

Muscle activities of the lower limb during level and uphill running

Toshiharu Yokozawa^{a,*}, Norihisa Fujii^b, Michiyoshi Ae^b

^aDepartment of Sports Sciences, Japan Institute of Sports Sciences, 3-15-1 Nishigaoka, Kitaku, Tokyo 115-0056, Japan

^bInstitute of Health and Sports Sciences, University of Tsukuba, 1-1-1 Tennodai, Tsukuba, Ibaraki 305-8574, Japan

Accepted 28 May 2007

Abstract

This study aimed to compare the muscle activities of the lower limb during overground level running (LR) and uphill running (UR) by using a musculoskeletal model. Six male distance runners ran at three running speeds (slow: 3.3 m/s; medium: 4.2 m/s; and high: 5.0 m/s) on a level runway and a slope of 9.1% grade in which force platforms were mounted. A musculoskeletal leg model and optimization were used to estimate the muscle activation and muscle torque from the joint torque of the lower limb calculated by the inverse dynamics approach. At high speed, the activation and muscle torque of the muscle groups surrounding the hip joints, such as the hamstrings and iliopsoas, during the recovery phase were significantly greater during UR than during LR. At all the running speeds, the knee extension torque by the vasti during the support phase was significantly smaller during UR. Further, the hip flexion and knee extension torques by the rectus femoris during UR were significantly greater than those during LR at all the speeds; this would play a role in compensating for the decrease in the knee extension torque by the vasti and in maintaining the trunk in a forward-leaning position. These results revealed that the activation and muscle torque of the hip extensors and flexors were augmented during UR at the high speed.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: Uphill running; Musculoskeletal model; Muscle torque; Activation level

1. Introduction

Hill training on uphill and downhill slopes has been frequently used by distance runners to improve their aerobic ability, strength of the lower limb muscles, mental toughness, and so on (Tulloh, 1998). Physiological variables such as oxygen consumption, heart rate, and blood lactate concentration were greater during uphill running (UR) than during level running (LR) (Gregor and Costill, 1973; Pivarnik and Sherman, 1990; Staab et al., 1992); this implies that the mechanical load on the lower limb muscles is also greater during UR than during LR.

Several studies have investigated the kinematic parameters during UR and compared them with those during LR (Klein et al., 1997; Milliron and Cavanagh, 1990; Paradisis and Cooke, 2001). In addition to the kinematic studies, analyses of the kinetics and muscle activities of the

lower limb can provide us with information regarding the load on the lower limb muscles during UR. However, few studies have focused on investigating the kinetic differences between LR and UR.

Swanson and Caldwell (2000) investigated the kinetics of the recovery leg and the electromyography (EMG) of the lower limb muscles during LR and UR on a treadmill at 4.5 m/s and 30% grade. They observed that the average hip power during the recovery phase and the EMG amplitude of the gluteus maximus (GMAX), rectus femoris (RF), vastus lateralis (VAS), gastrocnemius (GAS), and soleus (SOL) during the support phase (SP) were higher during UR. However, the grade of the uphill slope used in the study was extremely steep thereby rendering it unfit for training distance runners in the real world. In addition, the ground reaction forces (GRFs) were not measured; thus, the joint torques of the support leg could not be calculated. Gottschall and Kram (2005) investigated the GRFs during LR and UR on a treadmill at 3.0 m/s with different grades (3°, 6°, and 9°). They demonstrated that the normal impact

*Corresponding author. Tel.: +81 3 5963 0224; fax: +81 3 5963 0232.

E-mail address: yokozawa.toshiharu@jiss.naash.go.jp (T. Yokozawa).

force was smaller and the parallel propulsive force was greater during UR; however, they did not calculate the joint torques of the lower limb.

Most of the abovementioned studies used treadmill running as the experimental task. Some investigations have demonstrated that there were differences between treadmill running and overground running with regard to the stride length, stride frequency, angular kinematics, and the EMG activities of the lower limb muscles (Elliott and Blanksby, 1976; Frishberg, 1983; Nelson et al., 1972; Nigg et al., 1995; Wank et al., 1998). These differences have been attributed to several factors such as fluctuation in the treadmill belt speed, air resistance, and so on (Pugh, 1970; van Ingen Shuenau, 1980). This implies that there are differences in the biomechanical variables between treadmill running and overground running on uphill slopes.

A musculoskeletal model and optimization with an inverse dynamics approach have been used to estimate the forces of the lower limb muscles during locomotion (Anderson and Pandy, 2001; Brand et al., 1986; Crowninshield and Brand, 1981; Pedersen et al., 1997). The musculoskeletal model enables us to examine the activities of the agonists and antagonists as well as those of the monoarticular and biarticular muscles.

It is expected that the force and activation of the muscles surrounding the hip joint of the recovery leg and those surrounding the hip and knee joints of the support leg would be greater during UR. However, there is no study that has investigated this hypothesis. In order to utilize UR for hill training, it is important to identify the characteristics of the load acting on the lower limb muscles during UR with regard to the types of muscle contraction, activation, and forces exerted by the muscles. The purpose of this study was to compare the muscle activities of the lower limb during overground LR and UR by using a musculoskeletal model.

2. Methods

2.1. Data collection

Six male distance runners (height, 1.69 ± 0.02 m; body mass, 57.2 ± 4.7 kg; personal best record in a 5000-m race, $16 \text{ min } 6 \pm 37$ s) participated in the experiment. Prior to the experiment, the subjects were explained the purpose and significance of the study, details regarding the data collection, and safety measures regarding the experimental set-up. Subsequently, informed consent was obtained from all the subjects. A customized wooden runway (length, 12 m) was set on level (LR) and at a slope of 9.1% grade (UR; Fig. 1). After adequate warm up on the level

and sloping surfaces, the subjects were instructed to run along the runway at 3 running speeds, i.e., 3.3, 4.2, and 5.0 m/s, on both surfaces. Photocells were set at a distance of 5 m before and after the force platforms and measured the time required for covering a distance of 10 m to control the running speeds.

