($P < 0.05$) from the value calculated for level walking. †Denotes a value significantly different ($P < 0.05$) from the value calculated for upslope walking. Positive values correspond to extensor moments; negative values, to flexor moments.

Although the SO burst duration (Tb in Fig. 1) was independent of slope (Fig. 8), the MG burst duration was significantly affected by slope, i.e., the values for downslope and level walking were significantly smaller ($P < 0.05$) than the value for upslope walking (Fig. 8). LG burst durations for level and upslope walking were not statistically different but the burst duration for downslope walking was significantly smaller than the duration for upslope walking (Fig. 8; $P < 0.05$). Finally, there was no significant difference between burst durations for the level and upslope conditions for the P muscle, although both conditions were significantly greater than the burst durations measured for downslope walking.

The muscle burst cycle (Tc in Fig. 1) was found to be independent of slope in all four muscles, which is likely explained by the fact that the relatively similar stance times were used in the analysis (Table 1). Values varied between 810 and 870 ms (average = 840 ms) across the four muscles and three slope conditions.
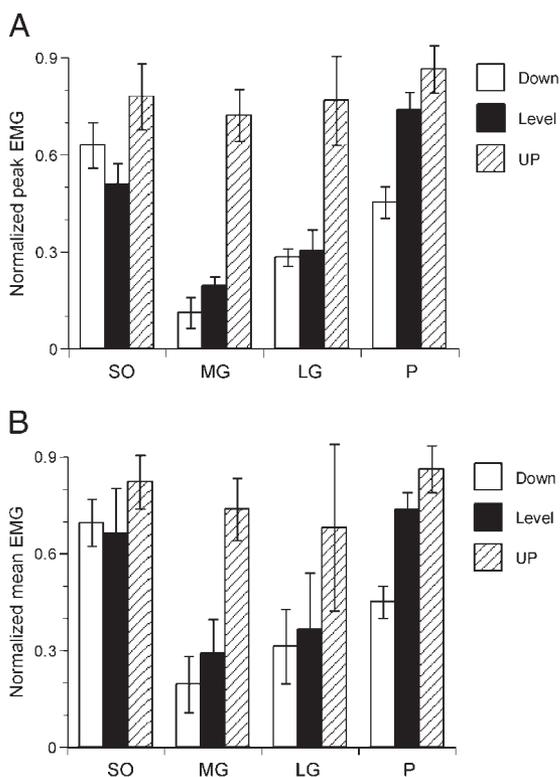
FIG. 7. Normalized peak (*A*) and mean values (*B*) of EMG bursts during level (0%), upslope (+50%), and downslope (−50%) overground walking for the SO, MG, lateral gastrocnemius (LG), and plantaris (P) muscles.
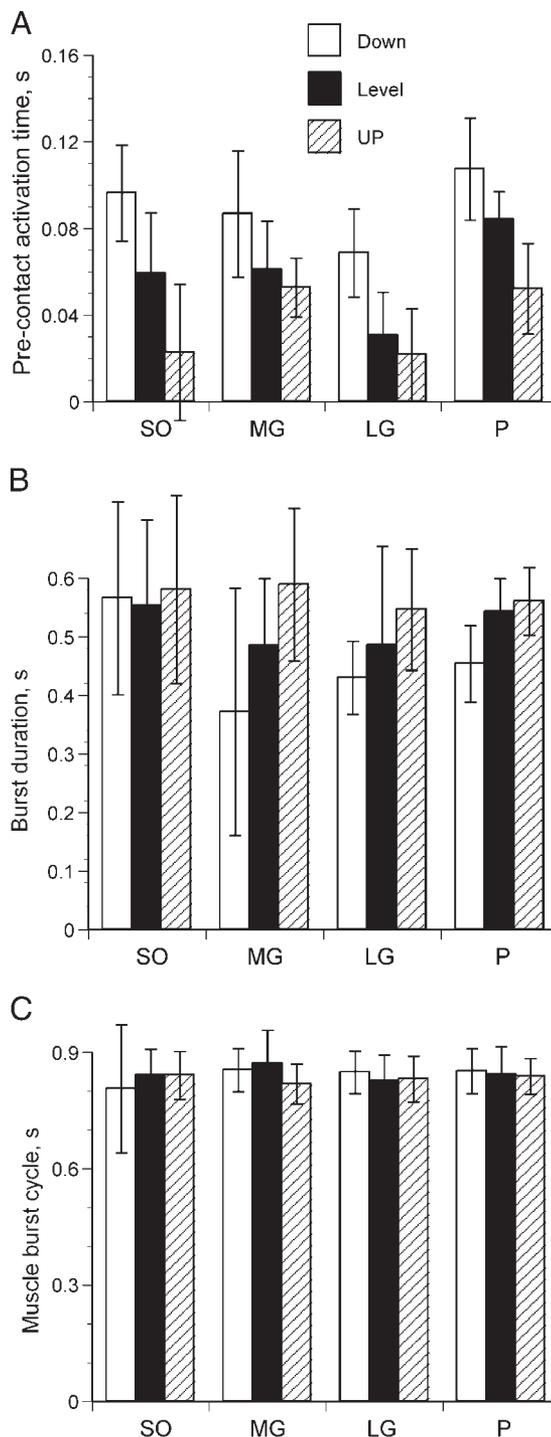
FIG. 8. Timing of EMG during level (0%), upslope (+50%), and downslope (−50%) overground walking for the SO, MG, LG, and P muscles. Ti, the precontact activation time, is the time between EMG onset and PC; Tb, the burst duration, is the time from burst onset to cessation; and Tc, the muscle burst cycle, is the time from burst onset to subsequent burst onset (see Fig. 1).

