Form Switching During Human Locomotion: Traversing Wedges in a Single Step

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Earhart, Gammon M. and Amy J. Bastian. Form switching during human locomotion: traversing wedges in a single step. J Neurophysiol 84: 605–615, 2000. We examined the neural control strategies used to accommodate discrete alterations in walking surface inclination. Normal subjects were tested walking on a level surface and on different wedges (10°, 15°, 20°, and 30°) presented in the context of level walking. On a given trial, a subject walked on a level surface in approach to a wedge, took a single step on the wedge, and continued walking on an elevated level surface beyond the wedge. As wedge inclination increased, subjects linearly increased peak joint angles. Changes in timing of peak joint angles and electromyograms were not linear. Subjects used two distinct temporal strategies, or forms, to traverse the wedges. One form was used for walking on a level surface and on the 10° wedge, another form for walking on the 20° and 30° wedges. In the level/10° form, peak hip flexion occurred well before heel strike (HS) and peak dorsiflexion occurred in late stance. In the 20°/30° form, peak hip flexion was delayed by 12% of the stride cycle and peak dorsiflexion was reached 12% earlier. For the level/10° form, onsets of the rectus femoris, gluteus maximus, and vastus lateralis muscles were well before HS and offset of the anterior tibialis was at HS. For the 20°/30° form, onsets of the rectus femoris, gluteus maximus, and vastus lateralis and offset of the anterior tibialis were all delayed by 12% of the stride cycle. Muscles shifted as a group, rather than individually, between the forms. Subjects traversing a 15° wedge switched back and forth between the two forms in consecutive trials, suggesting the presence of a transition zone. Differences between the forms can be explained by the differing biomechanical constraints imposed by the wedges. Steeper wedges necessitate changes in limb orientation to accommodate the surface, altering limb orientation with respect to gravity and making it necessary to pull the body forward over the foot. The use of different forms of behavior is a common theme in neural control and represents an efficient means of coordinating and adapting movement to meet changing environmental demands. The forms of locomotion reported here are likely used on a regular basis in real-world settings.

INTRODUCTION

Successful ambulation requires the ability to detect and compensate for obstacles in one’s path of progression. Complex reorganizations of the basic gait pattern are necessary to accommodate or avoid obstacles (McFadyen et al. 1994). To maximize safety and success, these adjustments must be made quickly and efficiently. One can make adjustments in response to direct contact with an obstacle, as is the case with stumbling corrective reactions (Berger et al. 1984), or anticipate the obstacle and make adjustments before contacting the obstacle (Drew et al. 1996). Adjustments made may vary according to the nature of the obstacle encountered.

The use of different strategies to accomplish a task, such as successful ambulation in the presence of varying environmental demands, has been examined in both human and animal literature. The terms “task” and “form” can be used to classify and describe movement strategies. A task can be defined as a movement performed to accomplish a specific goal. For example, in locomotion, the organism’s goal is to move its center of mass across a distance. Each particular way that a task can be executed is called a form of that task (Stein et al. 1986). There are several examples in the animal literature of different forms used to accomplish a given task. In the cat, different forms of locomotion for level, uphill, and downhill locomotion have been described (Carlson-Kuhta et al. 1998; Smith et al. 1998). Mortin et al. (1985) demonstrated three forms of the scratch reflex in the turtle, each form a distinct movement strategy but all forms with the same goal of reaching to and rubbing a stimulated site on the shell. A form can be distinguished from other forms based on differences in timing of activity at one joint with respect to activity at another joint. The selection of form varies according to the biomechanical constraints of the task. There are some regions called “transition zones,” where it is possible to accomplish a task successfully using either of two forms. The demonstration of a transition zone in which switching between strategies occurs provides strong evidence for the existence of two different forms of a task.

Different forms of a task in humans include forward and backward walking. Both have the goal of propelling the individual in a particular direction, but each is a distinct movement strategy with different kinetic and electromyographic features (Thorstensson 1986; Winter et al. 1989). Forward and backward walking also have different kinematic characteristics, although comparison of forward walking to time-reversed backward walking reveals that many kinematic features are preserved across the two forms (Grasso et al. 1998).

Several studies have examined properties of transitions between two forms of human locomotion, walking and running. It is possible to walk at a speed faster than that of a slow run, such that there is a set of speeds at which either a walk or a run...
is possible (Nilsson et al. 1985; Thorstensson and Robertsson 1987). This set of speeds represents the walk-run transition zone. Similar speed-based transition zones have been demonstrated for switching between trot and gallop in several animals, including horses, cats, dogs, and goats (Biewener and Taylor 1986; Heglund and Taylor 1988; Smith et al. 1993).

