Effects of Gradient Variations on Physiological Responses to a 30-minute Run

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This study investigated whether variations in gradient would affect the magnitude of physiological responses during a 30-minute run at an intensity of 70% of maximal oxygen capacity ($\dot{V}O_{2max}$). Forty untrained collegiate men were randomly assigned into 0%, −5%, −11% and −16% groups ($n = 10$ per group), and then performed a 30-minute run at gradients of 0%, −5%, −11% and −16%, respectively, at the intensity of 70% of their predetermined $\dot{V}O_{2max}$. Oxygen consumption ($\dot{V}O_2$), minute ventilation ($\dot{V}_E$), respiratory exchange ratio (RER), heart rate (HR), and rating of perceived exertion (RPE) were measured at 5, 10, 15, 20, 25 and 30 minutes, respectively, during each run. Blood lactate (LA) concentration was assessed by fingertip blood sample at 3 minutes after each run. The results showed that elevations in $\dot{V}O_2$, $\dot{V}_E$, RER and HR during running for the −11% and −16% groups were greater ($p < 0.05$) than for the −5% and 0% groups. For the −11% group, elevations of these measures were greater ($p < 0.05$) than those of these measures for the −5% group. However, the changes in these measures showed no significant difference ($p > 0.05$) between the 0% and −5% groups, or between the −11% and −16% groups. As for RPE and LA, no significant differences ($p > 0.05$) among the groups were observed. It is concluded that the steeper the gradient, the greater the increases in $\dot{V}O_2$, $\dot{V}_E$, RER and HR. This may be due to the fact that at a steeper downhill gradient (−16%), the quadriceps femoris muscle lengthens to a greater extent than at lower (−5%, −11%) and level gradients. [*J Exerc Sci Fit* • Vol 7 • No 2 • 85–90 • 2009]

Keywords: heart rate, lactate, lengthening exercise, muscle damage, oxygen consumption

Introduction

The extent of changes in oxygen consumption ($\dot{V}O_2$) can be used to evaluate how muscle groups in the human body respond to physical exercise (Dick & Cavanagh 1987; Costill 1970). Recent studies (Chen et al. 2008, 2007; Saunders et al. 2004) have shown that in tests of physical exercise, analyzing physiological parameters [maximal $\dot{V}O_2$ ($\dot{V}O_{2max}$), minute ventilation ($\dot{V}_E$), respiratory exchange ratio (RER), heart rate (HR), blood lactate (LA)] and kinematic parameters (stride length, stride frequency, and range of motion for the ankle, knee and hip joints) is an effective way to evaluate athletes' efficiency and performance. Chen et al. (2007) and Byrne et al. (2004) demonstrated that the extent of muscle damage suffered from performing a bout of downhill running (DHR) is somewhat similar to that suffered from running a marathon, suggesting that DHR can be used as a way of inducing muscle damage in laboratory experiments. The fact that DHR is an innate running form of the human body may explain why it has long been one of the most common methods used to induce damage in lower-limb muscle groups in studies of exercise-induced muscle damage (EIMD; Chen et al. 2008, 2007; Eston et al. 1996, 1995; Schwane et al. 1983).

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To date, only four previous studies have examined the effects of DHR, using under the intensity of 50%$\dot{V}O_{2max}$, on the upward drift in oxygen consumption (UDO; Westerlind et al. 1994, 1992; Dick & Cavanagh 1987; Klausen & Knuttgen 1971), and found a significant increase in $\dot{V}O_2$ during 30–45 minutes of lengthening exercise at 35%$\dot{V}O_{2max}$. In other studies (Chen et al. 2008, 2007; Braun & Dutto 2003; Eston et al. 2000, 1996; Smith et al. 1998; Pierrynowski et al. 1987; Byrnes et al. 1985), DHR is used merely as a means of inducing muscle damage in test subjects, while the actual topics of research (e.g. training, running economy) are explored from other angles. It should be noted that the DHR protocol in these studies used gradients of −10% to −15%, and required subjects to run at considerably higher intensities (70%$\dot{V}O_{2max}$ or 90%HR_{max}). Yet, because none of these later studies measured the effects of DHR on UDO, it is still unknown what influence an intensity of or exceeding 50% of $\dot{V}O_{2max}$ will have on UDO. Furthermore, it is generally necessary to wait 1–3 days after DHR before the symptoms of muscle damage become apparent (Chen et al. 2008, 2007; Byrne et al. 2004; Eston et al. 1995). If we are able to observe significant changes in physiological parameters (e.g. $\dot{V}O_2$) during DHR at different gradients, rather than waiting for a few days for muscle damage to occur, we would then be able to provide some evidence for the initial stages of EIMD.