DISCUSSION

The aim of this study was to quantify potential differences in muscle length and velocity changes, ground reaction forces, and muscle loads between downslope, level, and upslope walking in the cat. The rationale for investigating these mechanical variables lies in their relationship to muscle and cutaneous afferent signals, which are known to modulate

motoneuron output. These data may then help explain, for example, the unexpected flexor–extensor synergies reported for slope walking (Smith and Carlson-Kuhta 1995; Smith et al. 1998b). Specifically, muscle length and velocity changes might indicate the activity of group Ia and II afferents originating from muscle spindles, whereas the force applied to the paw pad, the activity of cutaneous receptors, and the joint moments relate to loading of the agonist muscles and might indicate the activity of group Ib afferents originating from Golgi tendon organs. Agonists are considered muscles whose generated moment at the joint has the same sign as the resultant joint moment (Andrews and Hay 1983).

Although we focused on muscle length and force feedback and feedback from cutaneous paw pad receptors, clearly there are other forms of sensory input that may influence motoneuron activity. For example, the vestibulospinal reflexes (arising from otolith membrans of the utriculus and sacculus, which sense head orientation with respect to the gravitational vertical) and the neck reflexes (arising from proprioceptors of dorsal neck muscles, which sense relative head position with respect to the body) could modulate hindlimb muscle activity (Wilson and Peterson 1981). These afferent signals seem especially relevant for the control of slope walking because head position might depend on slope (Gottschall et al. 2005). In this discussion, however, we will focus on muscle length– and force-dependent input and input from cutaneous paw pad receptors in full recognition of the potential afferent input from other sources.

The results of this study show that *1)* kinematic patterns of hindlimb joints respond to changes in slope in a manner similar to those reported in the literature, *2)* muscle-tendon unit (MTU) length changes and peak stretch velocities during the stance phase are largest in downslope and smallest in upslope walking, *3)* forces applied to the paw pad are largest in upslope and smallest in downslope walking, *4)* peaks of the ankle and hip extensor moments and knee flexor moments are the largest in upslope and smallest in downslope walking, and *5)* peak of the hip flexor moment is the largest in downslope walking. In the following discussion we present the similarities between our kinematic and EMG data and those described in previous detailed reports for slope walking (Carlson-Kuhta et al. 1998; Smith et al. 1998b). Further, we discuss the potential consequences of the differences observed in selected mechanical variables between the three walking conditions on muscle and cutaneous afferent signals and on their potential effect on the modulation of locomotor muscle activity.

