

## SWING- AND SUPPORT-RELATED MUSCLE ACTIONS DIFFERENTIALLY TRIGGER HUMAN WALK–RUN AND RUN–WALK TRANSITIONS

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### Summary

There has been no consistent explanation as to why humans prefer changing their gait from walking to running and from running to walking at increasing and decreasing speeds, respectively. This study examined muscle activation as a possible determinant of these gait transitions. Seven subjects walked and ran on a motor-driven treadmill for 40 s at speeds of 55, 70, 85, 100, 115, 130 and 145 % of the preferred transition speed. The movements of subjects were videotaped, and surface electromyographic activity was recorded from seven major leg muscles. Resultant moments at the leg joints during the swing phase were calculated. During the swing phase of locomotion at preferred running speeds (115, 130, 145 %), swing-related activation of the ankle, knee and hip flexors and peaks of flexion moments were typically lower ( $P < 0.05$ ) during running than during walking. At preferred walking speeds (55, 70, 85 %), support-related activation of the ankle and knee extensors was typically

lower during stance of walking than during stance of running ( $P < 0.05$ ). These results support the hypothesis that the preferred walk–run transition might be triggered by the increased sense of effort due to the exaggerated swing-related activation of the tibialis anterior, rectus femoris and hamstrings; this increased activation is necessary to meet the higher joint moment demands to move the swing leg during fast walking. The preferred run–walk transition might be similarly triggered by the sense of effort due to the higher support-related activation of the soleus, gastrocnemius and vastii that must generate higher forces during slow running than during walking at the same speed.

Key words: walking, running, gait transition, human, locomotion, preferred speed, electromyography, muscle activation, swing, stance, sense of effort.

### Introduction

Animals use different gaits to move at different speeds. Humans, for example, prefer to walk at relatively slow speeds and to run at faster speeds. It is not entirely clear why one gait is preferred over the other at a given speed and how the mechanics of walking and running affect our choice of gait (Alexander, 1989; Kram et al., 1997). The idea that the gait transition at increasing locomotion speeds is triggered by metabolic energy expenditure was initially proposed on the basis of the fact that bipeds and quadrupeds tend to use speeds closer to the most economical ones at each gait, which are quite apart from the gait transition speeds (Margaria, 1938; Hoyt and Taylor, 1981). The hypothesis that metabolic energy expenditure triggers the gait transition has not received support in recent studies. The transitions from trotting to galloping in horses (Farley and Taylor, 1991) and from walking to running in humans (Hreljac, 1993a; Minetti et al., 1994; Brisswalter and Mottet, 1996) occur at speeds slower than those predicted by the metabolic cost hypothesis. Although the metabolic cost per time or per distance travelled is higher during running than during walking at the transition speed, metabolic energy

expenditure per step appears to be the same for both gaits at the transition speed (Minetti et al., 1994). Thus, the metabolic hypothesis cannot be completely ruled out.

Farley and Taylor (Farley and Taylor, 1991) observed in horses carrying different weights that the trot–gallop transition occurred at different speeds but at the same level of the vertical ground reaction force. They proposed that the trot–gallop transition reduces the peak forces of the muscles. The walk–run transition in humans cannot be explained in the same way because the transition from walking to running increases peak vertical ground reaction forces (Nilsson and Thorstensson, 1989; Hreljac, 1993b).

The transition from walking to running in humans may be triggered by reaching a critical velocity of ankle flexion (Hreljac, 1995) and/or a critical angle between the thighs (Minetti et al., 1994) at fast walking speeds: both variables abruptly decrease after the walk–run transition. However, these possible limits of walking performance at fast speeds cannot explain the run–walk transition while locomotion speeds decrease (Kram et al., 1997) because the angle between the

thighs and the ankle flexion velocity change from smaller values during running to larger values during walking (Minetti et al., 1994; Hreljac, 1995).

One rather qualitative determinant of both the walk–run and run–walk transitions may be the rating of perceived exertion (Borg, 1973). At slow locomotion speeds (approximately below the gait transition speed), the rating of perceived exertion is lower during walking than during running; at faster speeds, the rating of perceived exertion is lower during running than during walking (Noble et al., 1973). The sense of perceived effort during low-intensity exercise (estimated by the rating of perceived exertion) is thought to originate from motor outflow commands to muscles (which can be quantified by muscle activation) and, to a lesser degree, from the afferent information about the actual force developed by the muscles (McCloskey et al., 1983). Thus, one can expect that the activation level of the leg muscles might behave similarly to the rating of perceived exertion and, thus, might explain both the walk–run and the run–walk transitions.

The purposes of this study were (i) to examine whether muscle activation values of major leg muscles could explain the walk–run and run–walk transitions in humans and, if so, (ii) to try to explain why locomotion at non-preferred speeds requires excessive muscle activation.

## Materials and methods

### Subjects

Seven male human subjects (age  $35 \pm 11$  years, height  $1.78 \pm 0.05$  m, mass  $72.5 \pm 10.9$  kg; means  $\pm$  s.d.) participated in the study after giving informed consent. The experimental protocol conformed with the Declaration of Helsinki for research involving human subjects and was approved by the Institutional Review Board. All subjects had prior experience of walking and running on a motor-driven treadmill. Before the experiments, each subject was required to warm up by walking and running on a treadmill at a self-selected speed for 15 min.

### Experimental protocol

In the first experiment, the preferred gait transition speed was determined by a procedure similar to that described by Hreljac (Hreljac, 1993a) and Kram et al. (Kram et al., 1997). This procedure was used to determine the walk–run transition at increasing speeds and the run–walk transition at decreasing speeds. The motor-driven treadmill was set at a relatively slow speed of  $1.4 \text{ m s}^{-1}$ , at which subjects could walk comfortably. Each subject had 1 min to try both walking and running and to select the gait that felt most comfortable. The subject then dismounted from the treadmill, the speed was increased by  $0.1\text{--}0.2 \text{ m s}^{-1}$ , and the subject again had 1 min to select a preferred gait. (The speed increment of  $0.1 \text{ m s}^{-1}$  was the smallest change in speed that could be reliably maintained and recorded by the treadmill.) The subject continued selecting the most comfortable gait until the speed reached  $3 \text{ m s}^{-1}$ , at which the subject always preferred running over walking. The slowest speed at which the subject selected running over walking as

his preferred gait was recorded. This procedure was repeated, but the initial speed was set at  $3 \text{ m s}^{-1}$  and decreased by  $0.1\text{--}0.2 \text{ m s}^{-1}$  to  $1.4 \text{ m s}^{-1}$ . The fastest speed at which the subject selected walking over running was recorded. Both procedures of determining gait transition speeds by incrementally increasing and decreasing speed yielded the same slowest running speed and the same fastest walking speed within each subject. Therefore, the preferred gait transition speed was defined as the mean of the two speeds determined as described above.