Therefore, this study was designed to test the hypothesis that when subjects engage in DHR at different gradients, the extent of their physiological responses is related to the gradient at which DHR takes place (−16% > −11% > −5% > 0%).

Methods

Subjects and general procedures

Forty untrained male students participated in this study that had been approved by the Institutional Ethics Committee, and gave an informed consent document in conformity with the Declaration of Helsinki. Their mean (± standard deviation) age, height, weight and $\dot{V}O_{2max}$ were 21.6 ± 1.7 years, 171.5 ± 5.4 cm, 66.5 ± 10.3 kg and 51.1 ± 5.6 mL · kg^{-1} · min^{-1}, respectively. $\dot{V}O_{2max}$ was determined by a graded maximal treadmill test using a motor-driven treadmill (Valiant; Lode B.V., Groningen, The Netherlands) and an automated gas analysis system (Vmax29c; SensorMedics Corp., Yorba Linda, CA, USA) using a similar protocol as described in previous studies (Chen et al. 2008, 2007). Following a general stretching exercise for 10 minutes, the subjects ran until volitional exhaustion while the treadmill velocity was increased by 1 mile · hour^{-1} every 2 minutes from 3 miles · hour^{-1} without gradient.

Subjects were placed into one of four groups (0%, −5%, −11% and −16%) by matching the baseline $\dot{V}O_{2max}$ among the groups. The sample size was estimated using data from a previous study (Chen et al. 2008), in which subjects similar to those in this study performed similar bouts of DHR. It was shown that such a study would need at least nine subjects per group, based on an effect size of 1, alpha level of 0.05 and a power (1 − beta) of 0.80. We recruited 10 subjects for each group. No significant differences ($p > 0.05$) in age, height, weight or $\dot{V}O_{2max}$ were evident among the groups. None of the subjects had engaged in any resistance or endurance training in the year immediately preceding the study, and none performed any recreational activities (e.g. hill running, soccer, volleyball) that include large eccentric components. All subjects were requested not to perform any unaccustomed exercise or vigorous physical activity, and asked not to take any anti-inflammatory agents or nutritional supplements during the experimental period.

$\dot{V}O_{2max}$ was assessed approximately 1 week prior to DHR. All subjects were familiarized with the treadmill test to be used for measuring $\dot{V}O_{2max}$ 2–3 days prior to the actual $\dot{V}O_{2max}$ test.

DHR

All subjects performed a 30-minute bout of DHR on the treadmill described earlier. The DHR protocol was similar to that of previous studies (Chen et al. 2008, 2007). After 10 minutes of general stretching, subjects ran on the treadmill at a 0° gradient for 5 minutes using self-selected speeds, followed by DHR. The gradient of the treadmill for the 0%, −5%, −11% and −16% groups was set at 0%, −5%, −11% and −16%, respectively, and the velocity was adjusted in the first 5 minutes to obtain the predetermined 70%$\dot{V}O_{2max}$ target for each subject. The velocity was not changed thereafter until completion of DHR, and the average speed of the treadmill for the 0%, −5%, −11% and −16% groups was 6.2 ± 0.7, 6.5 ± 0.7, 7.5 ± 0.8 and 7.8 ± 1.0 miles · hour^{-1}, respectively.

Criterion measures

Dependent variables were $\dot{V}O_2$, $\dot{V}_E$, RER, HR, rating of perceived exertion (RPE), and LA concentration. These measures, with the exception of LA, were assessed at 5, 10, 15, 20, 25 and 30 minutes during DHR for all groups. LA was measured before and at 3 minutes after each run.