We examined neural control strategies used to accommodate discrete alterations in surface inclination during walking. Subjects walked on a level surface in approach to a wedge, took a single step on the wedge, and continued walking on an elevated level surface beyond the wedge. This task is similar to walking from street to sidewalk by taking a single step on a handicapped access ramp. Wedges of various inclinations (10°, 15°, 20°, and 30°) were used. We hypothesized that several control mechanisms could be used to perform this task. First, subjects could use a single form of walking for all wedges, linearly adjusting features of the same basic temporal pattern in response to linear increases in wedge inclination. Most evidence from studies of slope walking supports this idea, although these studies tested steady-state locomotion on surfaces with inclinations of 12° or less (Patla 1986; Tokuhiro et al. 1985; Wall et al. 1981). Second, subjects could use a different form of walking for each different inclination. This strategy may not be efficient with respect to neural control, as many separate forms with unique temporal characteristics would be necessary to cover the range of surface inclinations encountered in everyday life. Third, subjects could use a particular form for one subset of inclinations and an alternate form for another subset of inclinations. Presumably, this would be a more efficient control strategy, as one basic temporal pattern could be used for a group of inclinations and finely adjusted within that group, rather than having to make more substantial adjustments to a single basic temporal pattern over a wide range of environmental conditions.

In the present study, we provide kinematic and electromyographic evidence for the use of two distinct temporal patterns to traverse the wedges presented. One form was used for walking on level surfaces and on a wedge with a 10° inclination; another form was used for walking on steeper wedges of 20° and 30° inclinations. We also provide evidence for a transition zone (15° inclination) in which either of the strategies can be used to traverse the wedge successfully. This is supported by the fact that subjects “switched” between the two strategies within this transition zone. Although transition zones and switching between forms have been demonstrated previously in humans (e.g., walk-run transitions), this is the first demonstration of switching within a forward walking task.

METHODS
Subjects
Fifteen healthy subjects without orthopedic or neurologic pathology participated in this study. Subjects ranged in age from 21 to 56 (mean ± SD = 26.86 ± 8.74) years. Seven subjects were male and eight were female. All subjects gave informed consent prior to testing. Note that one additional subject was tested, but was excluded from the study because she demonstrated toes first contact with the steepest wedge. All subjects included in the study struck all walking surfaces with the heel first or with a flat foot, rather than with toes first. We noted no differences in the patterns used for trials with heel first versus foot flat contact.

Paradigm
Subjects walked at a comfortable pace on a level surface approaching the wedge, took a single step on the incline, and continued walking on an elevated level surface beyond the wedge (Fig. 1). The wedge system had a height-adjustable platform providing an elevated level surface beyond the wedge that was even with the height of the wedge peak for all inclinations. All wedges were 0.98 m (3 ft) wide and 0.66 m (2 ft) long. Subjects performed 4–8 trials on each of the wedges: 10°, 20°, and 30° wedges. A 15° wedge was developed and added to the paradigm after the first five subjects had been tested. Thus, 10 of the 15 subjects also performed trials on a 15° wedge. All subjects also performed 4–8 trials of level walking during which no wedge was present. All trials of a given condition were performed as a block, and blocks were presented in randomized orders to all subjects.

Data collection
Kinematic and electromyographic (EMG) signals were recorded from the right side of the body for all subjects. We acknowledge that patterns on the left side of the body were likely also changing during this task, but patterns on the left were not recorded. Kinematic data were collected at 100 Hz using the Optotrak 3-D motion analysis system (Northern Digital, Inc., Waterloo, Ontario). Infrared-emitting diodes were placed on the right side of the body over the following anatomical landmarks (Fig. 1A): shoulder (acromion process), pelvis (iliac crest), hip (greater trochanter), knee (lateral femoral epicondyle), ankle (lateral malleolus), and foot (fifth metatarsal head). Joint angles for the hip, knee, and ankle were calculated based on the positions of these markers (Fig. 1A). Hip angle was defined as the angle between the thigh and the pelvis, knee angle as the angle between the thigh and the shank, and ankle angle as the angle between the shank and the foot. At the hip, an angle of 0° indicated that the pelvis and thigh were colinear. Hip angle values increased in the positive direction with increasing hip flexion and increased in the negative direction with increasing hip extension. At the knee, an angle of 0° represented full extension, and knee angle increased with increasing knee flexion. At the ankle, an angle of 0° represented vertical alignment of the shank with the foot flat on the floor. This conventional definition of ankle neutral corrected for the vertical offset of the ankle marker relative to the foot marker. Ankle angle increased in the positive direction with increasing dorsiflexion and increased in the negative direction with increasing plantarflexion.