The sagittal plane motion of the runners was captured by using a high-speed video camera (250 Hz; HSV-500C³, NAC Co., Tokyo, Japan). The GRF data were sampled at 500 Hz by using 2 Kistler force platforms (0.4 m \times 0.6 m; model 9281A, Kistler, AG) that were mounted in the runway (Fig. 1).

2.2. Data processing

Reflective markers were affixed to the body segment endpoints of the torso and lower limbs. These endpoints were digitized using a Frame-DIAS system (DKH Co., Tokyo, Japan) at 62.5 Hz during one running cycle (2 steps). Hip, knee, and ankle joint torques of the leg that was placed on the force platforms (FP-leg) were calculated from the GRF data and the two-dimensional coordinates reconstructed by applying direct linear transformation (DLT) method, and the data were smoothed using a Butterworth low-pass digital filter.

One running cycle was divided into the following 3 phases: the first half of the recovery phase (FRP), which began at toe-off of the FP-leg and terminated at the mid-support of the foot contralateral to the FP-leg; the second half of the recovery phase (SRP), from the mid-support of the foot contralateral to the FP-leg to foot contact of the FP-leg; and the SP, from foot contact to toe-off of the FP-leg.

2.3. Modelling of a musculoskeletal system and estimation of muscle forces of the lower limb

A two-dimensional model of FP-leg was developed by using SIMM (MusculoGraphics, Inc., Evanston, IL; Delp et al., 1990). Fig. 2 shows the musculoskeletal model developed in this study. The one-legged model comprised 33 Hill-type muscles. Although the hip adductors and abductors were included in this model, the muscle torques outside the sagittal plane generated by those were excluded for computational purposes, and only the hip extension and flexion torques by those were considered. The musculotendon complex comprised a contractile element, a passive elastic element in parallel with the contractile element, and a series elastic element serially connected with a pennation angle. The contractile element and the 2 passive elements followed the force-length-velocity characteristics and the stress-strain characteristics, respectively (Zajac, 1989). Equilibrium was maintained between the series elastic element (tendon) and the contractile and passive elastic elements (muscle). The maximum isometric force, optimal fibre length, tendon slack length, and pennation angle were derived from Yamaguchi et al. (1990). Seventeen major muscles out of 33 muscles were divided into the following 9 groups: GMAX; semimembranosus, semitendinosus, and long head of biceps femoris (HAMS); iliacus and psoas (ILP); adductor longus, adductor brevis, and adductor magnus (ADD); RF; vastus medialis, vastus intermedius, and VAS; medial and lateral GAS; SOL; and tibialis anterior (TA).

The problem regarding distribution of the total torque between muscles (Crowninshield and Brand, 1981) was resolved by using optimization. The objective function (J) was to minimize activation cubed, summed across all joints

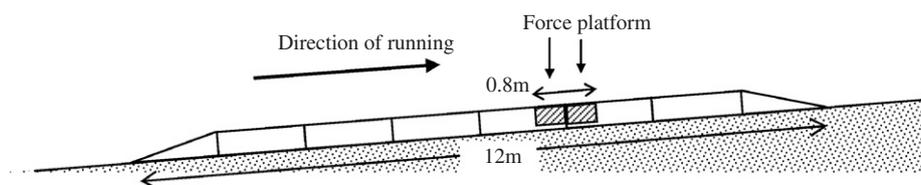


Fig. 1. Set-up of the runway and force platforms.

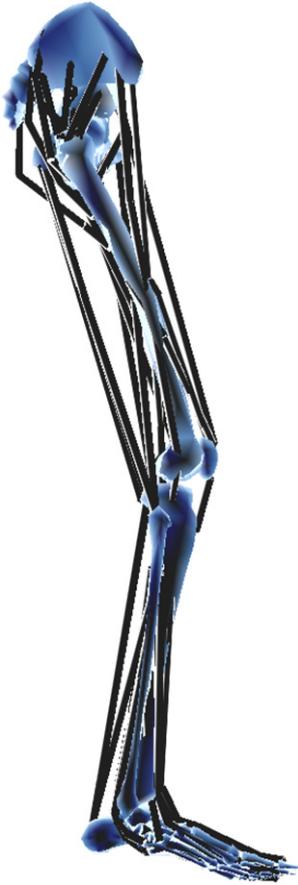


Fig. 2. The musculoskeletal model for the lower limb developed in this study, which comprises 33 Hill-type muscles.

(Anderson and Pandy, 2001; Crowninshield and Brand, 1981):

$$J = \sum_{m=1}^{33} (q_m)^3, \quad (1)$$

where q_m is the activation of muscle m . The net joint torques of all muscles were constrained to match those estimated by the inverse dynamics approach:

$$JT_j = \sum_{m=1}^{33} MT_{j,m}, \quad (2)$$

where JT_j is the torque of joint j , and $MT_{j,m}$ is the muscle torque generated by muscle m on joint j .

The optimization algorithm was formulated to determine the activation for each muscle so that the objective function of Eq. (1) was minimized and the constraint condition of Eq. (2) was satisfied. Subsequently, the muscle force, muscle torque, and contraction velocity were estimated from the optimized activation. The activation and contraction velocity of the muscle groups were defined as the average of the corresponding values of the muscles investigated, while the muscle torque of the muscle groups were the sum of the torques of the muscles investigated. For presentation of results, the muscle force and muscle torque were divided by the body mass. The time series data of all subjects were normalized to the time of a step as 50% and to one running cycle as 100%, and subsequently averaged.