During running, expired gas was continually collected using the same automated gas analysis system. The mean values of the 60 seconds at each time point (i.e. 5, 10, 15, 20, 25 and 30 minutes) during each run were obtained for $\dot{V}O_2$, $\dot{V}_E$ and RER. HR was measured using an HR monitor (Polar S610, Kempele, Finland) at 5, 10, 15, 20, 25 and 30 minutes during each run, and the mean value of the average 60 seconds was used for further analysis. RPE was assessed during the last 20 seconds at each time point (i.e. 5, 10, 15, 20, 25 and 30 minutes) using the Borg scale (Chen et al. 2008, 2007). LA was measured using fingertip blood and a portable lactate analyzer (Lactate Pro™ Tester Meter; Arkray Inc., Kyoto, Japan) before the 30-minute run, and at 3 minutes after.

Statistical analysis

Changes in $\dot{V}O_2$, HR, $\dot{V}_E$, RER, RPE and LA over time were analyzed by a one-way repeated-measures analysis of variance (ANOVA). When a significant time effect was found, a Tukey's *post hoc* test was conducted to detect the location of significance from the baseline. Changes in $\dot{V}O_2$, HR, $\dot{V}_E$, RER, RPE and LA during the different gradients of DHR (0%, −5%, −11%, −16%) were compared by a two-way mixed-design ANOVA. When a significant interaction effect (gradient × time) was evident, a Scheffé's *post hoc* test was conducted. Statistical significance was accepted at $p < 0.05$.

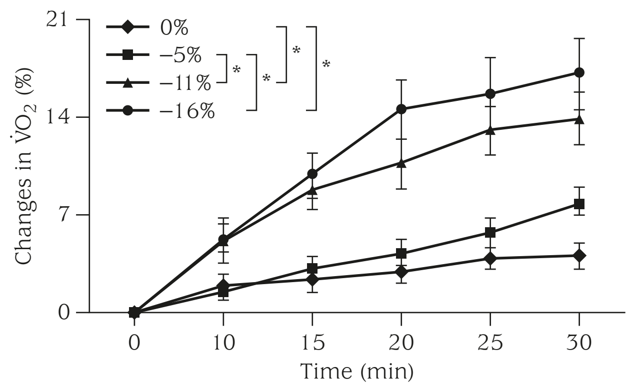

Fig. 1 Normalized changes in oxygen consumption ($\dot{V}O_2$; mean ± standard deviation) during a 30-minute run at the gradients of 0%, −5%, −11% and −16%. *Significant difference ($p < 0.05$) between groups.

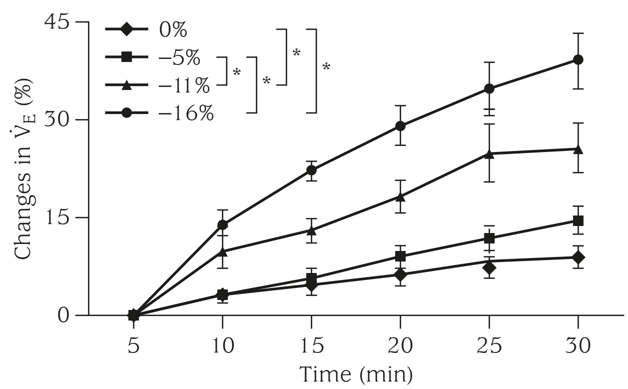

Fig. 2 Normalized changes in minute ventilation ($\dot{V}_E$; mean ± standard deviation) during a 30-minute run at the gradients of 0%, −5%, −11% and −16%. *Significant difference ($p < 0.05$) between groups.

Results

It was found that after 5 minutes of running (at gradients of 0%, −5%, −11% and −16%, respectively), subjects in the 0%, −5%, −11% and −16% groups all showed a $\dot{V}O_2$ of around 35.6 ± 2.0 mL · kg^{-1} · min^{-1}, $\dot{V}_E$ of around 58.8 ± 4.2 L · min^{-1}, RER of around 0.92 ± 0.01, HR of around 156.9 ± 5.8 beat · min^{-1} and RPE of around 10.2 ± 0.3. In addition, the LA values of all subjects prior to beginning their runs were found to be within the normal range (around 0.9 ± 0.1 μg · L^{-1}). In order to facilitate direct comparison of these four different gradients, the present study reported the normalized data of each variable instead of raw data (Figures 1–4).