FIG. 1. Illustration of marker placements, joint angle definitions, and the system of wedges used. Neutral joint angles (0°) are denoted by the dashed lines; joint angle values increased in the positive (+) direction from neutral as indicated by the curved arrows. For the wedge system, note that the height of the platform following the wedge is even with the top of the wedge. Subjects walked on a level surface approaching the incline, took a single step on the incline, and continued walking on a level surface beyond the incline.
Silver-silver chloride surface electrodes with on-site preamplifiers (Therapeutics Unlimited, Iowa City, IA) were placed on the right side of the body over the following muscles: rectus femoris (RF), gluteus maximus (GM), vastus lateralis (VL), lateral hamstring (LH), anterior tibialis (AT), and gastrocnemius (GA). EMG signals were amplified (75 Hz low-cut band-pass) and digitized at 1 kHz.

Analysis

Kinematic and EMG data were synchronized automatically by the Optotrak system. Three trials from each condition performed by each subject were analyzed. Thus, a total of 45 trials each of level, 10°, 20°, and 30° conditions, was analyzed, along with 30 trials of the 15° condition. Times for heel strike (HS) and toe off (TO) were selected manually from animated stick figure representations of each trial. We confirmed the accuracy of our method for HS and TO selections by collecting several walking trials during which HS and TO were registered on a force plate. Our manually selected HS and TO times were always within 10 ms (one frame) of the times indicated by the force plate data. For each subject, three trials from each condition were analyzed. Hip, knee, and ankle angles (Fig. 1) were calculated using the Optotrak data analysis package.

A stride was defined from TO prior to the wedge through TO from the wedge, thus including swing approaching and stance on the wedge. Stride was defined in this way because we were interested in the swing approaching the wedge and stance on the wedge. For each stride, we calculated 1) stride duration, 2) stride length, and 3) gait velocity to ensure that any changes we observed were not simply a reflection of changes in one or more of these variables.

Kinematic data were represented graphically in two ways: joint angle time series plots and joint angle-angle plots. Time series plots for the hip, knee, and ankle joints were used to examine single joint kinematics across conditions. Kinematic variables of interest included 1) the peak joint angles at the hip, knee, and ankle, and 2) the times at which these maxima occurred within the stride cycle. Angle-angle plots for hip versus ankle, knee versus hip, and ankle versus knee provided information about interjoint coordination.

EMG signals were rectified and low-pass filtered at 70 Hz (DataPac, Run Technologies, Inc., Laguna Hills, CA). All EMG signals were aligned on HS because we were particularly interested in the EMG events (onsets/offsets) that occurred at or around the time of HS on the wedge. EMG onsets were selected as the time when muscle activity level reached two times baseline for at least 50 ms. EMG offset times were selected as the time when muscle activity fell below two times baseline for at least 50 ms. Baseline was taken as the activity level during quiet stance. EMG onset and offset times were expressed as a percentage of the stride period, with HS defined as zero. EMG times that have negative values occurred prior to HS (swing phase), those with values of zero at HS, and those with positive values after HS (stance phase).

Separate repeated measures analyses of variance (ANOVA, $P < 0.05$) were used to compare variables of interest across different wedge inclinations. Duncan multiple range posthoc comparisons were performed for all significant $F$ values (Statistica, StatSoft, Inc., Tulsa, OK).

### Table 1. Stride length, duration, and gait velocity

<table>
<thead>
<tr>
<th>Condition</th>
<th>Stride Length, m</th>
<th>Stride Duration, s</th>
<th>Velocity, m/s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Level</td>
<td>1.32 ± 0.03</td>
<td>1.17 ± 0.03</td>
<td>1.14 ± 0.05</td>
</tr>
<tr>
<td>10 degrees</td>
<td>1.39 ± 0.04</td>
<td>1.26 ± 0.04</td>
<td>1.12 ± 0.05</td>
</tr>
<tr>
<td>20 degrees</td>
<td>1.36 ± 0.04</td>
<td>1.27 ± 0.05</td>
<td>1.08 ± 0.05</td>
</tr>
<tr>
<td>30 degrees</td>
<td>1.34 ± 0.04</td>
<td>1.28 ± 0.04</td>
<td>1.07 ± 0.05</td>
</tr>
</tbody>
</table>

Values are means ± SE (3 steps/subject; $n = 15$ subjects).

RESULTS

Kinematics: Level, 10°, 20°, and 30° conditions

### Stride Characteristics

Table 1 gives the means ± SE for stride length, stride duration, and gait velocity for the different conditions. Analysis of these variables revealed no significant differences across wedge conditions.