2.4. Statistical analysis

A two-way analysis of variance (ANOVA) with repeated measures on two independent factors (grade of slope \times running speed) was applied to test for significant differences in the variables between LR and UR. The level of significance was set at 5%.

3. Results

3.1. Comparison of the estimated muscle activation with EMG

Fig. 3 shows the average muscle activation and the EMG envelope by Yokozawa et al. (2005) in one running cycle for LR at the high speed. The activation patterns of most muscles were consistent with those of the EMG envelopes with the exception of some differences in the case of RF.

3.2. Muscle activation

Fig. 4 shows the average activation of the muscle groups in one running cycle for LR and UR at the 3 speeds. During LR and UR, the activation of ILP was the greatest among the 9 muscle groups. At the high speed, the activations of most muscle groups tended to be greater during UR than during LR, and significant differences between LR and UR were observed with regard to the activations of HAMS, ILP, ADD, and VAS at high speed ($p < 0.05$). However, there were no significant differences in the activations of the muscle groups between LR and UR at medium and slow speeds.

3.3. Muscle torque

Fig. 5 shows the average pattern of the net joint torque and muscle torques of the hip, knee, and ankle in one running cycle for LR and UR at high speed. The hip flexion torque was dominant in FRP, and ILP, ADD, and RF were the major contributors to the hip flexion torque. The hip extension torque was dominant from SRP to the middle part of SP during both LR and UR. HAMS contributed greatly to the hip extension torque; additionally, GMAX and ADD were involved in the generation of the hip extension torque during both LR and UR. During LR, the hip extension torque was dominant before toe-off, especially during 70–75% of one running cycle. During UR, RF acted as an antagonist to the hip extension torque, and the net torque of the hip joint was approximately zero in the second half of SP. During both LR and UR, the knee flexion torque by HAMS was dominant in SRP. The knee extension torque by VAS was large in SP, and HAMS and GAS acted as antagonists to the extension torque during both LR and UR. The plantar flexion torque by GAS and SOL was dominant in SP during both LR and UR. The dorsiflexion torque by TA was very small throughout one running cycle during both LR and UR.

Fig. 6 shows the average net joint torque and muscle torques of the hip in the 3 phases of LR and UR at all the speeds. At the high speed, the absolute values of the net hip torque and hip torque by ILP in FRP were significantly greater during UR than during LR ($p < 0.05$). The net hip torque at the high and medium speeds, the hip torque by HAMS at the high speed, and the hip torque by ADD at all the speeds in SRP were significantly greater during UR

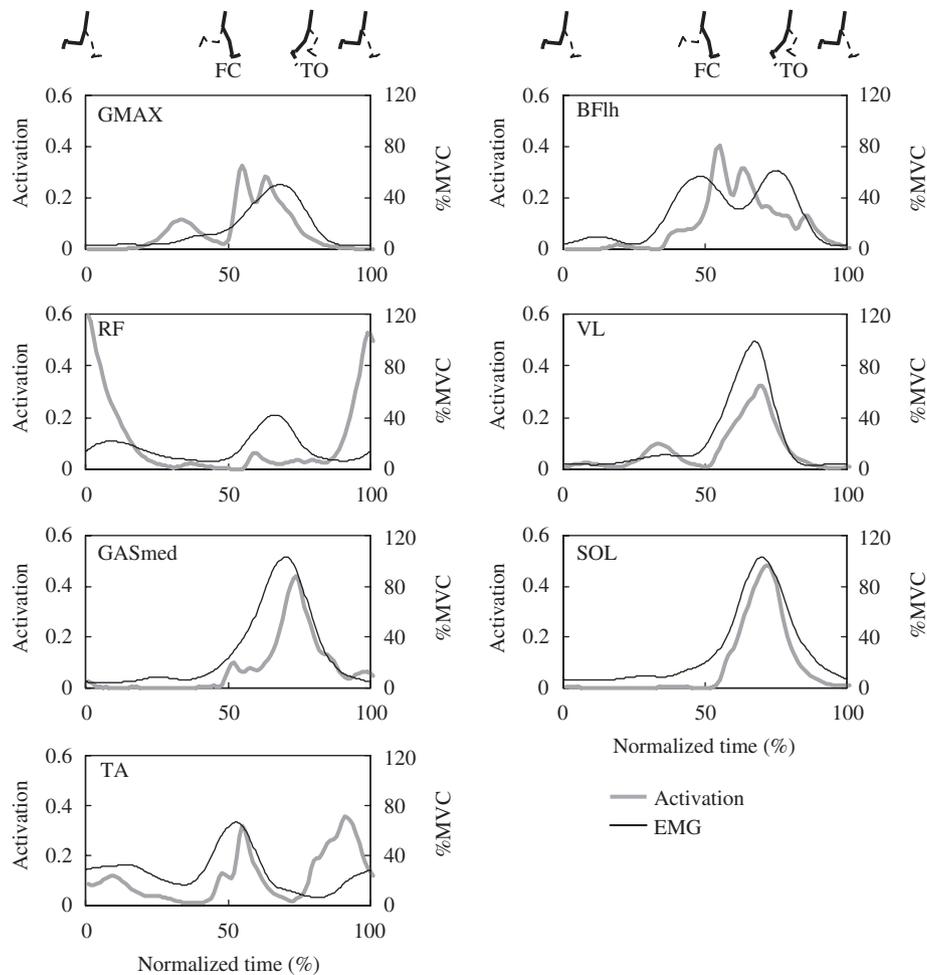


Fig. 3. Comparisons of estimated muscle activation with the EMG envelope divided by the mean amplitude at the maximum voluntary contraction (MVC) in gluteus maximus (GMAX), long head of biceps femoris (BF1h), rectus femoris (RF), and vastus lateralis (VL), medial gastrocnemius (GASmed), soleus (SOL), and tibialis anterior (TA) for level running at the high speed. FC is foot contact. TO is toe-off.