Kinematic response to slope walking

Reports in the literature suggest there are significant changes in posture and limb orientation in response to changes in slope during walking (Carlson-Kuhta et al. 1998; Higham and Jayne 2004; Smith et al. 1998b). The data reported here exemplify these changes and are similar to those reported by Smith et al. (1998b) for downslope walking (see their Fig. 5, i.e., joint angle patterns for all four joints) and Carlson-Kuhta et al. (1998) for upslope walking (see their Fig. 5, i.e., joint angle patterns for knee and ankle joints; no data are presented for the 50% condition for the hip and MTP joints). Data reported here regarding limb position at certain points in the step cycle as well as stance and swing durations are also similar to the

detailed reports in the literature (Carlson-Kuhta et al. 1998; Smith et al. 1998b). These findings suggest that the kinematic response of the cat to changes in slope during walking is consistent for the different populations reported.

For example, in all reports, Da always decreases and Dp always increases when slope changes progress from downslope to level to upslope walking. Hip height is smaller during both downslope and upslope compared with level walking and stance time, regardless of small changes in cycle period or walking speed, ranges from 61.6 to 67.6% of the gait cycle. Whereas Smith and colleagues (Carlson-Kuhta et al. 1998; Smith et al. 1998b) showed cycle periods to vary as a function of slope (see Table 1 in both reports), when step cycles within a more narrow range of stance times are selected for analysis, as in this study (i.e., between 450 and 600 ms), cycle period showed limited variability. This observation is supported by both the muscle EMG cycle period (Tc, Fig. 8) and the cycle periods projected from the monitored stance time and corresponding percentage of the step cycle.

In addition to the joint angle pattern similarities (Carlson-Kuhta et al. 1998; Smith et al. 1998b) joint position during selected points in the step cycle were similar to that in previous reports (Carlson-Kuhta et al. 1998; Smith et al. 1998b; Table 2 in both reports). Differences in the data between these previous reports and our study averaged approximately 10% for all data points reported (Table 2) with the greatest differences reported for downslope walking (about 14%) and the smallest differences reported for level walking (about 7%). Collectively, these data suggest that the response to changes in slope during walking in the cat is fairly robust and that any changes in neural control in response to these environmental changes may be similar across populations.

Potential effects of muscle length and velocity differences between the slope walking conditions on EMG locomotor patterns

Whereas Smith and colleagues used EMG and joint kinematics to support their proposed modifications to the Grillner model (1981) no estimates of muscle length were made and thus no discussion of potential length-dependent input was presented. Recordings of spindle afferent activity in cats walking on a level surface (Loeb et al. 1985a,c; Prochazka and Gorassini 1998; Severin 1970; Severin et al. 1967) have demonstrated a modest relationship between the activity of individual group Ia and II afferents and changes in the MTU length and velocity. The lack of unity in this relationship has been attributed, in part, to the effects of fusimotor, i.e., gamma activation (Loeb and Hoffer 1985b; Severin 1970), presynaptic inhibition (Cote and Gossard 2003; Menard et al. 2003), and the fact that muscle fascicle length and velocity and therefore spindle length and velocity may differ from those of the MTU, e.g., compliance in the tendon and aponeurosis (Griffiths 1991; Hoffer et al. 1989). Regarding the effect of these structures on strain distribution between muscle and connective tissue, preliminary data on muscle fascicle length changes during slope walking (Maas et al. 2005) suggest that the relationship between MTU and muscle fascicle length change is influenced by tendon compliance and muscle architecture. Using sonomicrometry methods described by Biewener et al. (1998), Maas et al. (2005) presented data suggesting the relationship between

fascicle and MTU length changes is different for the MG and SO during level and upslope walking. However, during downslope walking both muscles showed simultaneous increases in fascicle length and MTU length, i.e., when the MTU stretched the fascicles stretched, and the fascicle stretch of both SO and MG was much greater during downslope than that during level and upslope walking (Maas et al. 2005).

