

The effect of downhill running conditions on muscle damage in recreationally active adults

ROBERT SOUTHALL-EDWARDS¹, SUE INNES¹, AJMOL ALI², BEN JONES¹ 

¹*School of Sport, Rehabilitation and Exercise Sciences, University of Essex, Colchester, United Kingdom*

²*School of Sport, Exercise and Nutrition, Massey University, New Zealand*


ABSTRACT

Background: Downhill running (DR) has been used extensively to investigate recovery from muscle-damaging exercise. There is no consensus on the optimal conditions (duration, severity, intensity) for a DR protocol. The purpose of this research was to determine the most effective DR conditions to induce muscle damage. **Methods:** The research was comprised a 3x3 within-between participant design. Recreationally active males' (n = 12) muscle damage was assessed using gold standard indirect markers (force loss and muscle soreness) at baseline, 24 and 48h post one of three DR conditions (a. 45min at -10% gradient b. 45min at -12% c. 30min at -15%). DR was completed on a motorised treadmill at 70% velocity of $\dot{V}O_{2peak}$ achieved during an incremental exercise test to exhaustion. **Results:** Isometric force ($p = .005$, $\eta_p^2 = 0.45$) and muscle soreness ($p = .002$, $\eta_p^2 = 0.49$) were impaired 24h post-exercise; no difference ($p > .05$) was evident between conditions. At 48h the impairments in force loss and muscle soreness were no longer evident ($p > .05$) across all conditions. There was no difference ($p = .82$) in HR between the DR conditions. **Findings:** Independent of duration and gradient all conditions resulted in a similar response in force loss and muscle soreness, indicating muscle damage had occurred. Interestingly, the 30-min protocol produced the same response in less time, without requiring individuals to work at a greater intensity. Therefore, the 30-min condition is suggested as the most appropriate protocol for use in the scientific investigation of muscle damage from DR.

Keywords: Force loss; Muscle soreness; Gradient; Duration; Physiology; Exercise.

Cite this article as:

Southall-Edwards, R., Innes, S., Ali, A., & Jones, B. (2020). The effect of downhill running conditions on muscle damage in recreationally active adults. *Journal of Human Sport and Exercise, in press*. doi:<https://doi.org/10.14198/jhse.2022.172.15>

 **Corresponding author.** School of Sport, Rehabilitation and Exercise Sciences, University of Essex, Wivenhoe Park, Colchester, CO4 3SQ, United Kingdom.

E-mail: bjonesa@essex.ac.uk

Submitted for publication August 06, 2020

Accepted for publication October 01, 2020

Published *in press* October 28, 2020

JOURNAL OF HUMAN SPORT & EXERCISE ISSN 1988-5202

© Faculty of Education. University of Alicante

doi:10.14198/jhse.2022.172.15

INTRODUCTION

Eccentric (lengthening) muscle actions have been shown to produce more muscle damage than concentric or isometric actions (Hyldahl & Hubal, 2014). Previous research has used activities such as isolated eccentric contractions of localised muscle groups (elbow flexors/knee extensors) or exercises comprising of large amounts of eccentric muscle activity (e.g. eccentric squats), to investigate recovery from exercise-induced muscle damage (Clarkson & Hubal, 2002; Clarkson et al., 1992). These activities are known to cause muscle damage; however, they are not representative of exercise regularly conducted in day-to-day life. Downhill running (DR) provides a functional activity, containing exaggerated eccentric muscle activity, which is more indicative of movements in real-world sport and exercise. DR requires the muscle to work over a greater length and involves more angle changes than level running (Eston et al., 1995; Schwane et al., 1983). This leads to increased mechanical stress as brake force is generated during the eccentric actions and results in extensive muscle damage occurring (Park & Lee, 2015). Therefore, investigating recovery from muscle damage caused by DR appears a more ecologically valid method to provide useful information which can be applied to exercise activities of daily living.