($p < 0.05$). At all the speeds, the net hip torque and the hip torque by GMAX in SP were significantly smaller during UR ($p < 0.05$), and the absolute value of the hip torque by RF in SP was significantly greater during UR ($p < 0.05$).

Fig. 7 shows the average net joint torque and muscle torques of the knee in the 3 phases. There were no significant differences in the net joint torque and muscle torques of the knee in FRP between LR and UR at all the speeds. In SRP, the absolute values of the net knee torque and the knee torque by HAMS were significantly greater during UR at the high speed ($p < 0.05$). There was no significant difference in the net knee torque in SP between LR and UR at all the speeds. However, the knee extension torque by RF in SP was significantly greater during UR ($p < 0.05$), while the extension torque by VAS was significantly smaller during UR at all the speeds ($p < 0.05$).

Fig. 8 shows the average net joint torque and muscle torques of the ankle in SP. Since the ankle torque in the recovery phase was very small, it has not been shown in the figure. There were no significant differences in the net joint

torque and muscle torques of the ankle in SP between LR and UR at all the speeds.

4. Discussion

4.1. Activation of the lower limb muscles

The result that the estimated activation patterns of most muscles corresponded with those of the EMG envelopes (Fig. 3) indicates that it appears to be possible to compare the muscle activity of the lower limb during LR and UR although the two-dimensional model and the objective function used in the present study were not strictly valid. The muscle torque by RF in SP was estimated to be low so that the hip extension torque could be dominant; the actual torque value by RF may be larger in view of the EMG envelopes. It is important to recognize that motion and muscle torque outside the sagittal plane were excluded from this model. Therefore, it would be impossible to trust estimated muscle activities of the hip adductors and abductors. In addition, these muscles influenced the hip

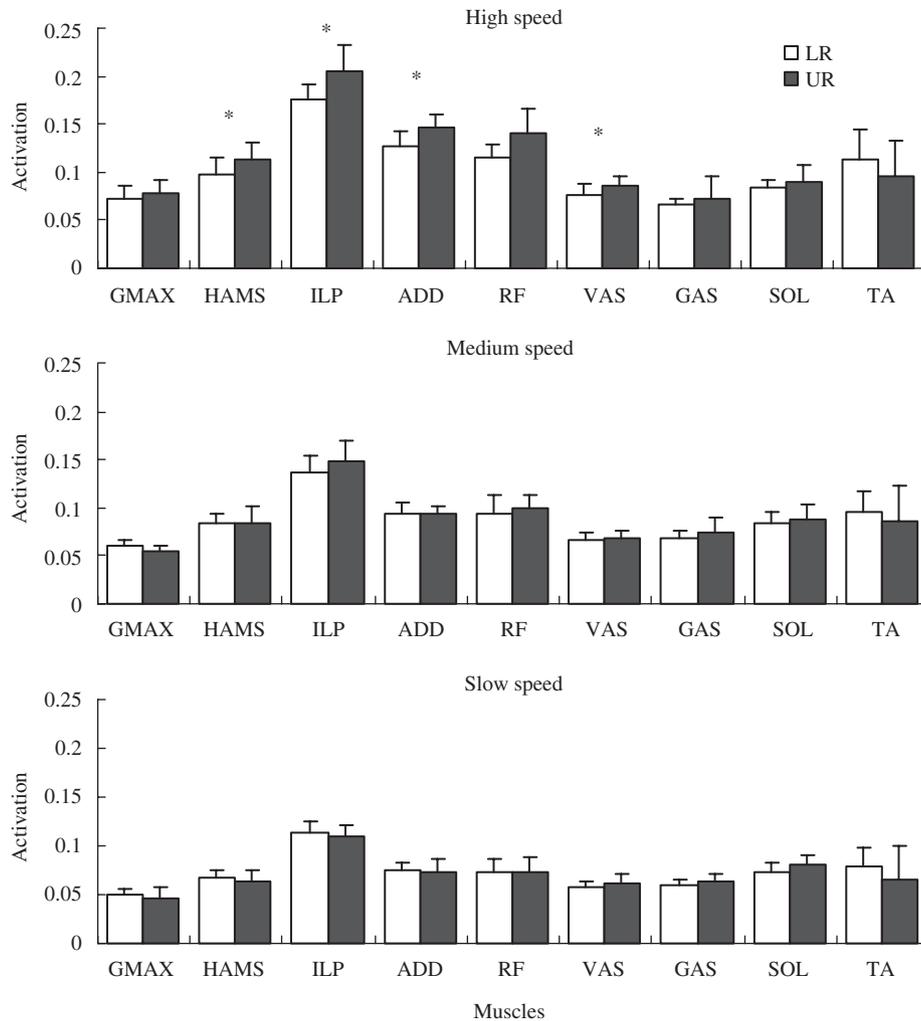


Fig. 4. Average activation of the muscle groups in one running cycle for level running (LR) and uphill running (UR) at the high (top), medium (middle), and slow (bottom) speeds. GMAX, gluteus maximus; HAMS, hamstrings; ILP, iliopsoas; ADD, adductors; RF, rectus femoris; VAS, vasti; GAS, gastrocnemius; SOL, soleus; TA, tibialis anterior. The symbol * indicates a significant difference between LR and UR at $p < 0.05$.

extension/flexion torques. The simplification used in this model may be one of the reasons for the decreased muscle torque by RF.

