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ORIGINAL ARTICLE

Level, uphill and downhill running economy values are strongly inter-correlated

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Abstract

Purpose Exercise economy is not solely an intrinsic physiological trait because economy in one mode of exercise (e.g., running) does not strongly correlate with economy in another mode (e.g. cycling). Economy also reflects the skill of an individual in a particular mode of exercise. Arguably, level, uphill and downhill running constitute biomechanically different modes of exercise. Thus, we tested the hypothesis that level running economy (LRE), uphill running economy (URE) and downhill running economy (DRE) would not be strongly inter-correlated.

Methods We measured the oxygen uptakes of 19 male trained runners during three different treadmill running speed and grade conditions: 238 m/min, 0%; 167 m/min, +7.5%; 291 m/min, −5%. Mean oxygen uptakes were 46.8 (SD 3.9), 48.0 (3.4) and 46.9 (3.7) ml/kg/min for level, uphill and downhill running, respectively, indicating that the three conditions were of similar aerobic intensity.

Results We reject our hypothesis based on the strong correlations of $r=0.909$, $r=0.901$ and $r=0.830$, respectively, between LRE vs. URE, LRE vs. DRE and URE vs. DRE.

Conclusion Economical runners on level surfaces are also economical on uphill and downhill grades. Inter-individual differences in running economy reflect differences in both intrinsic physiology and skill. Individuals who have experience with level, uphill and downhill running appear to be equally skilled in all three modes.

Keywords Locomotion · Metabolic cost · Oxygen consumption · Efficiency · Incline · Decline

Abbreviations

ANOVA	Analysis of variance
C_r	Cost of running per unit distance
DR	Downhill running
DRE	Downhill running economy
EMG	Electromyography
LR	Level running
LRE	Level running economy
RE	Running economy
UR	Uphill running
URE	Uphill running economy
$\dot{V}_E$	Volumetric flow rate of expired air
VEQ	Ventilatory equivalent $=\dot{V}_E/\dot{V}O_2$
$\dot{V}O_2$	Rate of oxygen uptake

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Introduction

Running economy (RE) is traditionally defined as "the steady-state oxygen consumption for a standardized running speed" (Conley and Krahenbuhl 1980) and a lower rate of oxygen consumption indicates better RE. Along with an individual's maximal oxygen uptake ($\dot{V}O_2$ max) and their lactate threshold, RE is a major determinant of success in competitive distance running (Joyner and Coyle 2008). Yet, exactly what factors determine an individual's RE remain unknown. Numerous review articles have delineated that factors such as muscle efficiency, intramuscular mitochondrial oxidative enzymes, anatomical differences, the ability to store and reutilize elastic energy, biomechanics, and skill are correlated with RE at the group level (Barnes and Kilding 2015; Cavanagh and Kram 1985; Lacour and Bourdin 2015; Moore 2016; Morgan et al. 1989). But, quantifying the contribution of each separate factor is more difficult. For example, Williams and Cavanagh (1987) examined the relationships between numerous physiological and biomechanical measures and RE in 31 participants. Although they were able to identify a few general correlations at the group level, Williams and Cavanagh (1987) were unable to accurately predict an individual's RE based a single or small subset of variables because RE is so multifactorial.

Running economy varies considerably among individuals; ranges up to 20% have been reported (Cureton and Sparling 1980; Daniels et al. 1977; Farrell et al. 1979). Similar variations in economy have also been reported for other modes of exercise. For example, Daniels et al. (1984) measured the submaximal oxygen uptake ($\dot{V}O_2$submax) in 13 trained runners during bench stepping, arm cranking, grade walking, cycling and running and found economy ranges of 12.6–25% across the five modes of exercise. Moreover, they found that an individual's economy in one mode of exercise did not strongly predict their economy during other exercise modes even when the same muscle groups were used. Thus, Daniels et al. (1984) concluded that economy does not appear to be an intrinsic general physiological trait for different modes of exercise within an individual. Rather, an individual's economy relative to others is specific to the mode of exercise.

Most people generally think of running as a single mode of exercise, but level, uphill and downhill running have distinctly different biomechanics and muscular actions (see review by Vernillo et al. 2017a). For example, during uphill running (UR), the muscles must generate net positive mechanical power, but during downhill running (DR), the muscles must dissipate mechanical power (Snyder et al. 2012). Compared to level running (LR), UR incurs smaller perpendicular impact and braking forces, requires greater propulsive forces and there is a greater tendency to land on the midfoot (Gottschall and Kram 2005). In contrast, DR incurs much larger impacts, greater braking forces and there is a tendency to land on the heels (Gottschall and Kram 2005). Hamill et al. (1984) reported that when runners switched from LR to DR, they experienced greater shock at the tibia, greater knee flexion velocities and more dorsiflexed ankles at contact. Yokozawa et al. (2007) demonstrated that compared to LR, UR involved greater muscle activation and extensor muscle torques at the hip and knee joints. More specifically, Cai et al. (2010) compared electromyographic (EMG) signals of the leg muscles during LR and UR and noted significantly greater EMG of the rectus femoris (RF) and the biceps femoris (BF) during UR. In contrast, quadriceps EMG initially does not differ between running on level vs. moderate downhill slopes at matched treadmill velocities (Abe et al. 2011; Mizrahi et al. 2001), although during downhill running, greater EMG signals emerge after 20 min (Mizrahi et al. 2001). The thorough review by Vernillo et al. (2017a) presents many other parameters that differ between LR, UR and DR. Overall, there is ample kinematic, kinetic and electromyographic evidence that level, uphill and downhill running could be considered different modes of exercise.