There is no consensus about which DR protocol is most effective in causing muscle damage. DR has been conducted at varying gradients (-4 to -16%) (Kolkhorst et al., 1996; Sorichter et al., 2001), over continuous (20-45 min) (Koskinen et al., 2001; Maeo et al., 2017; Malm et al., 2004; Peake et al., 2005b; Sorichter et al., 2001) or repeated (5-8 min) (Baumann et al., 2014; Eston et al., 2000; Kolkhorst et al., 1996; Nottle & Nosaka, 2007; Rowlands et al., 2001; van de Vyver et al., 2016; van de Vyver & Myburgh, 2014) durations and at varying intensities: velocity at $\dot{V}O_2$ max /peak (50-80%) (Féasson et al., 2002; Malm et al., 2004; Schwane et al., 1983), HR max (80%) (Nottle & Nosaka, 2007), predefined speed or a maximum tolerable velocity (Maeo et al., 2017). DR has been conducted using participants of varying fitness levels, ranging from healthy inactive/untrained individuals (Maeo et al., 2017; Sorichter et al., 2001), to highly active well-trained endurance athletes (Braun & Dutto, 2003; Peake et al., 2005b). Therefore, it is unclear what severity, intensity and duration of DR is most appropriate to produce muscle damage. Understanding what DR conditions may be most effective at producing muscle damage in recreationally active adults will allow for comparison of recovery with exercise resembling activities of daily living.

Direct assessment of muscle damage is highly invasive (i.e. muscle biopsies) or requires the use of expensive equipment (MRI) which may not always be available. Indirect markers are commonly used to quantify the magnitude and time course of muscle damage (Clarkson & Hubal, 2002; Hyldahl & Hubal, 2014). The loss of force-generating capacity is one of the most valid and reliable indirect indicators of exercise-induced muscle damage (Clarkson & Hubal, 2002; Warren et al., 1999). Concentric and eccentric exercise protocols both result in an immediate reduction in force-generating capacity. Following concentric activity, force generation returns to baseline within a few hours, however, after eccentric activities this recovery is prolonged, indicating the presence of muscle damage (Clarkson & Hubal, 2002). DR has been shown to reduce muscle force-generating capacity of between 10-30%, before returning towards baseline within 4-7 days (Baumann et al., 2014; Chen et al., 2007; Clarkson & Hubal, 2002; Close et al., 2004; Eston et al., 1995; Maeo et al., 2017; Malm et al., 2004; Nottle & Nosaka, 2007). Muscle soreness provides another commonly used indirect indicator of muscle damage and has been shown to increase significantly following DR, peaking 24-48 h post exercise, before returning to baseline within 5 days (Baumann et al., 2014; Braun & Dutto, 2003; Burr et al., 2015; Byrnes et al., 1985; Chen et al., 2007; Close et al., 2004; Eston et al., 2000; Maeo et al., 2017; Malm et al., 2004; Nottle & Nosaka, 2007; Rowlands et al., 2001; Schwane et al., 1983).

The purpose of this research is to determine the most appropriate DR conditions to induce muscle damage in recreationally active adults. The study aims to investigate how duration and gradient of DR affect the magnitude of muscle damage caused, assessed using indirect markers. It is hypothesised that all three DR conditions will elicit muscle damage responses. It is unknown to what extent gradient and duration will affect the muscle damage response.

MATERIAL AND METHODS

Participants

Participants were 12 healthy, recreationally active male adult volunteers, exercising two-five times per week (Table 1). Participants were screened for contraindicators to exercise using the Physical Activity Readiness Questionnaire (Par-Q). Ethical approval to conduct the research was granted by the University of Essex Ethics Committee and conformed to the Declaration of Helsinki. Written informed consent was provided by all participants.

Table 1. Participant demographics by downhill running condition.

Condition	Age (years)	Stature (m)	Mass (kg)	BMI (kg·m ²)	VO _{2peak} (ml·kg ⁻¹ ·min ⁻¹)
DR10	24.5 ± 7.4	1.76 ± 0.10	73.6 ± 4.2	23.8 ± 2.7	55.6 ± 7.5
DR12	24.8 ± 7.3	1.74 ± 0.07	70.7 ± 9.2	23.1 ± 1.7	51.4 ± 6.8
DR15	24.1 ± 6.4	1.77 ± 0.07	72.7 ± 5.8	23.3 ± 1.8	54.2 ± 6.1

DR10 = 45 min running downhill at 10% gradient (n = 4), DR12 = 45 min running downhill at 12% gradient (n = 4), DR30 = 30 min running downhill at 15% gradient (n = 4); ANOVA run to confirm no difference ($p > .05$) between condition for all outcomes.