Previous studies (Gregor and Costill, 1973; Pivarnik and Sherman, 1990; Staab et al., 1992) have revealed that physiological variables, such as oxygen consumption, heart rate, and blood lactate concentration, were greater during UR. Greater activation of HAMS, ILP, ADD, and VAS during UR at the high speed (Fig. 4) may provide a biomechanical explanation for the observed increases in these physiological variables.

However, there were no significant differences in the activation of the muscle groups between LR and UR at medium and slow speeds. Yokozawa et al. (2003) reported that the step frequency was greater during UR on a slope of 9.1% than during LR at 5.0 m/s despite the lack of any significant differences in the step length and step frequency between LR and UR at 4.2 and 3.3 m/s. Therefore, the increase in muscle activation during UR at high speed would facilitate an increase in the step frequency; however,

the muscle activation did not increase during UR when compared with LR at medium and slow speeds because the runners used the same step length and step frequency as those used during LR.

4.2. Muscle torque of the lower limb

Greater net hip flexion torque in FRP during UR at the high speed (Figs. 5 and 6) contributed to faster and greater hip flexion in the recovery phase (Yokozawa et al., 2003). The finding that ILP contributed more than RF to the hip flexion torque during UR may be attributed to the fact that there was no significant difference in the net knee torque between LR and UR (Fig. 7). Increased ILP activity during UR would play an important role in faster and greater hip flexion in FRP. In SRP, greater muscle torques by GMAX, HAMS, and ADD during UR at the high speed increased the net hip extension torque and knee flexion torque, which would subsequently contribute to rapid backward swing of the leg before foot contact (Yokozawa et al., 2003).

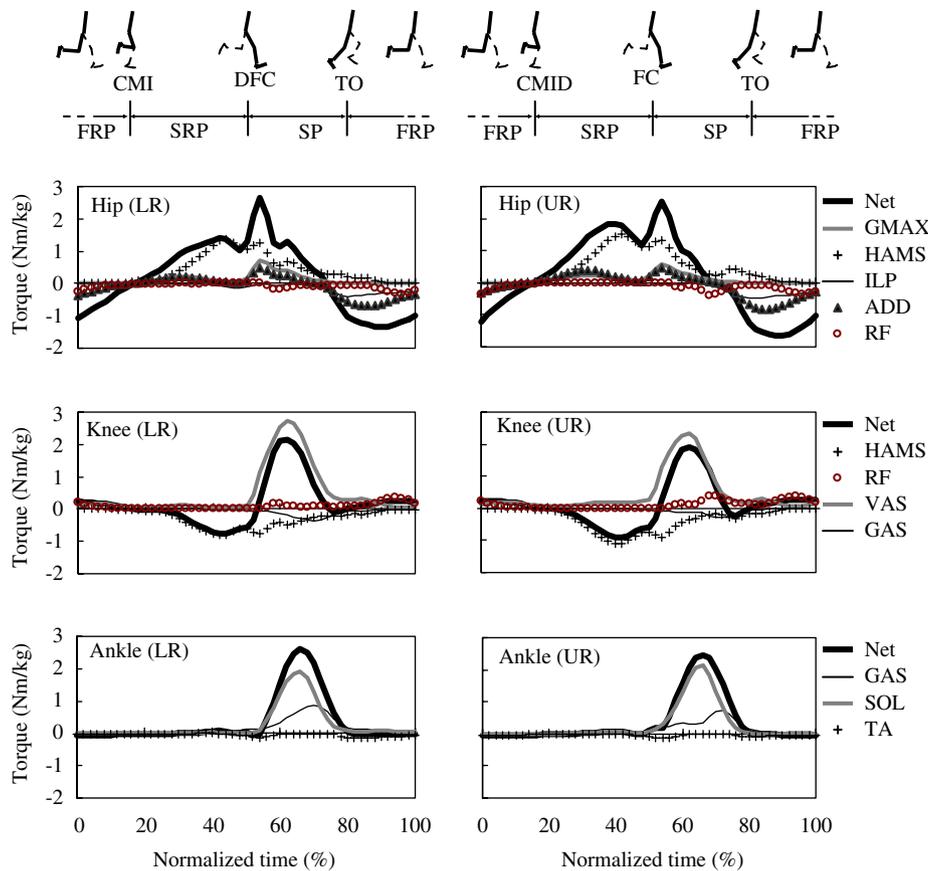


Fig. 5. Average pattern of the net joint torque (Net) and muscle torques of the hip (top), knee (middle), and ankle (bottom) in one running cycle for level running (LR; left) and uphill running (UR; right) at high speed. GMAX, gluteus maximus; HAMS, hamstrings; ILP, iliopsoas; ADD, adductors; RF, rectus femoris; VAS, vasti; GAS, gastrocnemius; SOL, soleus; TA, tibialis anterior. Positive values indicate extension (plantar flexion) torque and negative values indicate flexion (dorsiflexion) torque. CMID is the mid-support of the foot contralateral to the target leg. FC is foot contact. TO is toe-off. FRP is the first half of the recovery phase. SRP is the second half of the recovery phase. SP is the support phase.