After determining the gait transition speed, the subjects walked and ran on the treadmill for 40 s at speeds 55, 70, 85, 100, 115, 130 and 145 % of the transition speed. Speeds below and above 100 % were considered preferred walking and preferred running speeds, respectively. All 14 experimental conditions (two gaits  $\times$  seven speeds) were randomly ordered and separated by a 2 min rest period.

### EMG recording and analysis

During the last several seconds of each 40 s locomotion trial, electromyographic (EMG) activity was sampled from muscles of the right leg at 1000 Hz using standard surface electrodes. The muscles studied included the major flexors and extensors of the lower extremity: the tibialis anterior (TA, ankle flexor), soleus (SO, ankle extensor), gastrocnemius medialis (GA, ankle extensor and knee flexor), vastus medialis (VA, knee extensor), rectus femoris (RF, knee extensor and hip flexor), long head of the biceps femoris (BFL, knee flexor and hip extensor) and gluteus maximus (GLM, hip extensor). Bipolar surface pellet electrodes were placed on the skin overlying the belly of the muscles under study at a level of two-thirds of the belly length from its distal end (at a level of one-third for the SO and VA). EMG activity was recorded and amplified using a telemetry system (Konigsberg Instruments Inc., Pasadena, CA, USA) and a multi-channel A/D board (National Instruments, Austin, TX, USA) and fed into a PC at 1000 Hz.

After the locomotion experiment, the maximum level of EMG activity was determined during maximum voluntary contractions in which subjects applied maximum force against resistance in standard limb positions (similar to those described by Ericson et al., 1985). Maximum raw electromyograms were amplified, bandpass-filtered (30–450 Hz), rectified and low-pass-filtered with a cut-off frequency of 10 Hz to obtain a linear envelope for each test. The peak value of EMG envelope obtained for each muscle was used to normalise the EMG activity recorded during the locomotion experiment.

Raw EMG activity recorded during locomotion was digitally bandpass-filtered (30–450 Hz), full-wave-rectified, normalised to the maximum EMG envelope peak recorded during maximum isometric contractions, shifted in time by 40 ms to account for the electromechanical delay (Prilutsky et al., 1998a), and then averaged separately over the stance and swing phases. The electromechanical delay (EMD) is a phase delay between the time courses of EMG activity and the muscle force. This delay is caused by excitation–contraction coupling and by the dynamics of the muscle–tendon complex. The shift

of 40 ms seemed to align best the EMG activity and the muscle mechanical action (joint moments) in this study. The  $\pm 20$  ms change in the selected EMD altered averaged EMG values insignificantly (typically by less than 5 %).

The linear EMG envelope, normalised to the peak of maximum EMG activity, was also calculated for each muscle using low-pass digital filtering (Butterworth, zero-lag, fourth-order, cut-off frequency 10 Hz) of the rectified EMG activity without the EMD shift. Maximum peaks of the EMG envelopes for each muscle were used for further analysis. Three locomotion cycles of each subject were analysed for each experimental condition.

#### *Kinematic and kinetic analyses*

Reflective markers were attached to four leg joints (fifth metatarsophalangeal, ankle, knee and hip) and to the iliac crest of the right side (Prilutsky et al., 1998a; Prilutsky et al., 1998b). During the 40 s locomotion trials, the EMG signals were recorded, and subjects were simultaneously videotaped at 60 Hz (Peak Performance Technology Inc., Englewood, CO, USA). After the experiment, the recorded video images were digitised, and the resulting marker coordinates were filtered (Butterworth low-pass, zero-lag, fourth-order filter) with cut-off frequencies between 5 and 7 Hz. The filtered coordinates of markers were used to calculate the resultant joint moments at the ankle, knee and hip joints in the sagittal plane during the swing phase of locomotion (Prilutsky et al., 1998a). We chose to calculate joint moments because they reflect the total activation of muscles crossing the corresponding joint, given little co-activation of antagonists. Joint moments during the stance phase were not calculated in this study because the ground reaction forces necessary for the calculations could not be measured with our treadmill. To calculate the joint moments, it was assumed that the foot, shank and thigh are rigid bodies interconnected by frictionless hinge joints. The body segment parameters necessary for calculations were estimated using the regression equations of Zatsiorsky et al. (Zatsiorsky et al., 1990). The calculated joint moments of each subject were averaged over three cycles at each percentage of the swing phase of locomotion, and the peak values of joint moments were used for further analysis.

Selected kinematic variables of walking and running were also determined and averaged over three cycles.

#### *Statistical analyses*

Three-factor two (gait: walking and running) by seven (speed: 55, 70, 85, 100, 115, 130 and 145 % of preferred transition speed) by three (cycle) repeated-measures analyses of variance (ANOVAs) were performed to test the effects of gait and speed on the normalised swing- and support-related EMG activity averaged over the swing and stance phases, respectively. The same ANOVA design was used to test the effects of these factors on the peaks of normalised EMG envelopes of each muscle and also on selected kinematic variables. Two-factor two (gait) by seven (speed) repeated-measures ANOVAs were used to examine the effects of gait

and speed on peaks of joint moments averaged over three cycles. *Post-hoc* comparisons were performed using the Duncan test ( $\alpha=0.05$ ).

## **Results**

### *Gait transition speed*

The mean preferred gait transition speed in this study was  $2.1 \pm 0.2 \text{ m s}^{-1}$  (mean  $\pm$  s.d.,  $N=7$ ). No difference was found between the walk–run and the run–walk transition speeds. It should be noted, however, that a possible difference between the two transition speeds is likely to be smaller than  $0.1 \text{ m s}^{-1}$  (Thorstensson and Roberthson, 1987) and thus would not be detected in our study (see Materials and methods).

### *Muscle activation*

During both walking and running at all studied speeds, the SO, GA, VA and GLM had their activity bursts primarily during the stance phase (Fig. 1). This confirms that the function of these muscles in locomotion is to support and propel the body. Activation of the BFL was typically observed at the end of the swing phase with one exception (walking at the maximum speed), at which the BFL also had high levels of activation at the beginning of stance. The TA and RF muscles typically had two major periods of activity: at the beginning of stance and during swing (Fig. 1). Thus, the TA, RF and BFL are the major muscles controlling the swing leg.

The activation of muscles with swing-related function (TA, BFL and RF) was typically lower during running than during walking at preferred running speeds (115, 130 and 145 %). This was true for both the EMG activity averaged over the swing phase ( $P<0.05$ , Fig. 2A; with one exception, BFL at 115 %) and for the EMG envelope peaks associated with swing ( $P<0.05$ , Fig. 2B). At preferred walking speeds (55, 70 and 85 %), the two EMG indices of the TA, BFL and RF had a tendency to be lower during swing of walking than during swing of running. However, this result was statistically significant only for the averaged EMG activity of the TA (at 55 %) and BFL (at 55 and 70 %) and for the EMG envelope peaks of the TA (at 55 and 70 %) (Fig. 2A,B). The above results demonstrate that, as walking speeds increase beyond the transition speed, the switch from walking to running reduces the average and peak activation of the muscles active during swing. The stance-related EMG envelope peaks of the TA and RF did not have a clear gait-related tendency.