As shown in Figure 1, the elevation in $\dot{V}O_2$ during a 30-minute run was significantly greater for subjects in the −16% and −11% groups than for those in the −5% and 0% groups ($p < 0.05$). For the −11% group, elevation in $\dot{V}O_2$ was also significantly greater ($p < 0.05$) than that of the −5% group. However, no significant difference ($p > 0.05$) was seen between the −11% and −16% groups, and between the 0% and −5% groups. For the 0% group, $\dot{V}O_2$ was found to be 4% greater at the 30th minute of level running than at the 5th minute, but this was not a significant difference ($p > 0.05$). For the other three groups, in contrast, $\dot{V}O_2$ was significantly higher (i.e. −16% group, 17%; −11% group, 12%; −5% group, 7%; $p < 0.05$) at the 30th minute of DHR than at the 5th minute.

Similar results were found for $\dot{V}_E$, RER, and HR (Figures 2–4). From Figures 2 and 3, we can see that during the 30-minute run, subjects in the −16% and −11% groups showed a significantly greater ($p < 0.05$) increase in both $\dot{V}_E$ and RER than did those in the −5% and 0% groups. For the −11% group, elevation of these

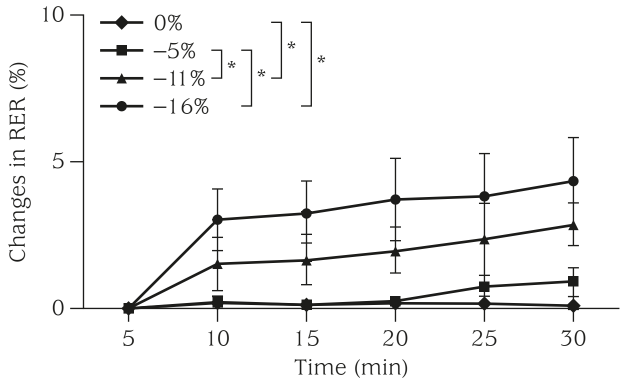

Fig. 3 Normalized changes in respiratory exchange ratio (RER; mean ± standard deviation) during a 30-minute run at the gradients of 0%, −5%, −11% and −16%. *Significant difference ($p < 0.05$) between groups.

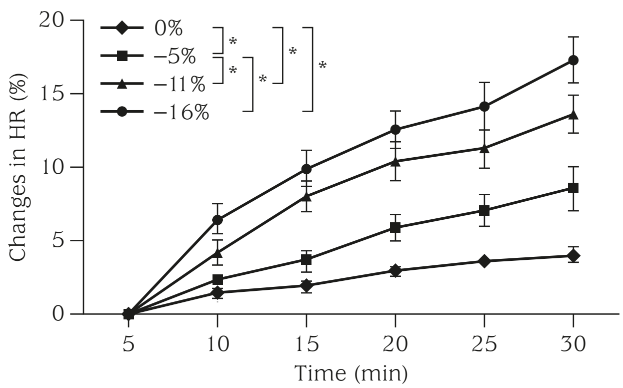

Fig. 4 Normalized changes in heart rate (HR; mean ± standard deviation) during a 30-minute run at the gradients of 0%, −5%, −11% and −16%. *Significant difference ($p < 0.05$) between groups.

measures were also significantly greater ($p < 0.05$) than those of these measures for the −5% group. However, there was no significant difference ($p > 0.05$) between the −11% and −16% groups, and between the 0% and −5% groups. HR data from Figure 4 show that during the 30-minute run, the increase in HR was greater ($p < 0.05$) for the −16% and −11% groups than for the −5% and 0% groups. HR increase of the −5% group was greater than that of the 0% group but smaller ($p < 0.05$) than that of the −11% group. However, no significant difference ($p > 0.05$) was found between the −11% and −16% groups.

Furthermore, the present study found that while running at each gradient leads to a significant increase in RPE (about 46–56%; $p < 0.05$), no significant difference ($p > 0.05$) in RPE values was seen among the four groups. Similar results were also noted for the degree of change in LA (about 13–14 $\mu g \cdot L^{-1}$) when this criterion was measured at 3 minutes after the subjects had finished running. Therefore, the results of these two variables are not shown in the text.

Discussion

The main findings of the present study showed that when subjects ran for 30 minutes at an intensity of 70% of $\dot{V}O_{2max}$, the extent of increase in $\dot{V}O_2$, $\dot{V}_E$, RER and HR was significantly greater for the −11% and −16% groups than for the −5% and 0% groups (Figures 1–4). However, no significant difference was seen between the −11% and −16% groups, and between the 0% and −5% groups (Figures 1–4). As for the extents of increase in RPE and LA, these were found to be unaffected by the gradient on which subjects ran. These results suggest that the greater the downhill slope, the more obvious the increase in physiological parameters.