Contrary to our expectation, the knee extension torque by VAS in SP was significantly smaller during UR at all the speeds. Fig. 9 shows the average pattern of the contraction velocity, muscle force, and theoretical maximum force of VAS in SP at the high speed. The theoretical maximum force was calculated based on the assumption that the activation was maximum (i.e., activation = 1) and considered as force exertion capacity based on the force-length-velocity characteristics. The contraction velocity of VAS during UR switched from lengthening to shortening earlier than that during LR in the middle of SP, and the shortening velocity of VAS during UR was greater. The muscle force and the maximum force of VAS tended to be smaller during UR from the middle to the end of SP. The theoretical maximum force decreases as the shortening velocity increases according to the force-velocity relationship. This indicates that VAS was not in an appropriate condition to exert a large force in SP during UR because of its greater shortening velocity.

One reason for the increased hip and knee torques by RF in SP during UR would be to compensate for the decrease in the knee extension torque by VAS. Heise et al. (1996) reported that economical runners exhibited a greater

amount of coactivation of RF and HAMS during SP when compared with noneconomical runners. In addition, the forward lean of the trunk is greater during UR throughout one running cycle (Paradis and Cooke, 2001; Yokozawa et al., 2003). This indicates that the increased coactivation of RF and HAMS during UR in the present study would help to maintain the trunk in a forward-leaning position.

The results of the present study suggested that the muscle activity surrounding the hip joint would be augmented and RF would be utilized effectively during UR at the high speed, which would provide useful information in designing training programs for distance runners. Further studies should focus on the energetics such as muscle power and muscle work in order to investigate the characteristics of UR as a training workout because runners need to increase the potential energy of their body centre of mass while running uphill.

5. Conclusions

This study revealed that the load on the lower limb muscles was greater during UR at the high speed due to

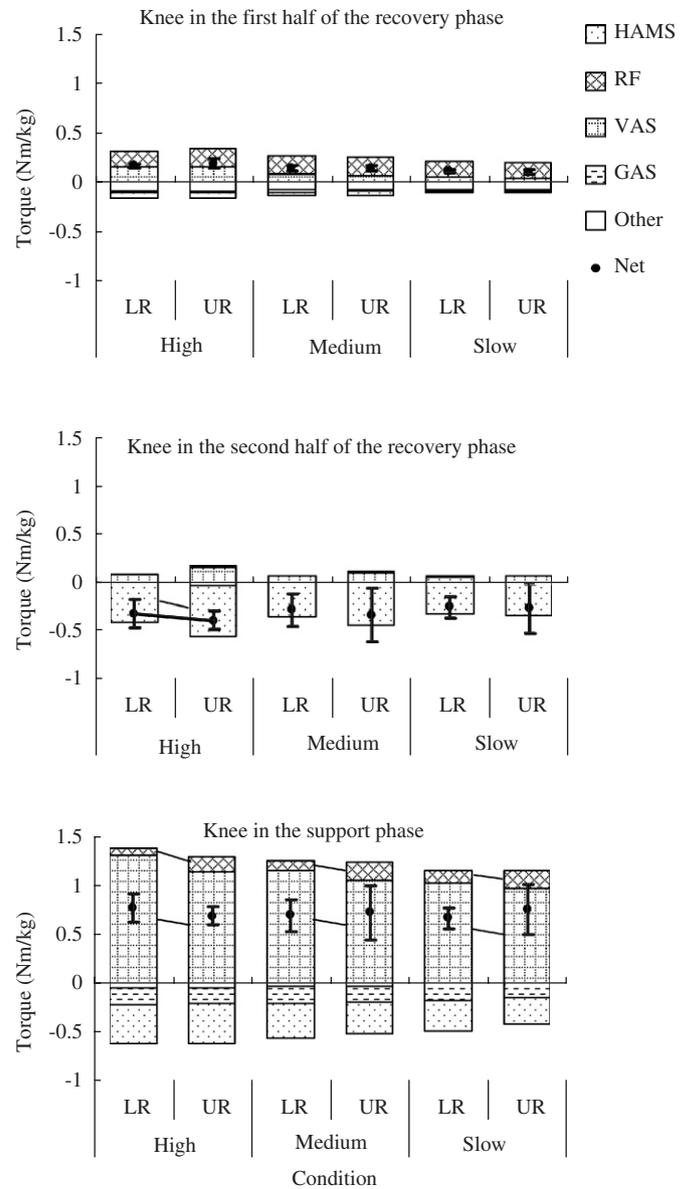
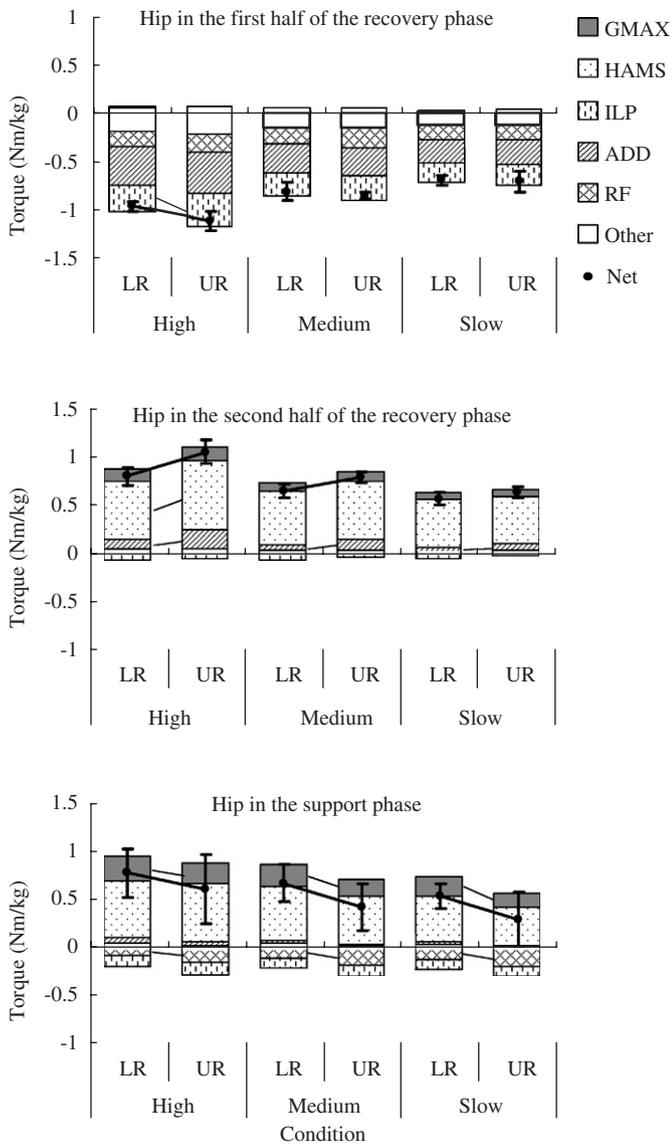