The averaged EMG activity of muscles with pure support-related functions (SO, GA, VA and GLM) was typically lower during walking than during running at preferred walking speeds (55, 70 and 85 %;  $P<0.05$ , Fig. 2A; with the exception of the GLM). At faster speeds, there were typically no statistically significant differences in the averaged EMG activity between walking and running ( $P<0.05$ , Fig. 2A; with the exceptions of the GA and GLM at speeds of 100 and 115 %). Although changes in EMG envelope peaks of the SO, GA, VA and GLM with speed and gait were similar, in general, to those of the averaged EMG activity, statistically significant

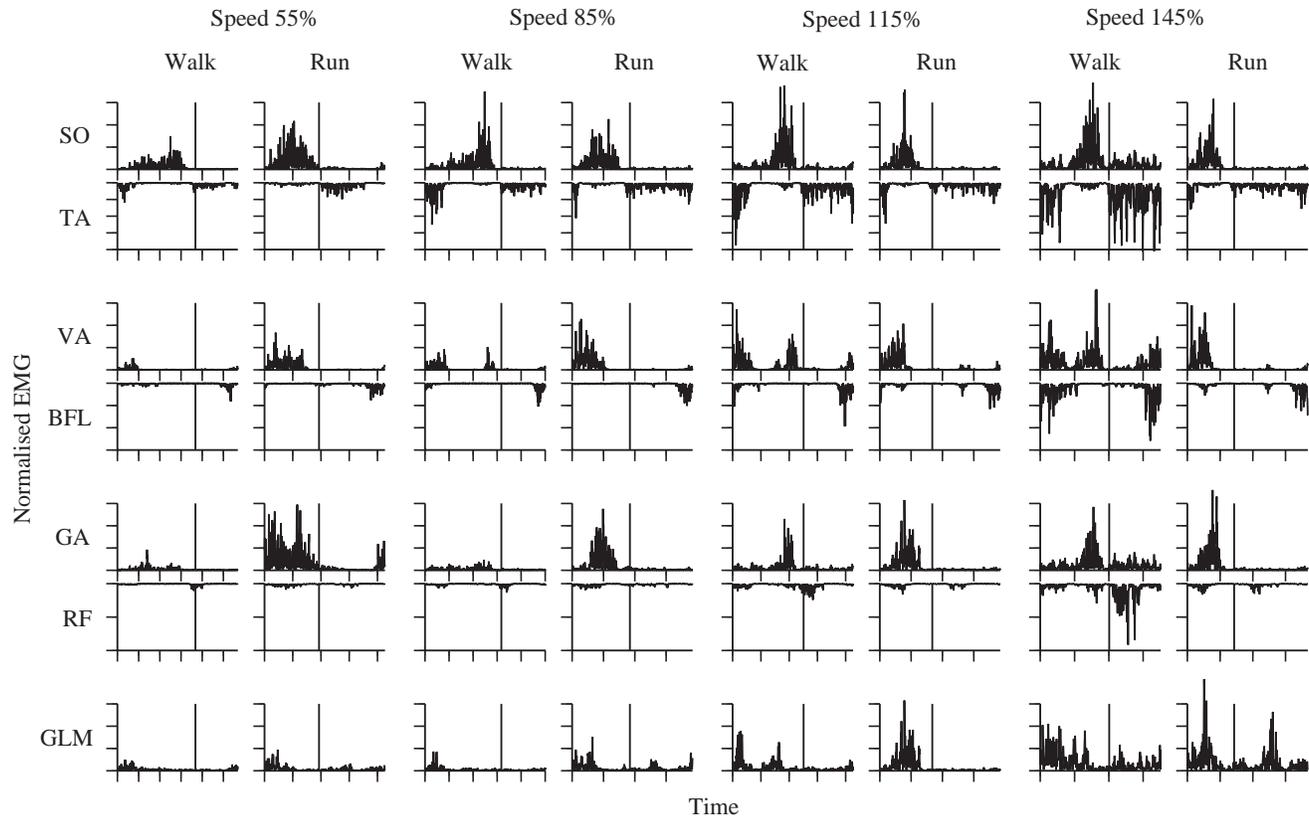


Fig. 1. Full-wave-rectified normalised electromyographic (EMG) recordings of major leg muscles during one cycle of walking and running at selected speeds of a typical subject. Speed is given as a percentage of the preferred gait transition speed. One vertical scale division in all plots corresponds to 100% of the corresponding peak of the EMG envelope in maximum isometric contraction; one horizontal scale division in all plots corresponds to 200 ms. EMG activity was shifted to the right along the time axis by 40 ms to account for the electromechanical delay between muscle activation and joint moments. Vertical lines separate the stance phase (on the left of the line) from the swing phase (on the right of the line). EMG activity of the ankle extensors (SO and GA), knee extensor (VA) and hip extensor (GLM) whose activation was primarily associated with the stance phase has positive values. EMG activity in the ankle flexor (TA), knee flexor (BFL) and hip flexor (RF) whose activation was primarily associated with the swing phase is inverted. SO, soleus; GA, gastrocnemius medialis; VA, vastus medialis; GLM, gluteus maximus; TA, tibialis anterior; BFL, long head of biceps femoris; RF, rectus femoris.

( $P < 0.05$ ) differences in the envelope peaks consistent with the averaged EMG activity were found only for the SO (at 55, 70%), the GA (at 55–100%) and the VA (at 55%) (Fig. 2B). This discrepancy was probably caused by a larger variability in the peak EMG compared with the averaged EMG activity. The above results indicate, in general, that, as speeds of running decrease below the transition speed, there is a tendency for a reduction in EMG activity in the support-related muscles after the switch from running to walking.

The sum of normalised swing- and support-related EMG activities, averaged over swing and stance, respectively, was lower during walking than during running at preferred walking speeds (55, 70 and 85%) and at the transition speed 100% ( $P < 0.05$ , Fig. 3A); it was lower during running than during walking at preferred running speeds of 130 and 145% (although the difference was significant only at 145%;  $P < 0.05$ , Fig. 3A). Similar results were generally obtained for the sum of EMG envelope peaks (described above, Fig. 2B) of all seven muscles. At preferred walking speeds of 55, 70 and 85%, the sum of EMG envelope peaks was lower during walking than

during running ( $P < 0.05$ , Fig. 3B); at preferred running speeds of 130 and 145%, the sum of EMG peaks was lower during running than during walking (Fig. 3B).

It should also be mentioned that, according to the ANOVA results, in most cases the averaged EMG activity and the EMG envelope peaks were significantly affected by gait, speed and/or the gait/speed interaction ( $F_{6,36} = 0.83\text{--}18.58$ ,  $P < 0.05$ ). In particular, both EMG indices increased with walking and running speed (Fig. 2, Fig. 3).