Given the parallel between MTU and fascicle length changes during downslope walking, the significantly larger MTU stretch magnitude of the ankle and knee extensors ($P < 0.05$, Table 3) and the significantly larger stretch velocity of MTU and muscle fascicles of the ankle extensors ($P < 0.05$, Table 3; Maas et al. 2005) during the stance phase, and assuming that gamma activation and presynaptic inhibition are not very different between the walking conditions studied here, one should expect greater activation of group Ia and II afferents of ankle, knee, and hip extensors and thus enhanced muscle activation during downslope walking (McCrea et al. 1995). Enhanced muscle activation in downslope walking, however, was not the case in all muscles studied. The SO and RF increased stretch (Table 3) and increased activity from level to downslope walking (Fig. 7; Smith et al. 1998b, their Fig. 8), whereas the MG and LG/P increased stretch (Table 3) and decreased activity (Fig. 7). Stretch of the IP was small and independent of slope (Table 3) but EMG increased in the IP from level to downslope walking (Smith et al. 1998b, their Fig. 8). Clearly the effect of stretch and the related effect of spindle afferents on EMG patterns in downslope walking remain open to debate.

In contrast, extensor muscle activity significantly increased during upslope walking compared with that during downslope and level conditions (Figs. 1 and 7; Carlson-Kuhta et al. 1998, their Figs. 8 and 9) despite very small stretch and even shortening of some extensors in early stance (Fig. 4, Table 3; Maas et al. 2005). It appears therefore that length-dependent proprioceptive feedback cannot entirely explain all of the changes in activation magnitude of the extensor muscles in the stance phase of slope walking either in this report or those data reported by Smith and colleagues. In fact, the increased stretch and activation in the SO during downslope compared with that during level walking suggest the length-dependent input enhances SO activity, whereas the data from the MG and LG/P (increased stretch in downslope walking) suggest length-dependent input does not enhance their activity (their EMG activity is the smallest in this condition).

Furthermore, Smith and colleagues reported that the anterior biceps femoris (ABF) and anterior semimembranosus (ASM) were inactive during downslope walking when the slope increased beyond about 15% slope. This finding was unexpected because the iliopsoas (IP), a hip flexor, was active in stance and the ABF and ASM, one-joint hip extensors, were not. Smith et al. (1998b) modified the Grillner model (1981), suggesting that the absence of EMG in the two single-joint hip extensors was a result of inhibition from the hip flexor center and mediated by length-dependent reciprocal inhibition from hip flexors (i.e., IP). Data presented here suggest this may not entirely be the case. Because the IP lengthens about the same in both level and downslope walking (Fig. 4) and because Smith et al. reported no inhibition during level walking, Smith et al.'s modification of the Grillner model (1981) cannot fully explain the absence

of EMG in the ABF and ASM, leaving the issue open to further study.

Finally, the EMG onset time (Ti, Fig. 1) appears to be closely related to the leg position at PC: the more extended at paw contact the hindlimb is (Table 1, Da), the earlier the ankle extensor activity starts with respect to stance (Figs. 1 and 8). As a result, precontact activation time decreased from about 70–110 ms in downslope, to 30–85 ms in level, and to 20–55 ms in upslope walking (Fig. 8). Position-sensitive afferents from the hip (Grillner and Rossignol 1978; Hiebert et al. 1996) and ankle flexors (Hiebert et al. 1996) have been suggested to initiate the stance-swing transition in walking cats. Similar length-sensitive afferents of hindlimb flexors could contribute to initiating the flexor–extensor phase transition because the MTU length of some of them (BFP and ST, knee flexors–hip extensors) reaches peak values at paw contact (Fig. 4B). (See experiment suggested in *Activity and proprioception of two-joint muscles*.)

Potential effects of cutaneous afferent signals from paw pad

Removing cutaneous feedback from the mechanoreceptors in the cat paw pad by anesthesia or neurectomy does not seem to affect locomotor patterns in normal walking (Duysens and Stein 1978; Forssberg et al. 1977). However, motor patterns seem to be affected in more demanding tasks (Bouyer and Rossignol 2003). Differences in ground reaction forces applied to the paws between different slope conditions (Fig. 5; Table 5) then might influence generated muscle activity. Indeed, the effects of stimulation of mechanoreceptors in the paw pad on regulation of muscle activation in locomotion are consistent in general with the effects of activating Ib tendon receptors. In particular, cutaneous stimulation of the pad receptors during stance prolongs and enhances extensor muscle activity (Duysens and Pearson 1976; Guertin et al. 1995; Loeb 1993; Schomburg et al. 1998). A potentially higher activation of pad skin receptors in upslope walking is thus consistent with enhanced activation of extensors compared with that in level walking (Figs. 1, 7, and 8; Carlson-Kuhta et al. 1998). Correspondingly, the reduced load on the hindlimbs in downslope walking, when larger loads are placed on the forelimbs, might contribute to the reduction of the stance duration and magnitude of extensor muscle activation (Figs. 1, 7, and 8; Smith et al. 1998b).