Since relative inter-individual economy varies from one mode of exercise to another, here we explored if level, uphill, and downhill running economy are interrelated. This topic is relevant for competitors in road, cross-country, fell, orienteering and mountain running events who must contend with level, uphill and downhill portions of the racecourses. The principle of specificity would suggest that for optimal racing performance on hilly terrain, athletes should train by running on level, uphill and downhill routes. However, some people live in areas of rather flat topography and thus cannot easily train outdoors on undulating or hilly terrain. One alternative for such topographically challenged athletes is to train on an inclinable/declinable treadmill. To provide a scientific basis for the specificity of running training, we asked: are the most economical runners on the level also the most economical runners downhill and/or uphill? We tested three null hypotheses: (1) level running economy (LRE) would not be strongly correlated with uphill running economy (URE), (2) LRE running economy would not be strongly correlated with downhill running economy (DRE) and (3) URE would not be strongly correlated with DRE.

Materials and methods

Participants

Nineteen healthy male trained runners [age: 29 ± 6.1 years (mean ± SD), body mass: 68.2 ± 7.7 kg] volunteered. All participants regularly encountered hills during their training runs and wore their own shoes during testing. Table 1 displays the participant demographics.

Protocol

Testing consisted of three visits to the laboratory separated by at least 72 h. During the first visit, each participant provided informed consent as per university policy and the 1964 Helsinki declaration. They then underwent a physical examination by a registered nurse. We instructed the participants to fast for at least 3 h prior to the second and third visits. During the second visit, each participant completed a $\dot{V}O_2$ max test on a Quinton model 18-60-1 treadmill (Seattle, WA, USA). Participants initially ran for 4 min at 200 m/min, 0% grade as a warm-up. After 4 min, we inclined the

Table 1 Participant demographics

Participant	Height (cm)	Mass (kg)	Age (years)	$\dot{V}O_2$ max (ml/kg/min)
1	175	66.8	37	67.6
2	176	63.6	32	74.7
3	172	66.1	32	67.4
4	188	80.8	25	67.9
5	184	78.5	24	69.3
6	169	59.0	22	65.6
7	176	65.6	30	69.3
8	181	71.7	32	64.4
9	171	65.4	25	66.6
10	180	63.8	37	71.2
11	160	50.0	30	75.9
12	182	66.3	23	76.0
13	180	76.3	31	66.1
14	184	73.5	23	69.5
15	176	68.1	42	63.7
16	177	65.8	26	73.7
17	183	74.5	24	61.5
18	184	79.4	22	58.0
19	172	60.9	38	66.9
Average	177.4	68.2	29.2	68.2
SD	6.7	7.7	6.1	4.7

treadmill to 5% and incremented the incline by 2.5% every 2 min thereafter until volitional fatigue.

Participants breathed through a Daniels low dead-space two-way breathing valve while wearing a nose clip and we collected their expired air with 200 l Douglas bags. We measured expired gas volume with a Parkinson–Cowan dry gas meter (Edmonton, UK) and corrected all volumes to standard temperature and pressure dry (STPD). We analyzed the composition of the expired air with a Beckman E-2 paramagnetic oxygen analyzer (Brea, California USA) and a Lira Model 300 infrared carbon dioxide analyzer (Mine Safety Appliances Company, Pittsburgh, Pennsylvania USA). We calibrated both devices before each test using known standard gas mixtures. The participants' $\dot{V}O_2$ max values (68.2 ± 4.8 ml/kg/min) indicated that they were aerobically fit.

During the third visit, after a 5-min warm-up at 200 m/min level, each participant performed three submaximal treadmill trials in random order, each lasting 7 min with 5 min of rest between trials. Based upon Margaria et al. (1963) and pilot experiments, we selected three running speed/grade combinations that require similar submaximal rates of oxygen consumption ($\dot{V}O_2$ submax). We chose: a level treadmill speed of 238 m/min, up 7.5% at 167 m/min and down 5% at 291 m/min. We intentionally avoided steeper downhill grades due to the large ground reaction impact forces associated with fast running down such grades (Gottschall and Kram 2005). To obtain the downhill grade, we mounted the rear feet of the treadmill atop a 15 cm wooden platform. To calibrate and monitor treadmill belt speed, we affixed a piece of reflective tape to the treadmill belt which triggered a photocell signal connected to an electronic frequency counter. We collected Douglas bags of expired air successively during minutes 6 and 7 and timed the collection period with a stopwatch. We averaged the two Douglas bag values to determine the oxygen uptake for each trial.