### Peak Joint Angles

Nearly all peak joint angle values changed as a function of increasing wedge inclination. Peak hip flexion (Fig. 2A, bold dots), peak knee flexion during stance (Fig. 2B, inverted triangles), and peak dorsiflexion (Fig. 2C, filled markers) decreased with increasing wedge inclination. These changes likely reflect the need for greater muscle force to overcome the increased resistance to motion at the wedge.

FIG. 2. Joint angle versus time plots of the hip (A), knee (B), and ankle (C) for level, 10°, 20°, and 30° conditions. Three trials for each wedge condition are drawn from toe off prior to the wedge through toe off from the wedge, thus depicting swing approaching and stance on the wedge. Heel strike is denoted by the vertical lines drawn through zero. Filled markers denote peak joint flexion and extension points; see text for details.
TABLE 2.  Peak joint angles during swing

<table>
<thead>
<tr>
<th>Condition</th>
<th>Peak Hip Flexion, deg</th>
<th>Peak Knee Flexion, deg</th>
<th>Peak Knee Extension, deg</th>
<th>Peak Ankle Plantarflexion, deg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Level</td>
<td>20.22 ± 3.51</td>
<td>64.20 ± 9.8</td>
<td>5.18 ± .70</td>
<td>−17.45 ± 1.73</td>
</tr>
<tr>
<td>10 degrees</td>
<td>20.88 ± 2.19</td>
<td>61.56 ± 4.20</td>
<td>11.17 ± 1.78</td>
<td>−16.22 ± 1.79</td>
</tr>
<tr>
<td>20 degrees</td>
<td>27.31 ± 2.58</td>
<td>66.07 ± 1.27</td>
<td>20.09 ± 2.31</td>
<td>−15.49 ± 1.97</td>
</tr>
<tr>
<td>30 degrees</td>
<td>32.61 ± 3.05</td>
<td>67.89 ± 1.55</td>
<td>27.71 ± 2.32</td>
<td>−13.90 ± 1.92</td>
</tr>
</tbody>
</table>

Values are means ± SE (3 steps/subject; n = 15 subjects). See text for description of statistically significant differences between conditions.

2C, filled squares) all increased with increasing wedge inclination. Statistically, peak hip flexion and peak knee flexion during stance were not different for the level and 10° conditions but were significantly different for all other comparisons. Peak ankle dorsiflexion was significantly different across all conditions.

Peak knee flexion during swing (Fig. 2B, filled triangles) did not change as wedge inclination increased and was not significantly different across conditions. Peak plantarflexion did not change substantially (Fig. 2C, filled diamonds), and only the 30° condition was different from the others (all P < 0.01). Tables 2 and 3 show mean peak joint angles during swing and stance, respectively.

Joint angle values at HS are presented in Table 3. Hip flexion, knee flexion, and ankle dorsiflexion at HS all increased incrementally as wedge inclination increased. For all joints, all comparisons across conditions were significant (all P < 0.01).

TABLE 3.  Joint angles at heel strike and peak joint angles during stance

<table>
<thead>
<tr>
<th>Condition</th>
<th>Hip Angle at HS, deg</th>
<th>Knee Angle at HS, deg</th>
<th>Ankle Angle at HS, deg</th>
<th>Peak Knee Flexion, deg</th>
<th>Peak Ankle Dorsiflexion, deg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Level</td>
<td>11.31 ± 1.50</td>
<td>12.27 ± 0.93</td>
<td>−3.89 ± 1.19</td>
<td>19.26 ± 1.42</td>
<td>13.81 ± 1.55</td>
</tr>
<tr>
<td>10 degrees</td>
<td>17.08 ± 2.04</td>
<td>19.67 ± 1.55</td>
<td>4.14 ± 1.37</td>
<td>23.92 ± 1.61</td>
<td>18.52 ± 1.39</td>
</tr>
<tr>
<td>20 degrees</td>
<td>25.34 ± 2.43</td>
<td>27.59 ± 1.74</td>
<td>12.43 ± 1.34</td>
<td>34.81 ± 1.82</td>
<td>26.95 ± 1.41</td>
</tr>
<tr>
<td>30 degrees</td>
<td>31.40 ± 3.07</td>
<td>35.27 ± 2.09</td>
<td>18.69 ± 1.48</td>
<td>41.15 ± 2.30</td>
<td>35.62 ± 1.36</td>
</tr>
</tbody>
</table>

Values are means ± SE (3 steps/subject; n = 15 subjects). See text for description of statistically significant differences between conditions. HS, heel strike.