#### Kinematics

With increasing speed, the swing duration during walking decreased, whereas the swing duration during running increased slightly (Table 1). As a result, swing durations were longer during running than during walking at speeds of 100, 115, 130 and 145% ( $P < 0.05$ ; Table 1). This difference increased from 50 ms at a speed of 100% to 124 ms at a speed of 145%. The magnitude of knee angle changes during swing increased with speed for both walking and running ( $P < 0.05$ ) and was statistically larger during running (68–79°) than

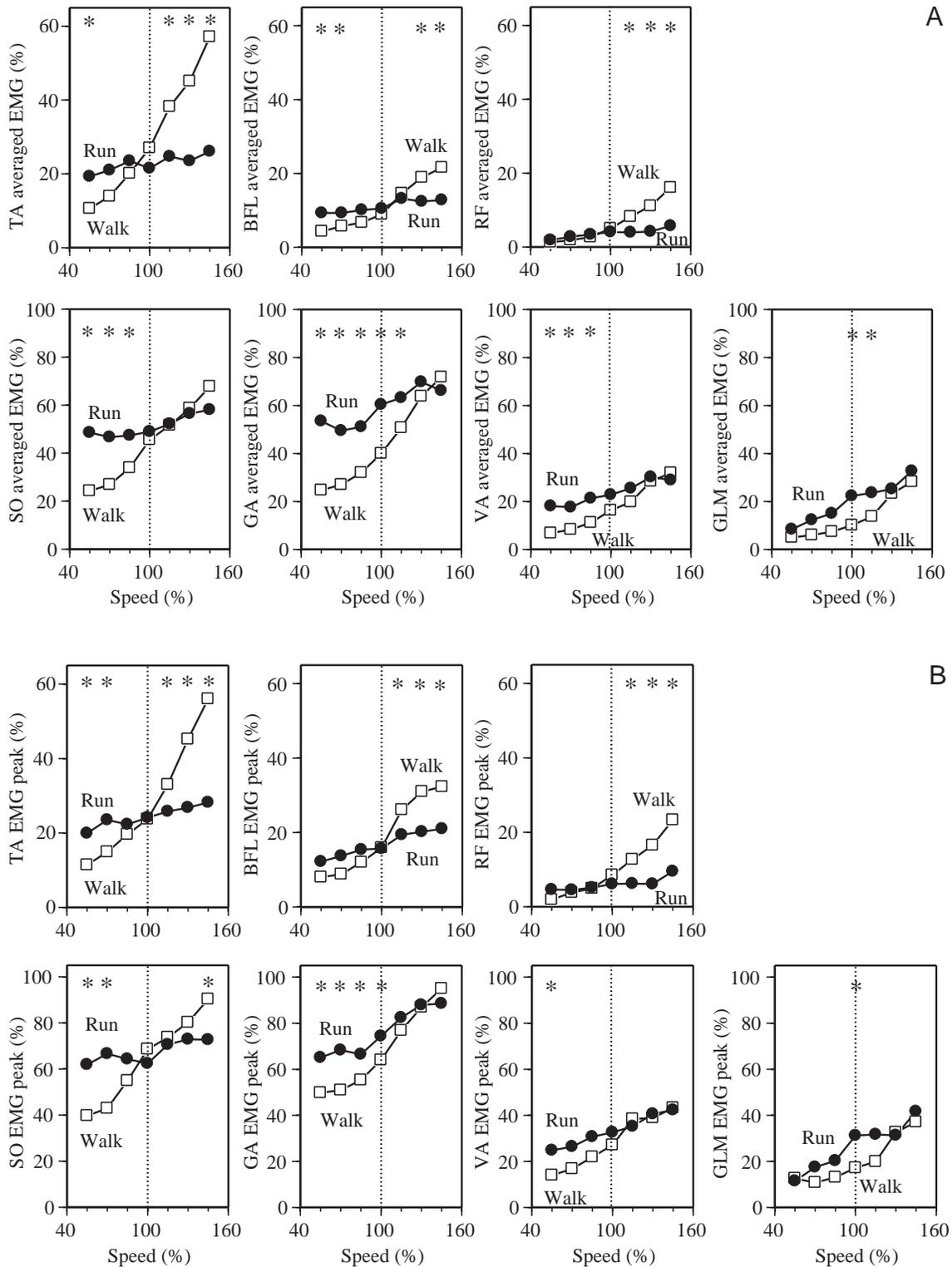


Fig. 2. Averaged normalised electromyographic (EMG) activity (A) and EMG envelope peaks (B) of leg muscles during walking and running at different normalised speeds. A speed of 100% corresponds to the gait transition speed ( $2.1 \pm 0.2 \text{ m s}^{-1}$ ). Swing-related muscles whose EMG activity was averaged over the swing phase (see A) include the tibialis anterior (TA), the long head of the biceps femoris (BFL) and the rectus femoris (RF). Support-related muscles whose EMG activity was averaged over the stance phase (see A) include the soleus (SO), the gastrocnemius medialis (GA), the vastus medialis (VA) and the gluteus maximus (GLM). An asterisk indicates a significant ( $P < 0.05$ ) difference in EMG activity between walking and running at the same speed. Normalised swing-related EMG activities in the TA, BFL and RF were typically lower during running than during walking at preferred running speeds (115, 130 and 145%), whereas support-related EMG activity in the ankle and knee extensors (SO, GA and VA) was typically lower during walking than during running at preferred walking speeds (55, 70 and 85%).

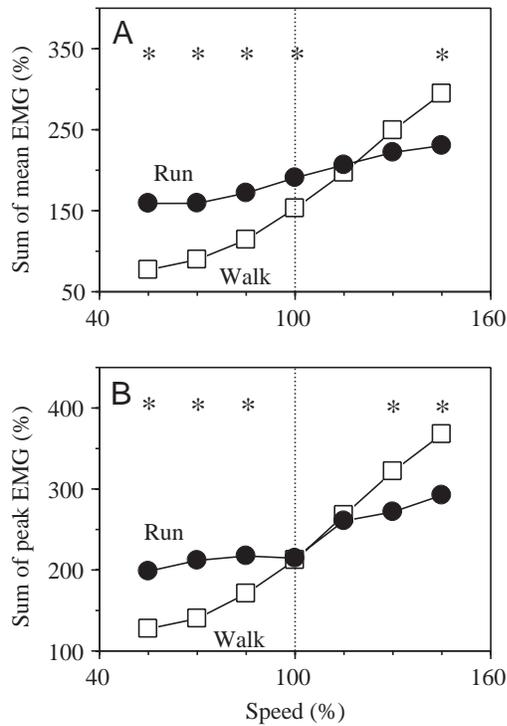


Fig. 3. General electromyographic (EMG) variables during walking and running at different normalised speeds. (A) Normalised EMG activity in the swing- and support-related muscles, averaged over swing and stance, respectively, and then summed across all muscles. (B) Peaks of linear EMG envelopes summed across all muscles. A speed of 100% corresponds to the gait transition speed ( $2.1 \pm 0.2 \text{ m s}^{-1}$ ). An asterisk indicates a significant ( $P < 0.05$ ) difference in EMG activity between walking and running at the same speed.

during walking ( $56\text{--}65^\circ$ ) at preferred running speeds 115, 130 and 145% ( $P < 0.05$ , Table 1). The average speed of ankle flexion and of angle change between the thighs during swing increased with locomotion speed ( $P < 0.05$ ). These two angular speeds were lower during running than during walking at preferred running speeds ( $P < 0.05$ , Table 1). The kinematic results presented in Table 1 appear to indicate higher mechanical demands on muscles controlling the swing leg during walking than during running at preferred running speeds.