Measures

Isometric knee extensor force (N) was assessed (1000 Hz) from maximal voluntary isometric contractions (MVIC), with a calibrated load cell dynamometer (Kin-Com dynamometer, Chattanooga Group Inc.; Hixon, TN, USA), attached around the participants' right leg superior to the ankle malleoli with a Velcro strap. Participants were seated upright, with the hip at 90° and knees at 80° flexion and instructed to remain seated with their arms across their chest (Konings et al., 2018). Participants performed a 3-s MVIC three times, with 60-s rest between contractions. They were requested to provide maximal effort on all contractions and provided with verbal encouragement. MVIC was taken as the peak force (N) observed during the 3-s contraction. The peak of the three MVIC trials was used in analysis.

A visual analogue scale (0-100 mm) was used to determine ratings of muscle soreness (Kargarfard et al., 2016). Muscle soreness ratings were assessed by participants rating the pain or discomfort they perceived during the MVIC.

Procedures

During visit 1 (Figure 1) participants completed an incremental exercise test (IXT) to exhaustion and a protocol to familiarise them with all outcome measures. One-week later participants completed baseline measurements for isometric force and muscle soreness (Visit 2) and were then randomly allocated to one of three DR conditions. Immediately following the downhill run (Post) a measurement of isometric force was obtained. Participants attended the lab 24 h (Visit 3) and 48 h (Visit 4) post DR to assess isometric force and muscle soreness status. The laboratory was kept at a consistent temperature (20 °C) for all visits.

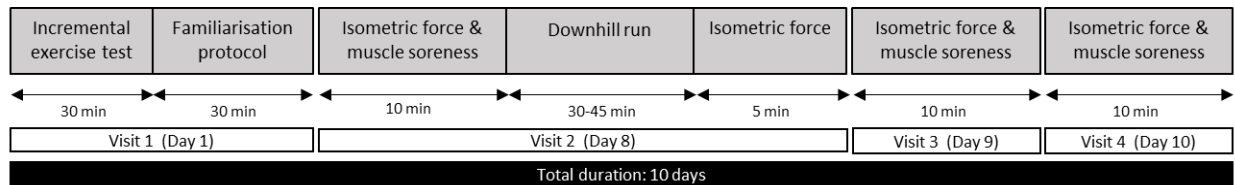


Figure 1. Schematic of experimental design to compare downhill running conditions.

The IXT was performed on a motorised treadmill (Saturn, HP Cosmos; Nussdorf, Germany) using 1 min stages, until participants achieved volitional exhaustion (Machado et al., 2013). Breath-by-breath online gas analysis (Oxycon Pro, Jaeger; Hoechberg, Germany) was used to determine $\text{VO}_{2\text{peak}}$ ($\text{ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$). The online gas analyser was calibrated before each procedure using a certified gas analyser. $\text{VO}_{2\text{peak}}$ was calculated from the mean maximal oxygen consumption over a 30-s period. Rating of perceived exertion (RPE) and HR (Polar RCX5, Polar Electro Oy; Kempele, Finland) were assessed to determine if maximal effort was achieved (Machado et al., 2013).

Participants completed one of three DR conditions on the motorised treadmill (Saturn, HP Cosmos; Nussdorf, Germany). The intensity of the downhill run was at 70% of the velocity when $\text{VO}_{2\text{peak}}$ was achieved during the IXT. The three DR conditions were 30 min at -15% gradient (DR15), 45 min at -12% (DR12) and 45 min at -10% (DR10); chosen based on commonly used intensities, gradients and durations of DR conditions within the literature (Baumann et al., 2014; Burr et al., 2015; Chen et al., 2007; Close et al., 2004; Féasson et al., 2002; Koskinen et al., 2001; Maeo et al., 2017; Park & Lee, 2015; Peake et al., 2005a; Peake et al., 2005b; Schwane et al., 1983; van de Vyver et al., 2016; van de Vyver & Myburgh, 2014) and following preliminary pilot investigations. Mean HR was calculated from 5-s interval recordings throughout each downhill run.

