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

Robert J. Gregor, D. Webb Smith, and Boris I. Prilutsky

Center for Human Movement Studies, School of Applied Physiology, Georgia Institute of Technology, Atlanta, Georgia

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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 hindlimb 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 Ia 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 (Abelow 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 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.
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 locomo-
tion 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 PegaXias-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 uninter-
rupted gait at constant speed through the walkway, and the hindlimb
under study made contact with both force platforms (Bertec) inde-
pendent 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 frames/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 elec-
trodes. EMG fine-wire electrodes (Teflon-insulated multistrand, 100
μm diameter, Cooner Wire, Chatsworth, CA) were passed subcuta-
neously from a head-mounted multipin connector and implanted
chronically in soleus (SO), lateral gastrocnemius (LG), medial gas-
trocnemius (MG), and/or plantaris (P) muscles. One cat had electrodes
implanted in the SO and MG muscles in the left hindlimb; a second
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 mea-
sured from PC to PO and expressed as a percentage of the step cycle.
Because walking speed affects the magnitude and profile of gait, kine-
matic 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 kine-
matic 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 con-
necting 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, LGP, 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 But-
nerworth filter with a cutoff frequency of 25 Hz. The normal (orthogon-
al to the walkway surface) and anterior–posterior (parallel to the walk-
way 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 repre-
sent 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 an-
tagonists 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-
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 stance (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.
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 conditions. Although the differences were significant (P < 0.05; Table 1).

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

<table>
<thead>
<tr>
<th>Kinematics</th>
<th>Downslope</th>
<th>Level</th>
<th>Upslope</th>
</tr>
</thead>
<tbody>
<tr>
<td>Da, m</td>
<td>+0.17 ± 0.01</td>
<td>+0.11 ± 0.02</td>
<td>±0.09 ± 0.01</td>
</tr>
<tr>
<td>Dp, m</td>
<td>+0.05 ± 0.03</td>
<td>+0.13 ± 0.03</td>
<td>+0.18 ± 0.01</td>
</tr>
<tr>
<td>Hh, m</td>
<td>+0.21 ± 0.01</td>
<td>+0.23 ± 0.02</td>
<td>+0.20 ± 0.01</td>
</tr>
<tr>
<td>Speed, m/s</td>
<td>+0.48 ± 0.09</td>
<td>0.54 ± 0.07</td>
<td>0.55 ± 0.05</td>
</tr>
<tr>
<td>% Stance</td>
<td>+64.4 ± 2.0</td>
<td>161.6 ± 2.9</td>
<td>67.6 ± 3.0</td>
</tr>
<tr>
<td>% Swing</td>
<td>+35.6 ± 2.0</td>
<td>138.4 ± 2.9</td>
<td>32.3 ± 3.0</td>
</tr>
</tbody>
</table>

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.

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

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

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.
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. 4A). 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 level and upslope walking ($P < 0.05$). 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 level and upslope walking ($P < 0.05$).

Interestingly, the iliopsoas (IP) muscle, a primary one-joint muscle, 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. 4A). 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

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Downslope</th>
<th>Level</th>
<th>Upslope</th>
</tr>
</thead>
<tbody>
<tr>
<td>SO</td>
<td>*9.1 ± 1.8</td>
<td>1.3 ± 1.3</td>
<td>1.3 ± 0.9</td>
</tr>
<tr>
<td>MG</td>
<td>*9.9 ± 1.8</td>
<td>1.0 ± 0.7</td>
<td>1.0 ± 0.7</td>
</tr>
<tr>
<td>LG/P</td>
<td>*8.8 ± 1.9</td>
<td>0.9 ± 0.6</td>
<td>0.9 ± 0.6</td>
</tr>
<tr>
<td>IP</td>
<td>*4.1 ± 0.9</td>
<td>5.1 ± 0.7</td>
<td>5.1 ± 0.7</td>
</tr>
<tr>
<td>RF</td>
<td>*15.7 ± 1.4</td>
<td>9.4 ± 1.3</td>
<td>9.4 ± 1.3</td>
</tr>
<tr>
<td>VL</td>
<td>*16.5 ± 1.7</td>
<td>1.1 ± 0.5</td>
<td>1.1 ± 0.5</td>
</tr>
<tr>
<td>SMA</td>
<td>0.1 ± 0.2</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>BFP</td>
<td>0.2 ± 0.1</td>
<td>2.5 ± 4.3</td>
<td>2.5 ± 4.3</td>
</tr>
<tr>
<td>ST</td>
<td>0.1 ± 0.1</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Downslope</th>
<th>Level</th>
<th>Upslope</th>
</tr>
</thead>
<tbody>
<tr>
<td>SO</td>
<td>*69 ± 11</td>
<td>38 ± 14</td>
<td>32 ± 17</td>
</tr>
<tr>
<td>MG</td>
<td>*55 ± 10</td>
<td>29 ± 13</td>
<td>26 ± 16</td>
</tr>
<tr>
<td>LG/P</td>
<td>*49 ± 9</td>
<td>28 ± 10</td>
<td>23 ± 15</td>
</tr>
<tr>
<td>IP</td>
<td>15 ± 3</td>
<td>16 ± 4</td>
<td>16 ± 4</td>
</tr>
<tr>
<td>RF</td>
<td>41 ± 10</td>
<td>41 ± 12</td>
<td>41 ± 6</td>
</tr>
<tr>
<td>VL</td>
<td>*36 ± 9</td>
<td>37 ± 22</td>
<td>28 ± 15</td>
</tr>
<tr>
<td>SMA</td>
<td>*47 ± 21</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>BFP</td>
<td>*26 ± 20</td>
<td>129 ± 22</td>
<td>129 ± 22</td>
</tr>
<tr>
<td>ST</td>
<td>*19 ± 13</td>
<td>127 ± 19</td>
<td>127 ± 19</td>
</tr>
</tbody>
</table>

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 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
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 down-
slope 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 walk-
ing 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 ob-
served 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.

![Ankle 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.](http://jn.physiology.org/)

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

<table>
<thead>
<tr>
<th>Force Component</th>
<th>Downslope</th>
<th>Level</th>
<th>Upslope</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fx</td>
<td>(-2.3 \pm 0.6)</td>
<td>(-0.8 \pm 0.4)</td>
<td>(3.2 \pm 0.8)</td>
</tr>
<tr>
<td>Fz</td>
<td>(+4.6 \pm 1.1)</td>
<td>(+5.3 \pm 1.2)</td>
<td>(6.0 \pm 1.3)</td>
</tr>
<tr>
<td>Fr</td>
<td>(+5.1 \pm 1.3)</td>
<td>(+5.4 \pm 1.2)</td>
<td>(6.8 \pm 1.7)</td>
</tr>
</tbody>
</table>

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.
Although the SO burst duration ($T_b$ 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 ($T_c$ 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.

### 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 membranes 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 sonomicroscopy 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 during downslope walking, the significantly larger MTU and upslope walking (Maas et al. 2005). It appears therefore that length-dependent reciprocal inhibition from hip flexors (i.e., when the MTU lengthens about the same in both level and upslope walking, when larger loads are placed on the forelimbs, might correspondingly, the reduced load on the hindlimbs in downslope 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 cutaneous afferent signals from paw pad

Removing cutaneous feedback from the mechanoreceptors in the cat paw pad by anesthesia or neurrectomy does not seem to affect locomotor patterns in normal walking (Duyens 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 (Duyens 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
was suggested to involve force-dependent inhibition from 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 Ia 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 semitendinosus (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 muscle afferent input.
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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