*Joint moments in swing*

As mentioned in the Materials and methods section, joint moments in the swing phase characterise swing-related muscle function quantitatively. Patterns of joint moments during the swing phase were, in general, similar across different speeds and gaits (Fig. 4). During approximately the first two-thirds of the swing of walking and running, the ankle moment was flexion at all speeds; during late swing, the moment was extension. At all speeds studied, the knee moment was extension during walking during the first half of swing, and it was flexion during the second half. During running at slow preferred walking speeds, the knee moment was flexion (speed 55%, Fig. 4) or close to zero (speed 85%) during the first part of swing and always flexion during the second part of swing. During running at preferred running speeds, the knee moment was slightly extension in the first half of swing and flexion in the second half of swing (Fig. 4). The hip moments during walking and running were similar at all speeds (Fig. 4): flexion during the first half of swing and extension during the second half of swing.

Peaks of flexion moments at the ankle, knee and hip and

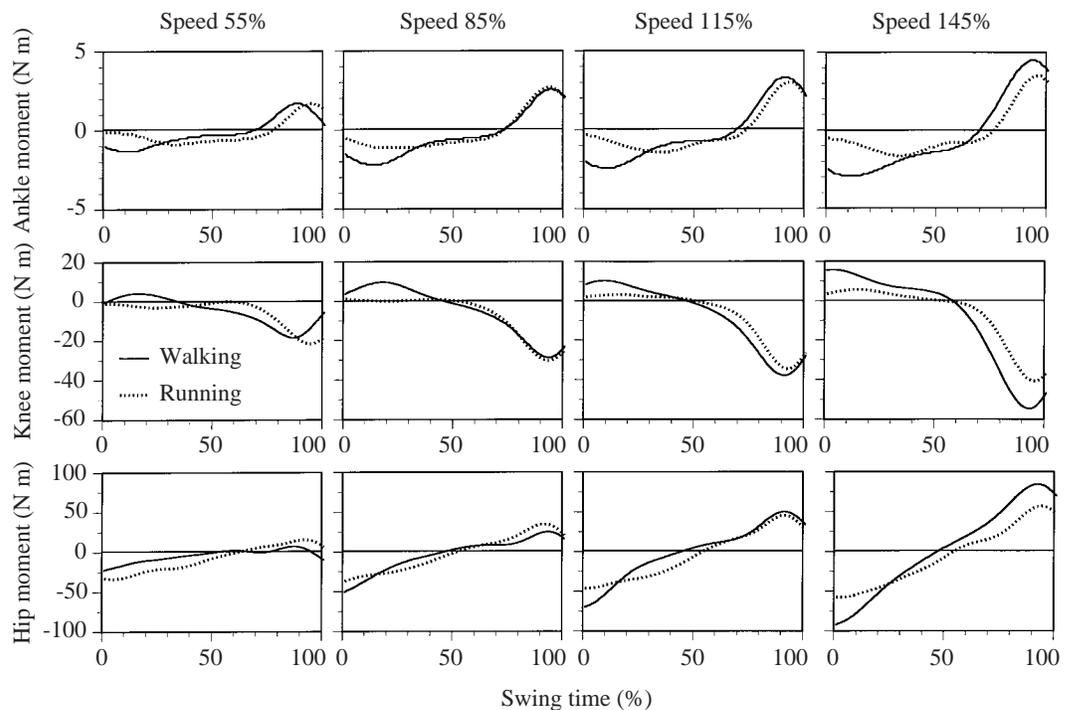


Fig. 4. Moments at the ankle, knee and hip joints during the swing phase of walking (solid lines) and running (broken lines) at selected speeds. Moments are averaged across three cycles of one subject. Extension moments are positive; flexion moments are negative. A speed of 100% corresponds to the gait transition speed ( $2.1 \pm 0.2 \text{ m s}^{-1}$ ).

Table 1. Selected kinematic variables of the swing phase of walking and running

Speed (%)	Gait	Swing duration (ms)	Range of knee motion (degrees)	Average speed of ankle flexion (degrees s <sup>-1</sup> )	Average speed of thigh angle change (degrees s <sup>-1</sup> )
55	W	406±53	60.4±4.4	49.3±20.1	65.9±3.4
	R	399±79	51.1±14.4*	59.8±36.3	65.5±9.8
70	W	368±41	60.9±3.9	60.1±22.9	80.5±5.2
	R	367±52	57.3±4.4	68.6±40.6	74.4±8.5
85	W	364±26	59.6±3.4	69.3±21.4	92.6±10.7
	R	389±40	59.5±6.2	65.4±27.4	83.9±10.8
100	W	345±25	59.6±5.5	81.7±21.6	105.3±12.2
	R	395±42	62.4±7.4	69.2±25.3	96.8±11.0
115	W	327±27	55.5±7.4*	86.1±16.2*	124.4±19.4*
	R	414±54	67.9±7.8	70.6±19.7	107.3±12.6
130	W	334±15	61.6±6.5*	89.4±22.7*	134.7±20.0*
	R	414±44	76.2±10.5	71.5±27.7	119.9±16.8
145	W	305±19	64.6±9.2*	102.1±23.5*	156.0±29.2*
	R	429±51	78.7±9.2	77.7±37.6	131.9±16.8

\*Statistically significant ( $P<0.05$ ) difference between walking (W) and running (R) at a given speed.

Values are means  $\pm$  S.D. ( $N=7$ ).