In summary, peak hip flexion, knee flexion, knee extension, and ankle dorsiflexion increased with increases in wedge inclination. However, the timing of peak hip flexion and peak ankle dorsiflexion did not vary incrementally with wedge inclination. Figure 3 summarizes the differences in timing of peak joint angles across conditions. Timing of peak hip flexion and peak ankle dorsiflexion show distinct groupings, indicating similarities between the level and 10° and between the 20° and 30° conditions but differences between the level/10 versus the 20°/30° conditions.

ANGLE-ANGLE PLOTS. Angle-angle plots for the swing and stance phases of the various conditions provided insights about interjoint coordination. Angle-angle plots for the swing phase of various conditions showed gradual changes that varied with wedge inclination. The changes in swing phase angle-angle plots reflected the incremental changes in peak joint angle values discussed previously. Angle-angle plots for the stance phase of various conditions are presented in Fig. 4. The hip versus ankle plots (Fig. 4A) for all conditions had two horizontally oriented segments with a more vertically oriented central segment between them. This central segment sloped downward and to the right in the level/10° conditions, but downward and to the left in the 20°/30° conditions. This difference in shape reflected the difference in timing of peak dorsiflexion discussed previously. Changes in the shape of the knee versus hip stance plots were more gradual, without any specific groupings (Fig. 4B).

The ankle versus knee curves showed patterns that fell into two distinct groupings. Ankle versus knee plots for the level and 10° conditions were S-shaped, while those for the 20° and 30° conditions were shaped like a side-lying letter C (Fig. 4C). The increase in ankle dorsiflexion during mid to late stance for the level/10° conditions created the S-shaped curve, while the absence of any such dorsiflexion during mid stance in the 20°/30° conditions created the C-shaped curve. We classified
the features of these plots to determine if there were statistically specific groupings. Plots were classified as category 0, 1, or 2 based on two characteristics: 1) overall shape and 2) location of the late stance portion of the graph (Fig. 4, D1 and D2, arrowheads) relative to the HS starting point (Fig. 4, D1 and D2, filled circles). Plots with an S shape received a subscore of 0; those with a side-lying C shape received a subscore of 1. Plots where the tail passed to the right of the HS starting point received a subscore of 0; those where the tail passed to the left of the HS starting point received a subscore of 1. The sum of the two subscores was used to categorize each trial. If two forms of walking were being used, most trials should have pure characteristics of one form or the other form (scores of either 0 or 2). Trials intermediate between the level/10° and the 20°/30° forms would have a score of 1. Overall, only 5 of 180 trials were given a score of 1. One hundred percent of the level trials and 93% (42 of 45) of the 10° trials received a score of 0. Ninety-five percent (43 of 45) of the 20° trials and 100% of the 30° trials received a score of 2.

**EMG timing: Level, 10°, 20°, and 30° conditions**

Like the kinematic patterns, EMG patterns were grouped in the level/10° and the 20°/30° conditions, with differences between the groupings. Specifically, the offset of AT and onsets of RF, GM, and VL changed from one pattern for level and 10° to another for 20° and 30° (Table 4). These muscles, with the exception of RF, appeared to shift as a group.

Figure 5 shows EMG records of a single subject for one trial of each condition. Plots are drawn for swing approaching the wedge and stance phase on the wedge. For level and 10° conditions, the onsets of RF, GM, and VL occurred well...
Values are means ± SE for significant changes in muscle onsets and offsets as a percentage of cycle (HS = 0%). For RF, GM, VL, and AT burst timing for level and 10° was similar, as was that for 20° and 30°. There were significant differences between the level/10° versus 20°/30° conditions, providing electromyographic evidence for two distinct forms of behavior (3 steps/subject; n = 15 subjects). EMG, electromyogram; RF, rectus femoris; GM, gluteus maximus; VL, vastus lateralis; AT, anterior tibialis.

ONSETS. Figure 6 shows group EMG timing data. Bars are aligned on HS and indicate the average times that each muscle was active for each condition. For RF, GM, and VL, there were no significant differences between the onset times for level and 10°, nor for the onset times for 20° and 30°. However, there were significant differences in onset time between level/10° and 20°/30° conditions (Fig. 6, A–C; all P < 0.001). Onset times for the LH (Fig. 6D) showed significant differences (P < 0.001) between all conditions except 20° and 30°. There were no significant differences in GA (Fig. 6F) onset time across conditions. Onset times for AT were not systematically evaluated because this muscle was often active throughout the entire swing phase.

OFFSETS. Offset times for AT showed groupings of level/10° and 20°/30° conditions (Fig. 6E). AT offset showed no significant differences between level and 10°, nor between 20° and 30°. Significant differences were present between the level/10° and the 20°/30° conditions (P < 0.001). Offset times for other muscles did not fall into those two groupings.