Fig. 6. Average net joint torque (“●” with standard error bars) and muscle torques (stacked bar graph) of the hip in the first half of the recovery phase (top), the second half of the recovery phase (middle), and the support phase (bottom) for level running (LR) and uphill running (UR) at the high, medium, and slow speeds. GMAX, gluteus maximus; HAMS, hamstrings; ILP, iliopsoas; ADD, adductors; RF, rectus femoris. Positive values indicate extension torque and negative values indicate flexion torque. The thick and thin lines connecting LR and UR indicate a significant difference between LR and UR at $p < 0.05$ in the net joint torque and muscle torque, respectively.

Fig. 7. Average net joint torque (“●” with standard error bars) and muscle torques (stacked bar graph) of the knee in the first half of the recovery phase (top), the second half of the recovery phase (middle), and the support phase (bottom) for level running (LR) and uphill running (UR) at the high, medium, and slow speeds. HAMS, hamstrings; RF, rectus femoris; VAS, vasti; GAS, gastrocnemius. Positive values indicate extension torque and negative values indicate flexion torque. The thick and thin lines connecting LR and UR indicate a significant difference between LR and UR at $p < 0.05$ in the net joint torque and muscle torque, respectively.

the increased activation of HAMS, ILP, ADD, and VAS. UR at the high speed increased the muscle torque of GMAX, HAMS, ILP, and ADD in the recovery phase, which would contribute to rapid forward and backward swings of the recovery leg and an increase in the step frequency. At all the speeds, the knee extension torque by VAS in the support phase was smaller during UR than during LR. However, it was inferred that the load on VAS during UR would not be smaller because of its greater shortening velocity. The increased RF

activity in SP during UR at all the speeds would compensate for the decrease in the torque by VAS, and it would contribute to maintaining the trunk in a forward-leaning position.

Conflict of interest

None.

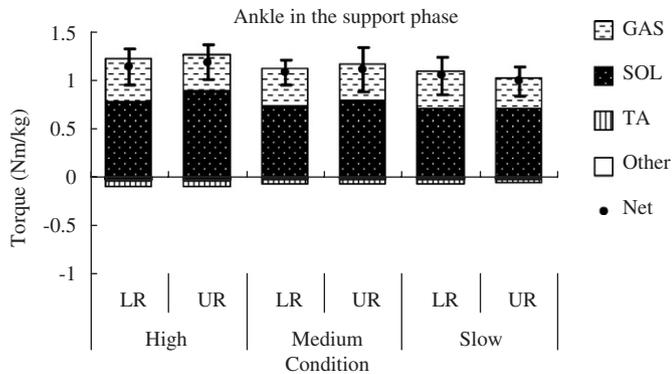


Fig. 8. Average net joint torque (“●” with standard error bars) and muscle torques (stacked bar graph) of the ankle in the support phase for level running (LR) and uphill running (UR) at the high, medium, and slow speeds. GAS, gastrocnemius; SOL, soleus; TA, tibialis anterior. Positive values indicate plantar flexion torque and negative values indicate dorsiflexion torque.

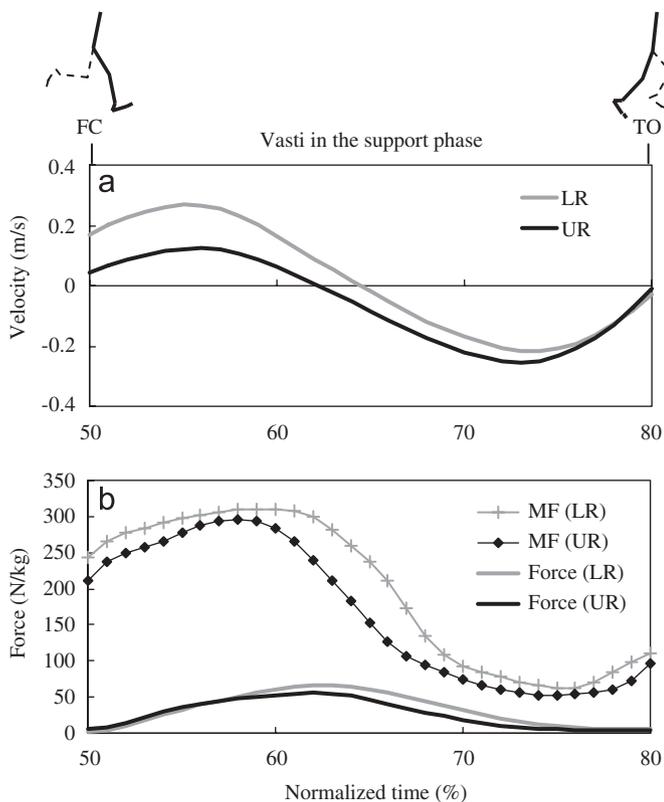


Fig. 9. Average pattern of the contraction velocity (a), and muscle force and theoretical maximum force (MF) (b) of the vasti during the support phase for level running (LR) and uphill running (UR) at high speed. Positive values of the contraction velocity indicate lengthening and negative values indicate shortening. FC is foot contact. TO is toe-off.