The present study found that when the 0% group ran for 30 minutes on level ground at an intensity of 70% of $\dot{V}O_{2max}$, subjects' $\dot{V}O_2$ levels showed no significant increase (Figure 1). This was similar to the findings of several previous studies (Westerlind et al. 1994, 1992; Dick & Cavanagh 1987; Byrnes et al. 1985). This may be related to the intensity of level running because Gleeson et al. (1995) found that the human body reaches its anaerobic threshold at an exercise intensity of around 80% of $\dot{V}O_{2max}$. If this is the case, the intensity of 70% of $\dot{V}O_{2max}$ used in the present study may be too low to cause a significant increase in the $\dot{V}O_2$ levels of subjects in the 0% group.

The present study found that the $\dot{V}O_2$ levels of subjects in the −16% (17%), −11% (12%) and −5% (6%) groups were all significantly higher at the 30th minute of DHR than they were at the 5th minute (Figure 1). Similar results were also found for $\dot{V}_E$, RER and HR (Figures 2–4). These findings support the contention of previous studies (Westerlind et al. 1994, 1992; Dick & Cavanagh 1987; Byrnes et al. 1985): performing one 30–45-minute bout of DHR can lead to a significant increase in $\dot{V}O_2$, $\dot{V}_E$, RER and HR. Of these, Byrnes et al. (1985) asked subjects to perform a 30-minute DHR (−10%) at an intensity of 157 $beat \cdot min^{-1}$, and the results showed that both $\dot{V}O_2$ and HR were around 6% higher at the 30th minute of DHR than at the 10th minute. Dick and Cavanagh (1987) had subjects perform a 40-minute DHR (−10%) at an intensity of 44%$\dot{V}O_{2max}$, and found that $\dot{V}O_2$ (10%), $\dot{V}_E$ (6%) and integrated electromyogram (23%) were all significantly higher at the

40th minute of DHR than at the 10th minute. Westerlind et al. (1992) had subjects perform a 30-minute DHR (–10%) at an intensity of 40%$\dot{V}O_{2max}$, with the result that HR (13%), $\dot{V}O_2$ (16%) and $\dot{V}_E$ (21%) were significantly higher at the 30th minute of DHR than at the 1st minute. In addition, DHR was found to have caused significant muscle damage in the subjects. Westerlind et al. (1994) found that when subjects performed a 45-minute DHR (–10%) at an intensity of 50%$\dot{V}O_{2max}$, both $\dot{V}O_2$ (5%) and HR (11%) increased significantly. From the results of the aforementioned and present studies, we can see that the level to which physiological parameters change following a bout of DHR seems to be influenced chiefly by both the gradient and the intensity at which subjects run.

Previous studies (Westerlind et al. 1992; Costill 1970) reported that physiological parameters ($\dot{V}_E$, RER, HR) could be the main factors behind the UDO that occurs when subjects perform concentric exercise at an intensity greater than 60%. The present study found that subjects in the –5% (9%), –11% (14%) and –16% (17%) groups that performed DHR, using 70%$\dot{V}O_{2max}$, all experienced a significantly greater increase in HR from the 5th minute to the 30th minute of exercise than did subjects in the 0% group (4%; Figure 4). Moreover, Westerlind et al. (1992) postulated that HR, or the amount of work done by the heart, may be related to the degree of change in $\dot{V}O_2$ during DHR. Because $\dot{V}O_2$, $\dot{V}_E$ and RER show a similar trend as HR when subjects engage in DHR (Figures 1–4), these results might indicate that when testing the effects of running at different gradients, these four physiological parameters can all serve as effective indexes to evaluate exercise intensity and physiological response.