### TABLE 4. EMG timing

<table>
<thead>
<tr>
<th>Condition</th>
<th>RF On</th>
<th>GM On</th>
<th>VL On</th>
<th>AT Off</th>
</tr>
</thead>
<tbody>
<tr>
<td>Level</td>
<td>–13.80 ± 1.03</td>
<td>–13.12 ± 1.11</td>
<td>–16.64 ± 0.83</td>
<td>2.21 ± 0.41</td>
</tr>
<tr>
<td>10 degrees</td>
<td>–11.80 ± 1.09</td>
<td>–11.01 ± 2.12</td>
<td>–14.47 ± 0.97</td>
<td>6.03 ± 1.30</td>
</tr>
<tr>
<td>20 degrees</td>
<td>–2.06 ± 0.73</td>
<td>–0.47 ± 0.72</td>
<td>–3.41 ± 1.29</td>
<td>20.41 ± 2.73</td>
</tr>
<tr>
<td>30 degrees</td>
<td>–0.34 ± 0.60</td>
<td>0.73 ± 0.96</td>
<td>–3.56 ± 1.14</td>
<td>22.90 ± 2.49</td>
</tr>
</tbody>
</table>

Figure 5. Electromyogram (EMG) records from trials of level (A), 10° (B), 20° (C), and 30° (D) for a single subject. Plots are drawn from toe off prior to the wedge through toe off from the wedge, thus depicting swing approaching and stance on the wedge. Heel strike is denoted by the vertical lines. Note that vertical scales are not constant across conditions, as the aim of the figure was to allow for accurate comparison of EMG timing rather than EMG amplitude (RF, rectus femoris; GM, gluteus maximus; VL, vastus lateralis; LH, lateral hamstring; AT, anterior tibialis; GA, gastrocnemius).
LATENCIES FROM AT OFFSET TO ONSET OF OTHER SHIFTED MUSCLES. We further evaluated EMG timing changes by calculating the latency between AT offset and the onset of each of the other time-shifted muscles (RF, GM, VL, LH). Comparable latencies across the different wedge conditions would indicate that the time shifts of the various muscles were similar and the muscles were shifting as a group. Conversely, changes in latencies across conditions would indicate that muscles were shifting individually rather than shifting as a group.

We found no significant differences in latencies between AT offset and the onsets of the GM, VL, or LH across wedge conditions. These muscles appeared to be shifting as a group. The latencies between AT offset and RF onset were similar for level and 10°, as well as for 20° and 30°, but there were significant differences between level/10° and 20°/30° (P < 0.01).

RELATIONSHIP OF KINEMATICS TO EMG. Figure 7 shows time series plots of joint angles and EMG for a 10° trial (Fig. 7A) and a 30° trial (Fig. 7B). Stick figures in Fig. 7 illustrate the configurations of the trunk and lower extremity at the time points indicated. Note that the stick figures show marker locations rather than joint angles. The ankle joint appears to be plantarflexed in many of the stick figures because of the vertical offset between the ankle and foot (fifth metatarsal) markers, whereas the joint angle traces indicate that the ankle was dorsiflexed through most of stance. This is because the definition of neutral ankle angle corrected for the offset between the ankle and foot markers (see METHODS).

In the 10° condition, peak hip flexion (pHF) occurred well before HS and the onset of GM activity followed after the reversal. In the 30° condition, pHF occurred at HS, and onset of GM activity occurred nearly simultaneously. At the knee, the timing of extensors changed as knee movement changed. For the 10° condition, knee extensor onsets coincided with attainment of peak knee extension prior to HS. For the 30° condition, the knee extensor onsets occurred at HS rather than prior to HS, but still coincided with peak knee extension prior to HS. The knee extensors remained active later into stance for the 30° condition and may have assisted in pulling the body forward over the foot. At the ankle, the AT appeared to subserve different functions,
depending on wedge inclination. In the 10° condition, AT offset occurred close to HS and AT activity may have eccentrically controlled lowering of the foot to the walking surface. Forward movement of the shank (and body) over the foot contributed to peak dorsiflexion (pDF). In the 30° condition, AT activity was prolonged and may have helped to pull the body forward over the foot, as the hip remained behind the foot for a longer period of time. Timing of peak dorsiflexion in the 30° condition was earlier than in the 10° condition and was nearly coincident with AT offset.