References

Anderson, F.C., Pandy, M.G., 2001. Static and dynamic optimization solutions for gait are practically equivalent. *Journal of Biomechanics* 34, 153–161.

Brand, R.A., Pedersen, D.R., Friederich, J.A., 1986. The sensitivity of muscle force predictions to changes in physiologic cross-sectional area. *Journal of Biomechanics* 19, 589–596.

Crowninshield, R.D., Brand, R.A., 1981. A physiologically based criterion of muscle force prediction in locomotion. *Journal of Biomechanics* 14, 793–801.

Delp, S.L., Lone, J.P., Hoy, M.G., Zajac, F.E., Topp, E.L., Rosen, J.M., 1990. An interactive graphics-based model of lower extremity to study orthopaedic surgical procedures. *IEEE Transaction on Biomedical Engineering* 37, 756–757.

Elliott, B.C., Blanksby, B.A., 1976. A cinematographic analysis of overground and treadmill running by males and females. *Medicine and Science in Sports and Exercise* 8, 84–87.

Frishberg, B.A., 1983. An analysis of overground and treadmill sprinting. *Medicine and Science in Sports and Exercise* 15, 478–485.

Gottschall, J.S., Kram, R., 2005. Ground reaction forces during downhill and uphill running. *Journal of Biomechanics* 38, 445–452.

Gregor, R.J., Costill, D.L., 1973. A comparison of the energy expenditure during positive and negative grade running. *Journal of Sports Medicine* 13, 248–252.

Heise, G.D., Morgan, D.W., Hough, H., Craib, M., 1996. Relationships between running economy and temporal EMG characteristics of bi-articular leg muscles. *International Journal of Sports Medicine* 17, 128–133.

Klein, R.M., Potteiger, J.A., Zebas, C.J., 1997. Metabolic and biomechanical variables of two incline conditions during distance running. *Medicine and Science in Sports and Exercise* 29, 1625–1630.

Milliron, M.J., Cavanagh, P.R., 1990. Sagittal plane kinematics of the lower extremity during distance running. In: Cavanagh, P.R. (Ed.), *Biomechanics of Distance Running*. Human Kinetics Publishers, Champaign, pp. 65–106.

Nelson, R.C., Dillman, C.J., Lagasse, P., Bickett, P., 1972. Biomechanics of overground versus treadmill running. *Medicine and Science in Sports* 4, 233–240.

Nigg, B.M., de Boer, R.W., Fisher, V., 1995. A kinematic comparison of overground and treadmill running. *Medicine and Science in Sports and Exercise* 27, 98–105.

Paradisi, G.P., Cooke, C.B., 2001. Kinematic and postural characteristics of sprint running on sloping surfaces. *Journal of Sports Sciences* 19, 149–159.

Pedersen, D.R., Brand, R.A., Devy, D.T., 1997. Pelvic muscle and acetabular contact forces during gait. *Journal of Biomechanics* 30, 959–965.

Pivarnik, J.M., Sherman, N.W., 1990. Responses of aerobically fit men and women to uphill/downhill walking and slow jogging. *Medicine and Science in Sports and Exercise* 22, 127–130.

Pugh, L.G.C.E., 1970. Oxygen intake in track and treadmill running with observations on the effect of air resistance. *Journal of Physiology* 207, 823–835.

Staab, J.S., Agnew, J.W., Siconolfi, S.F., 1992. Metabolic and performance responses to uphill and downhill running in distance runners. *Medicine and Science in Sports and Exercise* 24, 124–127.

Swanson, S.C., Caldwell, G.E., 2000. An integration biomechanical analysis of high speed incline and level treadmill running. *Medicine and Science in Sports and Exercise* 32, 1146–1155.

Tulloch, B., 1998. The role of cross-country in the development of a runner. *New Studies in Athletics* 13, 9–11.

van Ingen Shuenau, G.J., 1980. Some fundamental aspects of the biomechanics of overground versus treadmill locomotion. *Medicine and Science in Sports and Exercise* 12, 257–261.

Wank, V., Frick, U., Schmidtbleicher, D., 1998. Kinematics and electromyography of lower limb muscle in overground and treadmill running. *International Journal of Sports Medicine* 19, 455–461.

Yamaguchi, G.T., Sawa, A.G.U., Moran, D.W., Fessler, M.J., Winters, J.M., 1990. A survey of human musculotendon actuator parameters. In: Winters, J.M., Woo, S.L. (Eds.), *Multiple Muscle System*. Springer, New York, pp. 717–751.

- Yokozawa, T., Fujii, N., Enomoto, Y., Ae, M., 2003. Kinetic characteristics of distance running on the uphill (in Japanese). *Japanese Journal of Biomechanics in Sports and Exercise* 7, 30–42.
- Yokozawa, T., Fujii, N., Ae, M., 2005. Muscle force estimation of lower limb in running. In: *Proceedings of the 2005 International Symposium on Computer Simulation in Biomechanics*, Case Western Reserve University, Cleveland.
- Zajac, F.E., 1989. Muscle and tendon: Properties, models, scaling, and application to biomechanics and motor control. *Critical Reviews in Biomedical Engineering* 17, 359–411.