Statistical analysis

An *a priori* power analysis (G*POWER 3.1 Software, Düsseldorf, Germany) was conducted to determine significant power at an α -level of .05. Published DR force loss data was used to determine an effect size, revealing a total required sample size of 12 participants. Mean \pm standard deviation (SD), absolute and change from baseline values were calculated and presented in tables (Microsoft Excel, Microsoft Office 365 Pro Plus). Statistical analysis (SPSS v25.0, IBM Co., USA) was conducted with an alpha level of .05. One-way analysis of variance (ANOVA) was used to determine any difference between group in demographic measures at baseline. Two-way mixed method ANOVA was used to investigate any main effect of time, group or interaction effect for force loss and muscle soreness. One-way analysis of co-variance (ANCOVA) was conducted to determine differences between group while controlling for baseline. Post-hoc analysis of time was conducted using a paired samples t-test with a Bonferroni correction factor. Estimated marginal means were presented to illustrate change in force loss and muscle soreness after controlling for baseline. Effect sizes from ANOVA and ANCOVA were reported as partial Eta squared (η_p^2).

RESULTS

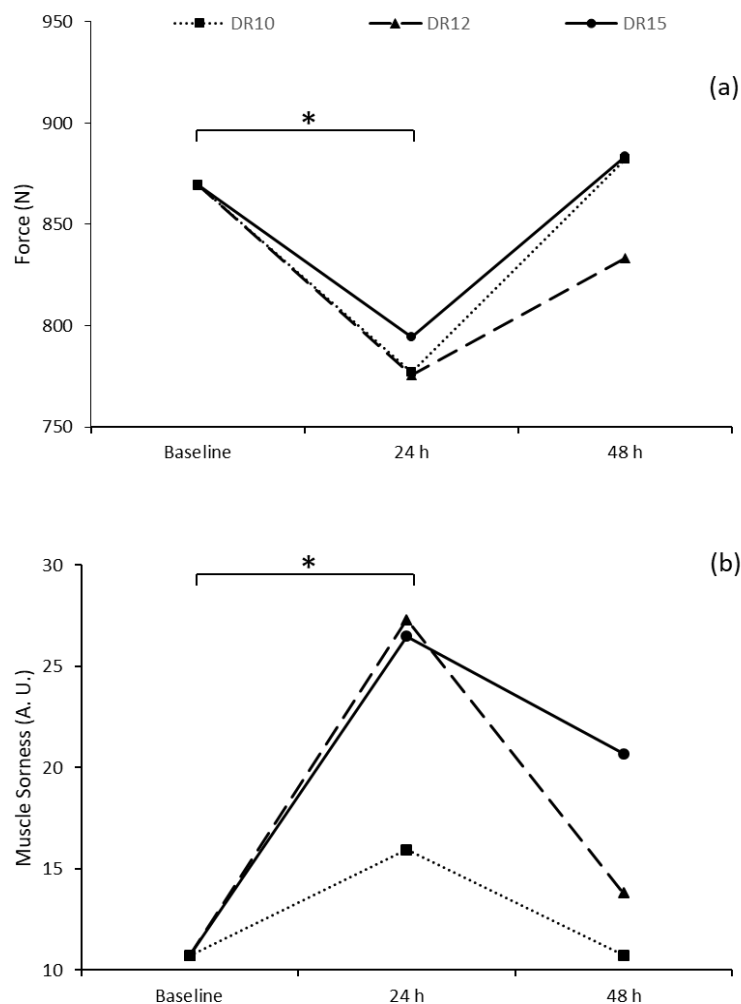
All DR conditions resulted in a reduction in force immediately post-exercise compared to baseline ($p = .001$, $\eta_p^2 = 0.72$; Table 2); there was no difference between condition ($p = .80$) or interaction of condition * time ($p = .89$). There was a main effect of time for isometric force ($p = .005$, $\eta_p^2 = 0.45$), with reduced force at 24 h ($p = .02$, $\eta_p^2 = 0.60$) compared to baseline but no difference between baseline and 48 h ($p = .87$). There was no effect of condition ($p = .76$) or interaction of condition * time ($p = .89$) for isometric force. When controlling

for baseline (Figure 2) there was no difference in isometric force between conditions at 24 h ($p = .94$) or 48 h ($p = .55$).