The fact that subjects in this study who engaged in DHR experienced different degrees of changes in physiological parameters ($\dot{V}O_2$, $\dot{V}_E$, RER, HR) is likely to be related chiefly to the different gradients (–5%, –11%, –16%) at which they ran. One limitation of the present study was the absence of treadmills equipped with force plates and high-speed video cameras, which would have enabled us to evaluate subjects' impact force, as well as the joint angle variations of the lower limbs during running. However, Gottschall and Kram (2005) showed a relationship between the gradient at which subjects ran and impact force as measured by a force plate on a treadmill. For example, the normal impact peaks of the –16%, –11% and –5% groups were found to be greater than that of the 0% group by 54%, 32% and 18%, respectively. Moreover, Buczek and Cavanagh (1990) found that when subjects were engaged in DHR at a gradient of –10%, the variation of the knee joint angle (35.1°) was significantly greater than that of subjects who ran on level ground (27.2°). More recently, Chen et al. (2007) postulated that when subjects are engaged in DHR, the quadriceps femoris muscle should extend and contract to a greater degree than when they run on level ground. This would cause the subjects to experience a gradual increase in both $\dot{V}O_2$ and $\dot{V}_E$ as they engage in DHR for longer periods of time. The above hypotheses would seem to suggest that the steeper the downhill slope at which subjects run, the greater the range of lengthening-contraction of the knee extensor, and, thus, the greater the extent of muscle damage.

Hreljac et al. (2000) reported that the primary biomechanical parameter distinguishing injured from never-injured runners is the extent of impact peak force. The extent of the vertical impact peak force for the injury group was 13% greater than that of the non-injury group, a difference equivalent to DHR at –5% in the Gottschall and Kram (2005) study. Other studies have also shown that high impact forces are related to an increase in the occurrence of injury (Grimston et al. 1994). These impact forces can be moderated by increasing the knee flexion angle at foot strike and decreasing stride length during downhill and level running, but such modifications are metabolically expensive (Derrick et al. 1998). In light of these findings, we did not rule out the possibility that the above hypotheses may help to explain why DHR at different gradients caused the physiological parameters of subjects in the present study to increase by different degrees.

The fact that DHR causes a significant increase in physiological parameters (Figures 1–4) might also be partly related to neurological factors and muscle stiffness. Eston et al. (1995) postulated that when humans engage in DHR, the knee extensors, anterior tibial muscles and hip extensors all perform lengthening contractions in order to help the body resist gravity. These contractions, in turn, lead to muscle damage. Westerlind et al. (1992) and Dick and Canavagh (1987) also suggested that the UDO occurring during DHR may be related to muscle damage. This could be due to the fact that DHR requires the use of more muscle groups than level running, leading to an increase in $\dot{V}O_2$. Klein et al. (1997) suggested that $\dot{V}O_2$ and $\dot{V}_E$ do not increase significantly until the latter stages of running, as the muscle damage that occurs during these stages causes a gradual increase in nerve activity. Dutto and Braun (2004) and Barry and Cole (1990) found that when DHR leads to muscle damage, significant muscle stiffness occurs. This stiffness then inhibits the body's ability to convert elastic energy into mechanical work, leading to a marked increase in $\dot{V}O_2$. Thus, subjects who engage in DHR at different gradients might experience different levels of muscle damage and muscle stiffness in the latter stages of running. This stiffness inhibits the body's ability to convert elastic energy into mechanical work, and in response, the body likely recruits more muscle fibers to assist with DHR. These hypotheses might be able to indirectly explain why subjects in this study who participated in the −5%, −11% and −16% groups experienced a significant increase in physiological parameters ($\dot{V}O_2$, $\dot{V}_E$, RER, HR) during the latter stages of DHR. Future studies are needed to test these issues.

In conclusion, the results of this study showed that when the subjects were engaged in DHR at a fixed intensity of 70% of $\dot{V}O_{2max}$, the range of the lengthening contractions of the quadriceps femoris muscles seems to increase as the gradient becomes steeper. This, in turn, leads to muscle damage and stiffness, which may, as subjects continue running, cause the body to recruit more muscle fibers to assist with DHR. In the end, this causes a marked decrease in running efficiency ($\dot{V}O_2$, $\dot{V}_E$, RER, HR). Therefore, these findings may provide a preliminary explanation for the different extents of muscle damage induced by DHR.

References

Barry DT, Cole NM (1990). Muscle sounds are emitted at the resonant frequencies of skeletal muscle. *IEEE Trans Biomed Eng* 37:525–31.

Braun WA, Dutto DJ (2003). The effects of a single bout of downhill running and ensuing delayed onset of muscle soreness on running economy performed 48 h later. *Eur J Appl Physiol* 90:29–34.