A speed of 100% corresponds to the gait transition speed ( $2.1\pm 0.2$  m s<sup>-1</sup>).

peaks of the hip extension moments increased with locomotion speed ( $P<0.05$ ) and were typically smaller during running than during walking at preferred running speeds (115, 130 and 145%;  $P<0.05$ , Fig. 5; with the exception of the hip flexion moment at 115%). These results are generally in agreement with the EMG results (Fig. 2A,B) for the muscles that have swing-related functions: the TA, which generates the ankle flexion moment during swing, BFL, which generates knee flexion and hip extension moments during late swing, and RF, which generates knee extension and hip flexion moments during early swing (Fig. 1, Fig. 4). Some of the above-mentioned moment peaks were smaller during walking than during running at preferred walking speeds ( $P<0.05$ , Fig. 5:

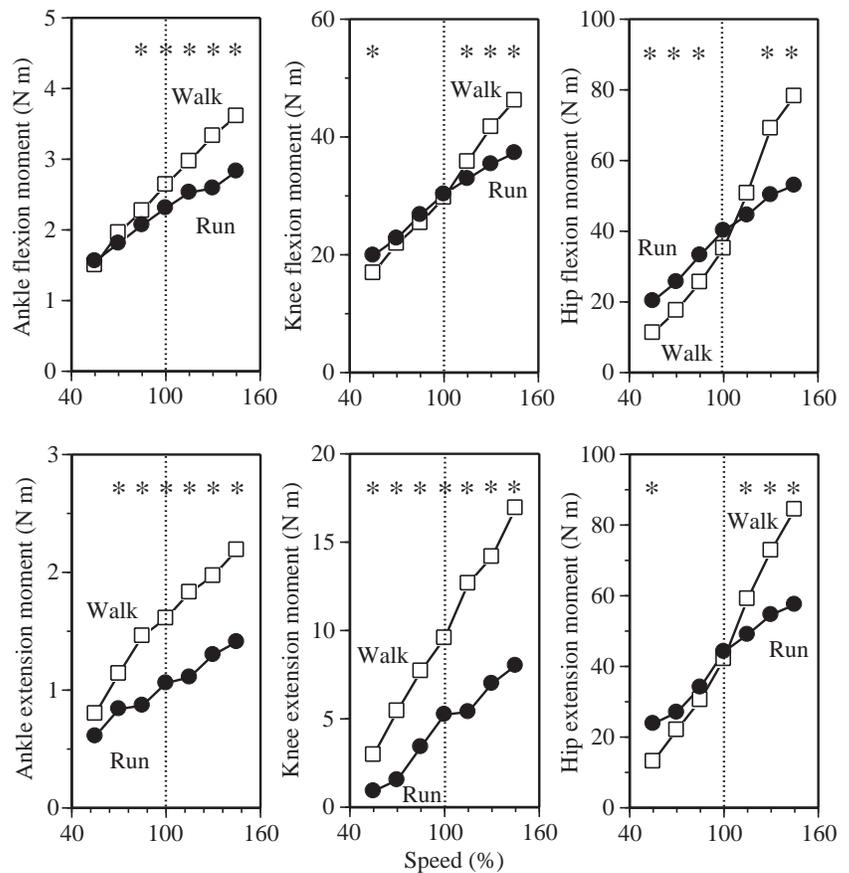


Fig. 5. Peaks of joint moments in swing during walking and running at different normalised speeds. A speed of 100% corresponds to the gait transition speed ( $2.1\pm 0.2$  m s<sup>-1</sup>). An asterisk indicates a significant ( $P<0.05$ ) difference in moment peaks between walking and running at the same speed. Peaks of ankle, knee and hip flexion moments and peaks of hip extension moments were typically smaller during running than during walking at preferred running speeds (115, 130 and 145 %).

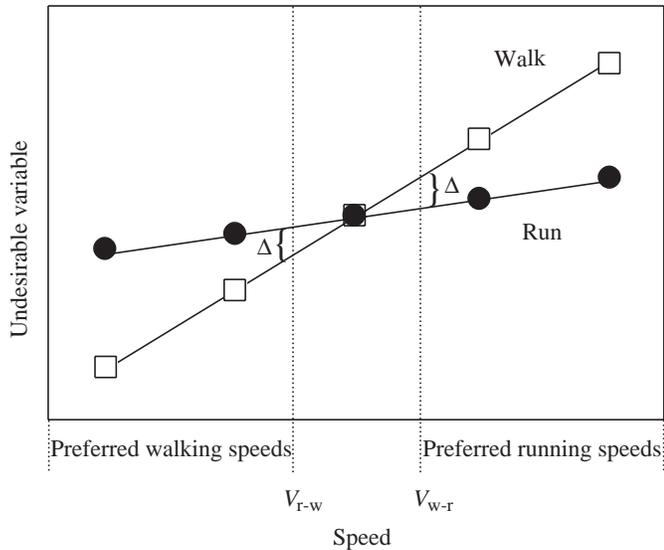


Fig. 6. Changes in a hypothetical undesirable variable that can trigger gait transitions. As walking speed increases and the magnitude of a variable during walking exceeds that during running by the threshold  $\Delta$ , the walk–run transition occurs at the speed  $V_{w-r}$  (right vertical line). As running speed decreases and the magnitude of a variable during running exceeds that during walking by the threshold  $\Delta$ , the run–walk transition occurs at the speed  $V_{r-w}$  (left vertical line). According to this definition of the gait transition trigger, the walk–run transition occurs at a faster speed than the run–walk transition.

knee flexion and hip extension moments at 55%, and hip flexion moments at 55, 70 and 85%).

Peaks of ankle and knee extension moments also increased with locomotion speed ( $P < 0.05$ ) and were larger during walking than during running at almost all speeds ( $P < 0.05$ , Fig. 5; with the exception of the ankle extension moment at 55%).

### Discussion

The purposes of this study were to examine whether activation of major leg muscles could be considered a trigger for the walk–run and run–walk transitions and, if it could, to explain why locomotion at non-preferred speeds requires excessive muscle activation.

To find a trigger for the walk–run transition, one might search for a certain undesirable variable that becomes larger during walking than during running as locomotion speed increases beyond the preferred transition speed and is reduced by switching from walking to running (Fig. 6: preferred running speeds). Similarly, an undesirable variable can be considered a trigger for the run–walk transition if it becomes larger during running than during walking as locomotion speeds decrease beyond the preferred transition speed (Fig. 6: preferred walking speeds).