Table 2. Isometric knee extensor force and muscle soreness baseline and change from baseline (Δ) values (mean \pm SD) following three downhill running conditions.

	Condition	Baseline	Post	Δ Post	24 h	Δ 24 h	48 h	Δ 48 h
Isometric Force (N)	DR10	939 \pm 365	727 \pm 307	-212 \pm 170	843 \pm 385	-92 \pm 49	951 \pm 326	12 \pm 69
	DR12	832 \pm 270	657 \pm 185	-175 \pm 114	740 \pm 253	-92 \pm 27	796 \pm 329	-36 \pm 79
	DR15	838 \pm 195	616 \pm 112	-222 \pm 155	764 \pm 158	-74 \pm 128	852 \pm 202	14 \pm 52
Muscle Soreness (A. U.)	DR10	3.3 \pm 3.2	-	-	6 \pm 7	3 \pm 5	3 \pm 4	-1 \pm 3
	DR12	18.4 \pm 19.1	-	-	37 \pm 25	19 \pm 8	22 \pm 22	4 \pm 6
	DR15	10.7 \pm 13.2	-	-	26 \pm 23	16 \pm 22	19 \pm 18	16 \pm 10

DR10 = 45 min running downhill at 10% gradient ($n = 4$), DR12 = 45 min running downhill at 12% gradient ($n = 4$), DR30 = 30 min running downhill at 15% gradient ($n = 4$).



(* Significant main effect of time ($p < .05$); Error bars omitted from figure to aid clarity of interpretation; DR10 = 45 min running downhill at 10% gradient ($n = 4$), DR12 = 45 min running downhill at 12% gradient ($n = 4$), DR30 = 30 min running downhill at 15% gradient ($n = 4$).

Figure 2. Isometric knee extensor force (a) and muscle soreness (b) following the three downhill running (DR) conditions when controlling for baseline.

There was a main effect of time for muscle soreness ($p = .002$, $\eta_p^2 = 0.49$), with reduced soreness at 24 h ($p = .036$, $\eta_p^2 = 0.75$) compared to baseline but no difference between baseline and 48 h ($p = .49$; Table 2). There was no main effect of condition ($p = .21$) or interaction of condition * time ($p = .22$) for muscle soreness. When controlling for baseline (Figure 2) there was no difference in muscle soreness between conditions at 24 h ($p = .55$) or 48 h ($p = .44$).

There was no main effect for condition on HR ($p = .82$). Mean HR was 145 ± 15 b.min⁻¹, 144 ± 14 b.min⁻¹ and 140 ± 1 b.min⁻¹ in DR15, DR12 and DR10 conditions, respectively.

DISCUSSION

The aim of this research was to investigate how the conditions (gradient and duration) of DR affect the magnitude of muscle damage caused in recreationally active adults. Immediately post exercise all three DR conditions resulted in a significant reduction (20-25%) in force-generating capacity. The force reduction was similar between conditions, indicating all three caused a similar level of muscle fatigue. One day later a significant reduction in force remained (8-10%) and this was similar across all conditions. The force loss still evident at 24 h indicates that all conditions were effective at causing muscle damage. The reductions observed in force loss immediately post exercise and at 24 h are in line with those previously reported following DR (Baumann et al., 2014; Chen et al., 2007; Clarkson & Hubal, 2002; Close et al., 2004; Eston et al., 1995; Maeo et al., 2017; Malm et al., 2004; Nottle & Nosaka, 2007). At 48 h force generation was no longer impaired, indicating muscle damage had recovered across all conditions.

A significant increase (12%) was observed in muscle soreness 24 h post exercise. At 48 h the increase was no longer present, suggesting muscle soreness had recovered. The observed increase at 24 h followed by decrease at 48 h in muscle soreness, is similar to those previously reported following DR (Baumann et al., 2014; Braun & Dutto, 2003; Burr et al., 2015; Byrnes et al., 1985; Chen et al., 2007; Close et al., 2004; Eston et al., 2000; Maeo et al., 2017; Malm et al., 2004; Nottle & Nosaka, 2007; Rowlands et al., 2001; Schwane et al., 1983). There was no significant difference between groups at any time, suggesting all conditions resulted in similar muscle soreness.