Buczek FL, Cavanagh PR (1990). Stance phase knee and ankle kinematics and kinetic during level and downhill running. *Med Sci Sports Exerc* 22:669–77.

Byrne C, Twist C, Eston R (2004). Neuromuscular function after exercise-induced muscle damage: theoretical and applied implications. *Sports Med* 34:49–69.

Byrnes WC, Clarkson PM, White JS, Hsieh SS, Frykman PN, Maughan RJ (1985). Delayed onset muscle soreness following repeated bouts of downhill running. *J Appl Physiol* 59:710–5.

Chen TC, Nosaka K, Tu JH (2007). Changes in running economy following downhill running. *J Sports Sci* 25:55–63.

Chen TC, Nosaka K, Wu CC (2008). Effects of daily 30-min run at different intensities on recovery from downhill running. *J Sci Med Sport* 11:271–9.

Costill DL (1970). Metabolic responses during distance running. *J Appl Physiol* 28:251–5.

Derrick TR, Hamill J, Caldwell GE (1998). Energy absorption of impacts during running at various stride lengths. *Med Sci Sports Exerc* 30:128–35.

Dick RW, Cavanagh PR (1987). An explanation of the upward drift in oxygen uptake during prolonged sub-maximal downhill running. *Med Sci Sports Exerc* 19:310–7.

Dutto DJ, Braun W (2004). DOMS-associated changes in ankle and knee dynamics during running. *Med Sci Sports Exerc* 36:560–6.

Eston RG, Finney S, Baker S, Baltzopoulos V (1996). Muscle tenderness and peak torque changes after downhill running following a prior bout of isokinetic eccentric exercise. *J Sports Sci* 14:291–9.

Eston RG, Lemmey AB, McHugh P, Byrne C, Walsh SE (2000). Effect of stride length on symptoms of exercise-induced muscle damage during a repeated bout of downhill running. *Scand J Med Sci Sports* 10:199–204.

Eston RG, Mickleborough J, Baltzopoulos V (1995). Eccentric activation and muscle damage: biomechanical and physiological considerations during downhill running. *Br J Sports Med* 29:89–94.

Gleeson M, Blannin AK, Zhu B, Brooks S, Cave R (1995). Cardiorespiratory, hormonal and haematological responses to submaximal cycling performed 2 days after eccentric or concentric exercise bouts. *J Sports Sci* 13:471–9.

Gottschall JS, Kram R (2005). Ground reaction forces during downhill and uphill running. *J Biomech* 38:445–52.

Grimston GM, Nigg BM, Fisher V, Ajemian SV (1994). External loads throughout a 45 min run in stress fracture and non-stress fracture runners. *J Biomech* 27:668.

Hreljac A, Marshall RN, Hume PA (2000). Evaluation of lower extremity overuse injury potential in runners. *Med Sci Sports Exerc* 32:1635–41.

Klausen K, Knuttgen H (1971). Effect of training on oxygen consumption in negative muscular work. *Acta Physiol Scand* 83:319–23.

Klein RM, Potteiger JA, Zebas CJ (1997). Metabolic and biomechanical variables of two incline conditions during distance running. *Med Sci Sports Exerc* 29:1625–30.

Pierrynowski MR, Tudus PM, Plyley MJ (1987). Effects of downhill or uphill training prior to a downhill run. *Eur J Appl Physiol Occup Physiol* 56:668–72.

Saunders PU, Pyne DB, Telford RD, Hawley JA (2004). Factors affecting running economy in trained distance runners. *Sports Med* 34:465–85.

Schwane JA, Johnson SR, Vandenakker CB, Armstrong RB (1983). Delayed onset muscular soreness and plasma CPK and LDH activities after downhill running. *Med Sci Sports Exerc* 15:51–6.

Smith LL, Bond JA, Holbert D, Houmard JA, Israel RG, McCammon MR, Smith SS (1998). Differential white cell count after two bouts of downhill running. *Int J Sports Med* 19:432–7.

Westerlind KC, Byrnes WC, Harris C, Wilcox AR (1994). Alterations in oxygen consumption during and between bouts of level and downhill running. *Med Sci Sports Exerc* 26:1144–52.

Westerlind KC, Byrnes WC, Mazzeo RS (1992). A comparison of the oxygen drift in downhill vs. level running. *J Appl Physiol* 72:796–800.