#### *Walk–run transition*

The results presented in Fig. 1 and Fig. 2 suggest that the

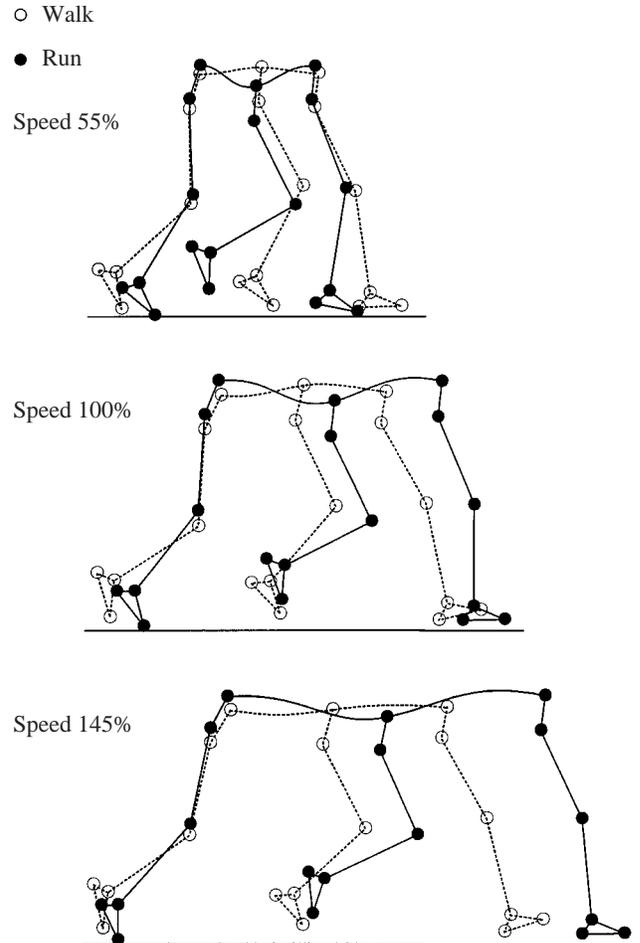


Fig. 7. Stick figure of the leg during swing during walking (open circles) and running (filled circles) at three normalised speeds for one subject. The three leg positions shown correspond to toe-off, middle swing and touch-down. Circles denote markers on the calcaneus, the fifth metatarsophalangeal joint, the lateral malleolus, the estimated centre of the knee joint, the greater trochanter and the iliac crest. Walking and running figures at a given speed are aligned such that the hip horizontal coordinates of the stick figures at toe-off coincide. The trajectory of the iliac crest is superimposed on the stick figures. The thigh angular amplitude is larger during walking than during running, whereas the vertical excursion of the iliac crest, the distance travelled during swing and the magnitude of knee flexion during swing are larger during running than during walking. A speed of 100% corresponds to the gait transition speed.

preferred walk–run transition may be triggered by the high swing-related activation of the TA, BFL and RF muscles during fast walking. Increased activation of these muscles during the swing phase of walking at fast speeds (Fig. 1, Fig. 2) is required to meet increased joint moment demands for acceleration and deceleration of the swing leg (Fig. 4, Fig. 5). The magnitude of thigh angular displacement during the swing phase was larger during walking than during running (Fig. 7; statistically significant differences occurred at speeds of 55–115%; see also Minetti et al., 1994). Also, the swing time was shorter during walking than during running at preferred

running speeds ( $P < 0.05$ ), and this difference doubled with increasing speed from 100 to 145 % (Table 1). As a consequence, the average angular thigh speed was significantly ( $P < 0.05$ ) higher during walking than during running at speeds 115, 130 and 145 % (Table 1). In addition, the knee joint is more extended during the swing phase of walking than during running (Table 1; Fig. 7; see also Grillner et al., 1979; Nilsson et al., 1985), which results in a larger moment of inertia of the leg with respect to the hip joint (Grillner et al., 1979; Nilsson et al., 1985). Thus, the higher angular speed of the thigh and the larger moment of inertia of the leg during walking at fast speeds require larger joint moments for acceleration (in the first half of swing; Fig. 4) and then deceleration (in the second half of swing; Fig. 4) of hip flexion (see also Prilutsky et al., 1998a; Winter, 1983a; Winter, 1983b) than during running at these speeds.

The angular acceleration and deceleration of the thigh developed during the swing phase by the hip flexors and extensors, respectively, causes the corresponding passive knee joint flexion (at the beginning of swing) and knee extension (during the second half of swing), respectively (Bernstein, 1935; Winter and Robertson, 1978). These knee flexion and extension movements are controlled by the activation of the RF and two-joint hamstrings, including the BFL, that produce braking knee extension and knee flexion moments, respectively (Cavanagh and Gregor, 1975; Winter, 1983a; Winter, 1983b; Prilutsky et al., 1996; Prilutsky et al., 1998a). Thus, relatively large knee extension and flexion moments during the swing phase of fast walking are associated with large hip flexion and extension moments and the corresponding high levels of activation of the RF and BFL (Fig. 1, Fig. 2, Fig. 4, Fig. 5).

The larger peaks of the ankle flexion moment and the higher levels of activation of the ankle flexor TA during walking compared with running at preferred running speeds (Fig. 1, Fig. 2, Fig. 4, Fig. 5) are also related to the shorter swing duration and the higher average angular speed of ankle flexion during walking than during running at speeds of 115–145 % (Table 1). This result is consistent with the observation that the peak angular velocity of ankle flexion during walking at preferred running speeds is abruptly reduced after switching to running (Hreljac, 1995).

The flexion moments at the ankle, knee and hip and the extension moment at the hip during swing (Fig. 4, Fig. 5) substantiate the EMG results and the conclusion that the high swing-related activation levels of leg muscles might be responsible for triggering the walk–run transition. Peaks of these joint moments, as for the swing-related activation of the corresponding muscles (Fig. 2; TA, BFL and RF), become larger during walking than during running after the preferred transition speed (Fig. 5). Since antagonistic co-activation among major leg muscles is relatively low during the swing phase (Fig. 1), it can be argued that the ankle flexion moment during the first two-thirds of swing (Fig. 4, Fig. 5) is primarily created by the ankle flexor TA; the knee flexion and the hip extension moments during the second half of swing (Fig. 4, Fig. 5) are primarily produced by the two-joint knee flexor and

hip extensor muscles, including the BFL (Fig. 1, Fig. 2), and the hip flexion moment during the first half of swing (Fig. 4, Fig. 5) is probably produced by the hip flexors RF (Fig. 1, Fig. 2) and iliacus (Inman, 1953).

Ankle and knee extension moment peaks during the swing phase of walking at the majority of studied speeds exceeded those during running ( $P < 0.05$ , Fig. 5). Therefore, it is unlikely that ankle and knee extension moment peaks during swing would trigger the gait transition (see Fig. 6), especially considering that the largest extension moment peaks obtained during the swing phase (Fig. 4) are approximately 10 % of the corresponding moment peaks developed during the stance phase of walking (Winter, 1983a).

#### *Run–walk transition*

The run–walk transition during decreasing locomotion speeds could be triggered by the high support-related activation of the ankle and knee extensors (SO, GA and VA) during the stance phase of slow running (Fig. 1, Fig. 2). The higher activation levels of these muscles during stance of slow running is likely to be required for deceleration and subsequent acceleration of the body, whose vertical displacement (judging from the iliac crest displacement) is larger during running than during walking at all speeds studied ( $P < 0.05$ ; see also Fig. 7). Peaks of vertical ground reaction forces are also larger during running than during walking at the same speeds (Nilsson and Thorstensson, 1989; Hreljac, 1993b) and, according to Farley and Taylor (Farley and Taylor, 1991), should require higher muscle forces.