Taken together, the observed force loss and muscle soreness indicate that all three DR conditions were effective at causing significant muscle damage 24 h post exercise, before recovery was observed at 48 h. The hypothesis that all three DR conditions will elicit muscle damage responses is therefore accepted. Interestingly it would appear that increased duration and gradient do not increase the extent of muscle damage, as may have been intuitively expected. However, the 30-min condition is able to produce the same muscle damage in less time, therefore reducing the time commitment for both investigator and participant. Additionally, there was no difference in average HR across the conditions, suggesting running downhill at the steeper gradient did not involve additional cardiovascular strain. Therefore, it is likely the shorter condition would be more amenable to participants, especially if working with those not accustomed to running for prolonged periods.

Laboratories provide a controlled environment where recovery from exercise can be monitored. However, the protocols used do not necessarily replicate activities as they are undertaken in the "real world". Research has begun to move away from lab-based muscle damage protocols and investigate recovery from sport activities (Brown et al., 2016a; Brown et al., 2016b; Doma et al., 2018). It is important to first establish laboratory-based protocols which can be compared with "real world" activities to better understand the differences/similarities in recovery. Appropriate protocols (such as DR) are required, which are comparable

in duration and intensity to common activities. Current Government guidelines recommend activities be conducted in 30-min bouts (GOV.UK, 2019). Therefore, the 30-min DR condition presented here is ideal for comparisons with common 30-min exercise activities. This approach will ensure scientific rigour is maintained when carrying out muscle damage research in more ecologically valid environments.

CONCLUSIONS

In summary, all three DR conditions were effective in causing a similar magnitude of muscle damage when completed by recreationally active adults. Interestingly, the 30-min condition completed at a steeper gradient (15%), produced the same muscle damage response in less time, without requiring individuals to work at a greater intensity. Therefore, researchers looking to induce muscle damage using DR should employ the 30-min protocol. This will offer time-saving benefits and may be superior for individuals not accustomed to prolonged periods of running.

AUTHOR CONTRIBUTIONS

Robert Southall-Edwards, Dr Sue Innes and Dr Ben Jones, all developed the study design. Robert Southall-Edwards undertook the data collection with Dr Sue Innes, Dr Ajmol Ali and Dr Ben Jones supervising the findings of this work. Robert Southall-Edwards and Dr Ajmol Ali completed the statistical analysis. All authors discussed the results and contributed to the final manuscript.

SUPPORTING AGENCIES

No external funding was provided for this project.

DISCLOSURE STATEMENT

The authors have no conflicts of interest that are directly relevant to the content of this manuscript.

ACKNOWLEDGEMENTS

The authors thank the volunteers for the participation in the research.

REFERENCES

- Baumann, C. W., Green, M. S., Doyle, J. A., Rupp, J. C., Ingalls, C. P., & Corona, B. T. (2014). Muscle injury after low-intensity downhill running reduces running economy. *J Strength Cond Res*, 28(5), 1212-1218. <https://doi.org/10.1519/jsc.0000000000000422>
- Braun, W. A., & Dutto, D. J. (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(1-2), 29-34. <https://doi.org/10.1007/s00421-003-0857-8>
- Brown, M. A., Howatson, G., Keane, K., & Stevenson, E. J. (2016a). Exercise-induced muscle damage following dance and sprint-specific exercise in females. *J Sports Med Phys Fitness*, 56(11), 1376-1383.
- Brown, M. A., Howatson, G., Keane, K. M., & Stevenson, E. J. (2016b). Adaptation to Damaging Dance and Repeated-Sprint Activity in Women. *Journal of strength and conditioning research*, 30(9), 2574-2581. <https://doi.org/10.1519/jsc.0000000000001346>