Potential effects of changes in muscle force–dependent afferent signals

At rest, activation of extensor Ib tendon force receptors causes inhibition of extensor motoneurons (Jami 1992). However, during the stance phase of locomotion, activation of the same receptors (by low-threshold <2 T electrical stimulation) leads to prolongation and enhancement of extensor activation (positive force feedback: Burke 1999; Gossard et al. 1994; McCrea 1998; McCrea et al. 1995; Pearson 1995; Pearson and Collins 1993; Pearson et al. 1992; Prochazka et al. 1997; Whelan and Pearson 1997; Whelan et al. 1995). This observation is attributed to the reconfiguration of group Ib reflexes during locomotion as opposed to rest.

The significant increase in peaks of the resultant extensor moments at the ankle, knee, and hip during upslope walking

(Fig. 6; Table 6) indicates greater forces exerted by the extensor muscles and thus stronger force-dependent afferent signals from them. A significant increase in activation of major extensors during upslope walking as opposed to level walking (Fig. 7; Carlson-Kuhta et al. 1998, their Figs. 8 and 9) is consistent with the notion of positive-force feedback according to which a greater load on extensors leads to their stronger excitation and prolongation of the extensor phase. Although Carlson-Kuhta et al. (1998; their Table 1) report no increase in stance duration with change in upslope grade (level to 100% upslope), interpretation of those data remains unclear because the cycle period decreased, suggesting the speed of walking actually increased. In contrast, when stance duration was constrained within a more narrow range, i.e., 450–600 ms (Table 1), a significant increase in stance duration was observed during upslope walking than that during level walking (Table 1). These data also support the notion of positive force feedback as discussed above.

Finally, the surprising results of Smith et al. (1998b) concerning the increase in stance-related activity of hip flexors (iliopsoas and rectus femoris), the corresponding reduction in stance-related activity of hip extensors (anterior biceps femoris, anterior semimebranosus), and a virtually constant activation magnitude of knee extensors (vastus lateralis) as the grade of downslope walking increased are consistent with changes in peaks of hip flexor and knee extensor moments reported here (Fig. 6; Table 6) and was predicted by Smith et al. (1998b). The hip flexor moments are exerted during the last 2/3 of stance at −50% slope condition (Fig. 6), and the peaks of knee extensor moments differ little (but significantly) among most slope conditions (Table 6). The significantly earlier transition between the hip extensor to hip flexor activation phases in stance of downslope walking cannot be explained by exaggerated group Ia and II afferents' activity from the one-joint hip flexor IP because its MTU velocity and length change in stance are similar among the three walking conditions (Figs. 4 and 5; Tables 3 and 4). More likely the hip flexor group Ib afferents are responsible for the early extension-to-flexion phase transition during stance of downslope walking.

Activity and proprioception of two-joint muscles

Several observations in this study (exaggerated SO activity in stance of downslope walking; Fig. 7) and the study of Smith et al. (1998a,b) (absence of stance-related activity of one-joint hip extensors in downslope walking; their Fig. 10) could not be easily explained by the inferred cutaneous and proprioceptive afferent signals discussed above. In particular, MTU length-dependent afferent feedback from LG/P, MG, and SO in initial stance in downslope walking might be expected to be similar among the four muscles (Fig. 4; Table 3), as well as the expected force-dependent and cutaneous input from these muscles and the paw pad (Figs. 5 and 6). Given these facts, changes in activity of SO, LG, MG, and P muscles in downslope walking should be similar. Activity of MG and P, however, was significantly lower than that in level walking, but SO activity significantly increased (Fig. 7). The differential activation of these and other one- and multijoint synergists has been reported often for locomotion and other motor tasks and was suggested to involve force-dependent inhibition from the two-joint muscles onto the one-joint muscles of the synergist

group (for review see Prilutsky 2000). The extent to which the force-dependent inhibition from LG and MG onto SO described by Nichols (1989, 1994) and discussed by Gregor et al. (2001) participates in the regulation of synergistic activity is not completely clear. Nevertheless, if one assumes this inhibition is present in locomotion, the unloading of the ankle extensors and knee flexors, LG and MG, in downslope walking might reduce their activity and, in turn, the force-dependent inhibition of SO. As a result, SO activity might stay the same or even increase in downslope walking.