**15° condition**

To further test whether subjects were using two forms to accomplish the task or whether this was a graded response, we studied subjects walking on a 15° wedge. Most subjects (8 of 10) demonstrated switching between forms on the 15° wedge. Both kinematic and electromyographic data supported the use of two distinct forms on different trials of the 15° condition.

Figure 8 shows angle-angle stance plots and EMG records for a single subject on two trials of the 15° condition. This subject demonstrated switching between forms on the 15°

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**FIG. 7.** Relationships of muscle activity to kinematics for one stride in the 10° condition (A) and one stride in the 30° condition (B) from a single subject. Stick figures depict body position at toe off (TO), peak hip flexion (pHF), heel strike (HS), and peak dorsiflexion (pDF). Plots below stick figures show joint angle time series for the hip, knee, and ankle along with EMG activity of GM, VL, and AT.
wedge. On one trial (Fig. 8A), the subject used the level-like strategy. On this trial the ankle versus knee stance plot was S-shaped, GM and VL onsets were well before HS, and AT offset was at HS. On the other trial (Fig. 8B), the subject used the 30°-like strategy. On this trial, the ankle versus knee stance plot was sidelying C-shaped, GM and VL onsets were at HS, and AT offset was well after HS.

Of the 10 subjects who performed trials on the 15° wedge, eight demonstrated switching between the two forms. (One subject used a 30°-like strategy for all trials, and one subject used an intermediate form for all trials.) Switching back and forth between strategies appeared to occur randomly throughout the series of trials. To determine whether subjects were using the two forms described earlier to traverse the 15° wedge, we first categorized ankle angle versus knee angle plots as 0, 1, or 2. A total of 30 trials from the 15° condition were categorized. Of these trials, 43% (13 of 30) were level-like and given a value of 0, 47% (14 of 30) were 30-like and given a value of 2, and 10% (3 of 30) were given a value of 1 because they possessed kinematic characteristics intermediate between the two pure forms.

Following categorization of trials based on the shape of ankle versus knee angle plots, we tested whether the temporal features of the categorized trials were consistent with those of the two forms described earlier. Kinematic data from all level-like trials were averaged, as were data from all 30°-like trials. Timing of ankle dorsiflexion was significantly different between the level-like and 30°-like trials. Peak dorsiflexion timing for the level-like trials was the same as the actual level trials and for the 30°-like trials was the same as the actual 30° trials. However, timing of pHF was not different for level-like and 30°-like trials and was the same as the actual 30° trials (all P < 0.01).

Variables examined included ankle, knee, hip, and trunk angles at HS, center of mass and hip positions relative to ankle position at HS, and foot orientation with respect to the horizontal. None of these variables was a consistent predictor of form.

**DISCUSSION**

This study demonstrates switching between forms during a forward walking task in humans. Subjects used one form for level walking and the single step on the 10° wedge and another form for single steps on the 20° and 30° wedges. The level/10° form was characterized by peak hip flexion during mid-swing, peak dorsiflexion during late stance, RF, GM, and VL onsets prior to HS, and AT offset near HS. The 20°/30° form was characterized by pHF near HS, peak dorsiflexion during mid-stance, RF, GM, and VL onsets at HS, and AT offset well after HS. Switching between the two forms was demonstrated on the 15° wedge, suggesting the presence of a transition zone at 15°.

Studies that have examined steady-state locomotion on inclines have not reported such switching but have reported some of the changes noted here. Wall et al. (1981) noted similar increases in hip and knee flexion with increasing slope. Delays in the onsets of RF and GM for 9° and 12° steady-state slope walking have also been reported (Tokuhiro et al. 1985). There has been no study to date that has used both EMG and kinematics to examine slope walking in humans on inclinations as steep as 20° and 30° and no study examining a task where only a single step was taken on the incline. The present task may be useful for studies involving subjects with neurological deficits who cannot perform other more demanding switches between forms, such as changing from a walk to a run.

**Why did subjects switch forms?**

Kinematic and electromyographic changes may be explained by differences in the biomechanical constraints of the task. As wedge inclination increased, hip and knee flexion and ankle dorsiflexion increased during both swing and stance. These changes were necessary to orient the leg appropriately to...
accommodate the steeper obstacles (Patla and Prentice 1995). The need to flex the hip and knee more for steeper wedges led to a change in the relative orientation of the trunk and limb with respect to gravity. For steeper wedges, the limb was oriented more anteriorly with respect to the trunk, such that the body had to be actively pulled forward over the foot through early and mid-stance.