- Burr, J. F., Boulter, M., & Beck, K. (2015). Arterial stiffness results from eccentrically biased downhill running exercise. *J Sci Med Sport*, 18(2), 230-235. <https://doi.org/10.1016/j.jsams.2014.03.003>
- Byrnes, W. C., Clarkson, P. M., White, J. S., Hsieh, S. S., Frykman, P. N., & Maughan, R. J. (1985). Delayed onset muscle soreness following repeated bouts of downhill running. *J Appl Physiol* (1985), 59(3), 710-715. <https://doi.org/10.1152/jappl.1985.59.3.710>
- Chen, T. C., Nosaka, K., & Tu, J. H. (2007). Changes in running economy following downhill running. *J Sports Sci*, 25(1), 55-63. <https://doi.org/10.1080/02640410600718228>
- Clarkson, P. M., & Hubal, M. J. (2002). Exercise-induced muscle damage in humans. *Am J Phys Med Rehabil*, 81(11 Suppl), S52-69. <https://doi.org/10.1097/00002060-200211001-00007>
- Clarkson, P. M., Nosaka, K., & Braun, B. (1992). Muscle function after exercise-induced muscle damage and rapid adaptation. *Med Sci Sports Exerc*, 24(5), 512-520. <https://doi.org/10.1249/00005768-199205000-00004>
- Close, G. L., Ashton, T., Cable, T., Doran, D., & MacLaren, D. P. (2004). Eccentric exercise, isokinetic muscle torque and delayed onset muscle soreness: the role of reactive oxygen species. *Eur J Appl Physiol*, 91(5-6), 615-621. <https://doi.org/10.1007/s00421-003-1012-2>
- Doma, K., Leicht, A., Sinclair, W., Schumann, M., Damas, F., Burt, D., & Woods, C. (2018). Impact of Exercise-Induced Muscle Damage on Performance Test Outcomes in Elite Female Basketball Players. *J Strength Cond Res*, 32(6), 1731-1738. <https://doi.org/10.1519/jsc.0000000000002244>
- Eston, R., Lemmey, A., McHugh, P., Byrne, C., & Walsh, S. (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(4), 199-204. <https://doi.org/10.1034/j.1600-0838.2000.010004199.x>
- Eston, R. G., Mickleborough, J., & Baltzopoulos, V. (1995). Eccentric activation and muscle damage: biomechanical and physiological considerations during downhill running. *Br J Sports Med*, 29(2), 89-94. <https://doi.org/10.1136/bjism.29.2.89>
- Féasson, L., Stockholm, D., Freyssenet, D., Richard, I., Duguez, S., Beckmann, J. S., & Denis, C. (2002). Molecular adaptations of neuromuscular disease-associated proteins in response to eccentric exercise in human skeletal muscle. *The Journal of physiology*, 543(1), 297-306. <https://doi.org/10.1113/jphysiol.2002.018689>
- GOV.Uk. (2019, 7th September). UK Chief Medical Officers' Physical Activity Guidelines. Gov UK. <https://www.gov.uk/government/collections/physical-activity-guidelines>
- Hyldahl, R. D., & Hubal, M. J. (2014). Lengthening our perspective: morphological, cellular, and molecular responses to eccentric exercise. *Muscle Nerve*, 49(2), 155-170. <https://doi.org/10.1002/mus.24077>
- Kargarfard, M., Lam, E. T., Shariat, A., Shaw, I., Shaw, B. S., & Tamrin, S. B. (2016). Efficacy of massage on muscle soreness, perceived recovery, physiological restoration and physical performance in male bodybuilders. *J Sports Sci*, 34(10), 959-965. <https://doi.org/10.1080/02640414.2015.1081264>
- Kolkhorst, F. W., Mittelstadt, S. W., & Dolgener, F. A. (1996). Perceived exertion and blood lactate concentration during graded treadmill running. *Eur J Appl Physiol Occup Physiol*, 72(3), 272-277. <https://doi.org/10.1007/bf00838651>
- Konings, M. J., Parkinson, J., Zijdwind, I., & Hettinga, F. J. (2018). Racing an Opponent: Alteration of Pacing, Performance, and Muscle-Force Decline but Not Rating of Perceived Exertion. *Int J Sports Physiol Perform*, 13(3), 283-289. <https://doi.org/10.1123/ijssp.2017-0220>
- Koskinen, S. O., Hoyhtya, M., Turpeenniemi-Hujanen, T., Martikkala, V., Mäkinen, T. T., Oksa, J., Rintamäki, H., Lofberg, M., Somer, H., & Takala, T. E. (2001). Serum concentrations of collagen degrading enzymes and their inhibitors after downhill running. *Scand J Med Sci Sports*, 11(1), 9-15. <https://doi.org/10.1034/j.1600-0838.2001.011001009.x>