Concerning the unexpected lack of activity of ABF and ASM in stance of downslope walking, the similar length changes in IP during downslope and level walking do not seem to support the idea that the absence of activity in one-joint hip extensors is caused by the length-dependent reciprocal inhibition from one-joint hip flexors (see above). A second possible hypothesis rests with the lengthening observed in the increasingly active rectus femoris (RF) during downslope walking that is significantly different from the lengthening observed during level walking (Fig. 4A, Table 3). Eccles et al. (1957, 1958) showed the RF has a length-dependent inhibitory effect on the ABF and the ASM and semitendonosus (ST). The RF also has an excitatory effect on the sartorius, which in turn has an inhibitory effect on the ASM. Given the statistically significant increase in RF lengthening (Table 3) and the increased EMG activity (see Smith et al. 1998b, their Fig. 8) in downslope walking, the possibility exists that length-dependent inhibitory signals from the RF affect the ABF, ASM, and ST diminishing their activity during downslope walking. Self-reinnervating the RF and observing EMG in the ABF and ASM during downslope walking may provide data to test this hypothesis.

In conclusion, the mechanisms responsible for modification of muscle activation patterns in slope compared with level walking have not been adequately explained. For instance, suggested reconfigurations of the unit burst model of the central pattern generator for slope walking (Smith et al. 1998a,b) have difficulty explaining changes in the magnitude and timing of activity in the majority of sampled muscles (Pearson 2000). Afferent input in slope walking might modulate muscle activation differently from that in level walking because of differences in mechanical conditions between the tasks (Pearson 2000). To better understand the potential role of mechanical conditions of downslope and upslope walking in modulating afferent input and muscle activity, we quantified MTU length changes and velocity of the major hindlimb muscles, ground reaction forces, and joint moments during walking on inclined (±50%) and level surfaces. These mechanical variables are presumably related to feedback input from length-/velocity-sensitive muscle afferents (Hoffer et al. 1989; Prochazka and Gorassini 1998), pressure-sensitive mechanoreceptors in the paw pad (Strange and Hoffer 1999), and force-sensitive muscle afferents (Jami 1992; Prochazka and Gorassini 1998). We found that during stance of downslope walking, the stretch magnitude and peak stretch velocities of MTU of ankle and knee extensors were significantly larger than those in level and upslope walking, suggesting a larger afferent input from group Ia and II afferents. The resultant ground reaction force applied to the hindlimb and peaks of ankle and hip extensor moments were substantially greater in upslope walking than those in the level and downslope conditions, suggesting larger cutaneous and group Ib

afferent input in upslope walking. The larger magnitude and duration of EMG bursts of MG, LG, and P in upslope walking compared with those of other walking conditions are consistent with the notion of the positive force feedback during locomotion (Gossard et al. 1994; McCrea 1998; Pearson and Collins 1993). The contribution of muscle length–dependent feedback to the activity of MG, LG, and P is apparently much smaller because the activity of these muscles is significantly reduced in downslope walking. The SO activity, however, might depend more strongly on input from spindle afferents because the SO activity is larger in downslope than that in level walking. Length-sensitive afferents from two-joint knee flexors–hip extensors BFP and ST might contribute to triggering the transition from flexion to the extension phase of the CPG because EMG onset of ankle extensors occurs when MTU lengths of these muscles are close to maximum before paw contact in the three walking conditions.

Although our inferences about afferent input made from mechanical variables in this study are indirect and do not take into account the possible influence of gamma activation and presynaptic inhibition, we believe these results add to the understanding of the possible effects of mechanical conditions on afferent input and muscle activation patterns.

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