At the hip, the increase in flexion on steeper wedges led to a delay in the timing of pHF relative to HS. GM onset was also delayed and coincided with hip movement reversal from flexion to extension. GM activity following HS likely contributes to forward propulsion of the body over the foot during stance on the steeper wedges. At the knee, the need for greater flexion at HS and more propulsive force to overcome gravity on steeper wedges may be related to the delayed onsets of RF and VL. For the steeper wedges, knee extensor activity from HS through mid-stance may assist in pulling the femur forward over the tibia. At the ankle, increased dorsiflexion was required to traverse steeper wedges. Peak dorsiflexion was reached earlier in stance on the steeper wedges. The prolonged activity of AT following HS on the steeper wedges may serve to pull the body forward over the foot following HS.

Comparison to stair ascent

On the steeper wedges, the hip remains behind the foot for a greater portion of stance and more propulsive force may be required to move the body forward over the incline. This need to pull the body forward over the foot may be analogous to the “pull-up” phase of stair ascent (McFadyen and Winter 1988). The pull-up phase of stair ascent, which begins at the start of single limb support and continues through mid-swing of the contralateral limb, is characterized by upward vertical movement of the body and activity of the hip and knee extensors. We propose that the hip and knee extensors may be serving pull-up functions in the 20°/30° wedge conditions. However, a major difference between pull-up of stair climbing and wedge walking occurs at the ankle. Plantarflexor (soleus) muscle activity occurs during pull-up in stair climbing. In contrast, dorsiflexor (AT) activity occurs during pull-up in wedge walking. This difference may be a function of differing position of the line of gravity with respect to the foot during the pull-up phases of stair climbing and wedge walking.

Form switching in other situations

Other demonstrations of form switching can be explained based on the biomechanical constraints or demands of the task. For example, the turtle uses different forms of scratch to rub different regions of the shell (Stein et al. 1986). Because of biomechanical restrictions of the musculoskeletal system, the turtle simply cannot reach all regions of the shell using a single strategy and must employ three different forms to successfully rub regions spanning from the midbody to the tail. Each form of scratch has very different timing of knee activity with respect to hip activity, and this temporal difference serves as an excellent discriminator among the forms. Another example of switching that may have a biomechanical basis is the trot-gallop transition in horses. This transition is thought to occur when musculoskeletal forces reach a critical level, with the change of form resulting in a reduction of peak forces and potential reduction in the risk of injury (Farley and Taylor 1991).

The switching demonstrated here may be triggered by biomechanical factors. The need to pull the body forward on steeper wedges but not on level surfaces or less steep wedges creates the dichotomy of forms demonstrated here. We were not able to identify a single variable (e.g., amount of hip flexion at HS) that triggered the form switch and hypothesize that the trigger to switch from one form to another is multifactorial. The combination of body orientation with respect to the foot, joint orientations with respect to gravity, joint ranges of motion, and foot orientation on the inclines may determine which of the two forms will be used for a particular situation. Based on a combination of factors, subjects may or may not need to actively pull the body forward over the foot during different trials on the 15° wedge. As such, subjects may have a level-like ankle pattern on some 15° trials and a 30°-like ankle pattern on other 15° trials.

The walk to run transition is similar to our task in that it is not easily explained by a single triggering variable. Although well studied, there is no consensus that a single factor is responsible for the walk to run switch. An early hypothesis, that the walk-run transition occurred at the speed at which a walk became less efficient than a run, has been refuted (Hreljac 1993; Minetti et al. 1994). Some now argue that perceived comfort levels, which are influenced by several factors including inter-thigh angle and internal work levels, determine the walk-run transition speed (Minetti et al. 1994). Others suggest that a loss of pattern stability, characterized by increase stride duration variability around the transition speed, triggers the switch from walk to run (Brissswalter and Mottet 1996; Diedrich and Warren 1995). An alternative explanation, based on the inverted pendulum model of walking, states that the walk-run transition is a direct result of system dynamics. Kram et al. (1997) report that subjects switch from walking to running at a particular Froude number, a ratio of centripetal to gravitational force. Thus the walk-run transition may be influenced by multiple factors, as is the transition between forms demonstrated here.

The use of different forms of behavior is a common theme in the neural control of movement across species. Different strategies are employed based on the different biomechanical demands of a given task. The use of distinct forms is an efficient means for the nervous system to control movement, rather than attempting to adjust a single form to all situations in which a task must be performed. Instead, different forms with distinct temporal characteristics can be used for different subsets of a task and the spatial features of each form then finely adjusted over a narrower domain. We have demonstrated shifts in kinematic and electromyographic temporal patterns that support the use of two different forms for different wedge inclinations. The forms used to traverse wedges in the experimental situations described are likely used on a regular basis in real-world settings, as this task is similar to walking from the street onto the sidewalk by taking a single step on a ramp designed to allow handicapped access.

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