- Machado, F. A., Kravchychyn, A. C., Peserico, C. S., da Silva, D. F., & Mezzaroba, P. V. (2013). Incremental test design, peak 'aerobic' running speed and endurance performance in runners. *J Sci Med Sport*, 16(6), 577-582. <https://doi.org/10.1016/j.jsams.2012.12.009>
- Maeo, S., Ando, Y., Kanehisa, H., & Kawakami, Y. (2017). Localization of damage in the human leg muscles induced by downhill running. *Sci Rep*, 7(1), 5769. <https://doi.org/10.1038/s41598-017-06129-8>
- Malm, C., Sjodin, T. L., Sjoberg, B., Lenkei, R., Renstrom, P., Lundberg, I. E., & Ekblom, B. (2004). Leukocytes, cytokines, growth factors and hormones in human skeletal muscle and blood after uphill or downhill running. *J Physiol*, 556(Pt 3), 983-1000. <https://doi.org/10.1113/jphysiol.2003.056598>
- Nottle, C., & Nosaka, K. (2007). Changes in power assessed by the Wingate Anaerobic Test following downhill running. *J Strength Cond Res*, 21(1), 145-150. <https://doi.org/10.1519/00124278-200702000-00026>
- Park, K. S., & Lee, M. G. (2015). Effects of unaccustomed downhill running on muscle damage, oxidative stress, and leukocyte apoptosis. *J Exerc Nutrition Biochem*, 19(2), 55-63. <https://dx.doi.org/10.5717%2Fjenb.2015.15050702>
- Peake, J. M., Suzuki, K., Hordern, M., Wilson, G., Nosaka, K., & Coombes, J. S. (2005a). Plasma cytokine changes in relation to exercise intensity and muscle damage. *Eur J Appl Physiol*, 95(5-6), 514-521. <https://doi.org/10.1007/s00421-005-0035-2>
- Peake, J. M., Suzuki, K., Wilson, G., Hordern, M., Nosaka, K., Mackinnon, L., & Coombes, J. S. (2005b). Exercise-Induced Muscle Damage, Plasma Cytokines, and Markers of Neutrophil Activation. *Medicine & Science in Sports & Exercise*, 37(5), 737-745. <https://doi.org/10.1249/01.mss.0000161804.05399.3b>
- Rowlands, A. V., Eston, R. G., & Tilzey, C. (2001). Effect of stride length manipulation on symptoms of exercise-induced muscle damage and the repeated bout effect. *J Sports Sci*, 19(5), 333-340. <https://doi.org/10.1080/02640410152006108>
- Schwane, J. A., Watrous, B. G., Johnson, S. R., & Armstrong, R. B. (1983). Is Lactic Acid Related to Delayed-Onset Muscle Soreness? *Phys Sportsmed*, 11(3), 124-131. <https://doi.org/10.1080/00913847.1983.11708485>
- Sorichter, S., Mair, J., Koller, A., Calzolari, C., Huonker, M., Pau, B., & Puschendorf, B. (2001). Release of muscle proteins after downhill running in male and female subjects. *Scand J Med Sci Sports*, 11(1), 28-32. <https://doi.org/10.1034/j.1600-0838.2001.011001028.x>
- van de Vyver, M., Engelbrecht, L., Smith, C., & Myburgh, K. H. (2016). Neutrophil and monocyte responses to downhill running: Intracellular contents of MPO, IL-6, IL-10, pstat3, and SOCS3. *Scand J Med Sci Sports*, 26(6), 638-647. <https://doi.org/10.1111/sms.12497>
- van de Vyver, M., & Myburgh, K. H. (2014). Variable inflammation and intramuscular STAT3 phosphorylation and myeloperoxidase levels after downhill running. *Scand J Med Sci Sports*, 24(5), e360-371. <https://doi.org/10.1111/sms.12164>
- Warren, G. L., Lowe, D. A., & Armstrong, R. B. (1999). Measurement tools used in the study of eccentric contraction-induced injury. *Sports Med*, 27(1), 43-59. <https://doi.org/10.2165/00007256-199927010-00004>