The suggested role of the support-related activation of the SO, GA and VA in triggering the run–walk transition appears less convincing than the role of the swing-related activation of the TA, BFL and RF in the walk–run transition. First, the joint moments were not determined for the stance phase, and it is not known whether they were larger during stance of running than during walking at slow speeds in this study. Also, the activity of the GA and VA at 100 and 115 % of the transition speed was typically higher during running than during walking (and, for a speed of 115 %, that result might have been statistically significant if more subjects had been investigated; Fig. 2). This does not correspond to the trigger definition adopted in this study (Fig. 6). However, since the difference in the activation of the GA and VA between running and walking at 100 and 115 % was relatively small (6–14 % and 8–18 %, for the EMG activity peaks of the two muscles, respectively) compared with substantially greater differences at speeds of 55, 70 and 85 % (18–25 % and 29–44 %, respectively), it is possible that the support-related EMG activity during walking and running at 100 and 115 % was perceived by the subjects as the same.

Assuming that the perception threshold for a change in an undesirable variable has a finite value, the preferred run–walk transition speed should theoretically be slower than the walk–run transition speed. When preferred running speeds decrease and approach the gait transition speed range (Fig. 6; the area between the two vertical lines), the advantage of

switching to walking can only be detected when the difference in the variable between running and walking reaches the perception threshold ( $\Delta$ , Fig. 6). This will occur at the left vertical line in Fig. 6, which corresponds to the theoretical run-walk transition speed,  $V_{r-w}$ . With increasing preferred walking speeds, the walk-run transition occurs when a reduction in the variable due to switching to running becomes detectable (at the right vertical line in Fig. 6,  $V_{w-r}$ ). This explanation for the difference in the walk-run and run-walk transition speeds is consistent with the findings of Thorstensson and Roberthson (Thorstensson and Roberthson, 1987), but inconsistent with our results since we did not find differences between the two speeds. An explanation for this discrepancy is that the difference between the two transition speeds appears to be smaller than  $0.1 \text{ m s}^{-1}$  (Thorstensson and Roberthson, 1987), and the minimal speed increment for measuring gait transitions in our study was  $0.1 \text{ m s}^{-1}$  because of the technical limitations of the equipment. So, we may not have been able to detect the presumed difference between the two speeds. In the region between the walk-run and the run-walk transition speeds, the subject would not be able to decide which gait was more preferable. This prediction was partly supported in this study: the subjects often hesitated in choosing the preferred gait in the vicinity of the gait transition speed.

#### *Other possible triggers of the gait transitions and relationships between them*

Although only major extensor and flexor leg muscles were investigated in the present study and many more muscles, including those that create moments outside the plane of progression, are likely to be involved in locomotion, at least 75% of the total mechanical work for walking and running is supplied by joint moments in the plane of progression (Eng and Winter, 1995; Prilutsky and Zatsiorsky, 1992), which confirms the major contribution of the muscles studied here to walking and running. Therefore, the similarity between changes in the summed EMG activities of the muscles studied (Fig. 3A,B) and changes in the perceived exertion of walking and running at different speeds (Noble et al., 1973) may indicate that these two variables are closely related, especially considering the role of the motor commands in the sense of effort (McCloskey et al., 1983).

The results of the present study are consistent, in general, with the previous studies on determinants of the gait transition in humans. The lower total muscle activation during walking compared with running at preferred walking speeds (Fig. 3) is expected to lead to a lower rate of perceived effort (McCloskey et al., 1983) and a lower metabolic energy expenditure (Woledge et al., 1985; Minetti and Alexander, 1997). Both these expectations have been confirmed experimentally (Margarita, 1938; Noble et al., 1973). The lower total muscle activation (Fig. 3) and the smaller flexion moment peaks during swing during running compared with walking at preferred running speeds (Fig. 5) are also consistent with a smaller angle between the thighs and 'internal work' (Minetti

et al., 1994), a more flexed leg during swing (Grillner et al., 1979; Nilsson et al., 1985), smaller peaks of ankle flexion velocity (Hreljac, 1995), a lower rate of perceived effort (Noble et al., 1973) and lower metabolic energy expenditure (Margarita, 1938) during running at preferred running speeds.

Since the potential determinants of the gait transitions found in this and other studies are closely related, it is difficult to pinpoint just one primary reason for the gait transitions in humans. As discussed by Farley and Taylor (Farley and Taylor, 1991) and Minetti et al. (Minetti et al., 1994) and observed in the present study, subjects are capable of selecting a preferred gait at given speeds within several seconds or even steps. This suggests that the gait selection is more likely to be based either on mechanical factors (Farley and Taylor, 1991; Hreljac, 1995; Kram et al., 1997) or on the sense of effort originating from motor commands and afferent signals from muscles and joints rather than from receptors sensing metabolic changes in the body, which take longer than several seconds to establish a steady state. However, the total averaged EMG activities during walking and running with changing speeds (Fig. 3A) behave very similarly to the metabolic cost. In particular, the total averaged EMG activity and the metabolic cost are higher during running than during walking at the preferred transition speed (Hreljac, 1993a; Minetti et al., 1994; Brisswalter and Mottet, 1996). The sum of EMG peaks (Fig. 3B) also greatly resembles the metabolic cost plots reported by Mercier et al. (Mercier et al., 1994, their fig. 1). Moreover, the fact that the metabolic cost is typically lower for preferred gaits than for non-preferred ones (except in the vicinity of the preferred gait transition; Hreljac, 1993a; Minetti et al., 1994; Brisswalter and Mottet, 1996; but see Mercier et al., 1994) suggests that the metabolic cost may be a contributing factor to gait selection (Minetti et al., 1994; Minetti and Alexander, 1997), at least at speeds that are far from the preferred transition speed.

The idea that the gait transition with increasing locomotion speed could be caused by a mechanical trigger was supported by the observations that certain mechanical variables (ground reaction forces in horses, Farley and Taylor, 1991; the angle between the thighs in humans, Minetti et al., 1994; peak ankle angular velocity in humans, Hreljac, 1995) abruptly decrease at the preferred gait transition. Apart from the fact that these mechanical variables cannot explain the gait transition in the opposite direction at decreasing speeds (Kram et al., 1997), a non-preferred gait is still possible beyond the preferred transition speed despite exaggerated 'mechanical trigger' values: in this study, for example, all subjects could walk at 145% of the preferred transition speed.

The dynamics of an inverted-pendulum system has also been considered a possible trigger of the gait transition (Kram et al., 1997). Although the preferred gait transition speed decreases with decreasing gravitational force in accordance with the predictions of the inverted-pendulum model, it has still not been explained why humans and bipedal birds prefer to switch from walking to running at speeds of approximately half the maximum walking speed predicted by the model (Kram et al., 1997).

Taken together, the results of the present study and the data from the literature (see the above) support the hypothesis that the walk–run and run–walk transitions are triggered by an increased sense of effort due to exaggerated muscle activation required to meet the increased mechanical demands of non-preferred gaits. According to this hypothesis, the exaggerated swing-related activation of the TA, BFL and RF is primarily responsible for the walk–run transition at increasing speed, whereas the high support-related activation of the SO, GA and VA triggers the run–walk transition at decreasing speeds.

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