The data in this paper were collected in 1985, when RE was traditionally quantified as $\dot{V}O_2$ (ml/kg/min). Today, we and other scientists advocate using units of metabolic energy (Fletcher et al. 2009; Kipp et al. 2018; Beck et al. 2018). However, since we matched the exercise intensity during LR, UR and DR, the metabolic fuel mixtures were likely very similar and thus $\dot{V}O_2$ reflects the rate of metabolic energy consumption. We appreciate that some scientists prefer to express running economy in units of oxygen or energy per distance (C_r). Indeed, we have used such calculations ourselves when we are comparing individuals or groups (or even species) at different level running velocities. However, in the present study, all subjects ran at the same three combinations of incline and velocity. Thus, if we were to divide the oxygen consumption rates for each subject by the same three running velocities (i.e., three mathematical constants), the results of our correlation analysis (i.e. our main hypotheses) would not change at all. Moreover, our study was designed to build upon Gregor and Costill (1973) who compared level, uphill and downhill at the same velocity but at very different intensities and therefore different mixtures of metabolic substrates. We chose to present our data as $\dot{V}O_2$ values (ml/kg/min), because it allowed us to directly compare the exercise intensity across conditions. If we reported C_r values, they would be numerically very different for the three conditions when in fact, the three conditions were at very similar intensities. Because we provide the $\dot{V}O_2$ data for each individual subject in all three conditions, readers can easily calculate C_r.

Statistical analysis

Using R-Studio (http://www.rstudio.com), we performed one-way repeated measures ANOVA to test for differences between conditions. When a significant effect was detected by the ANOVA, we performed pair-wise Bonferroni follow-up comparisons. We also calculated both Pearson product-moment and Spearman Rho correlations between all three possible pairs of running conditions. The former technique used the actual $\dot{V}O_2$ submax values, while the latter used each participant's rank in economy at each of the three conditions. We used Cohen's criterion for a strong correlation of an r value greater than 0.50 (Cohen 1988) and we applied a $p < 0.05$ criterion for statistical significance. Since we performed three regression analyses, to control for false positives, we used a Bonferroni correction to the p value, $0.05/3 = 0.0167$.

Results

Running economy values for each participant at the three grade and speed conditions are shown in Table 2. In general, we met our goal of matching the exercise intensity between the three speed and grade conditions. LRE and DRE were not significantly different ($p > 0.99$) nor were URE and DRE ($p = 0.145$). The average URE 48.0 ml/kg/min was statistically greater ($p = 0.012$) than the LRE (46.8 ml/kg/min), but the difference was only 2.5%.

The submaximal oxygen uptakes of the runners averaged 68.6 ± 5.60, 70.3 ± 5.04 and $68.8 \pm 5.36\%$ of their $\dot{V}O_2$ max during the level, uphill and downhill trials, respectively. The greatest $\%\dot{V}O_2$ max recorded for any of the 57 trials was 79.7%. Given the aerobic fitness of our participants, it is reasonable to assume that at these intensities, they were at steady state and below their lactate thresholds.

Inter-individual variation in RE within this group of runners was similar across all three speed and grade conditions. The inter-individual RE ranges were 27.8%, 22.9%, and 24.3%, respectively, for the level, uphill, and downhill runs. The coefficients of variation across the three conditions were 8.2%, 7.0% and 7.7%, respectively.

We found strong correlations among LRE, URE and DRE using the Pearson product-moment method. The correlation between LRE and URE was $r = 0.909$ ($p = 7.12\text{E}^{-8}$). Figure 1 shows this relationship. The regression equation was:

$$\text{URE} = 10.052 + (0.811 \times \text{LRE}).$$

The 95% confidence limits for r, intercept and slope were (0.775, 0.964) (1.129, 18.974) and (0.621, 1.001), respectively.

Between LRE and DRE, the correlation coefficient was $r = 0.901$ ($p = 1.478\text{E}^{-07}$). Figure 2 shows this relationship. The regression equation was:

$$\text{DRE} = 6.988 + (0.855 \times \text{LRE}).$$

The 95% confidence limits for r, intercept and slope were (0.751, 0.961) (−2.918, 16.895) and (0.644, 1.066), respectively.

Between DRE and URE, the correlation coefficient was $r = 0.830$ ($p = 1.082\text{E}^{-05}$). Figure 3 shows this relationship. The regression equation was:

$$\text{DRE} = 4.576 + (0.884 \cdot \text{URE}).$$

The 95% confidence limits for r, intercept and slope were (0.604, 0.932) (−10.017, 19.170) and (0.580, 1.187), respectively.

We also numerically ranked the runners based on their $\dot{V}O_2$ submax values to determine if individuals were consistently more or less economical when compared with the

Table 2 Submaximal oxygen uptake (ml/kg/min)

Participant	Level	Uphill	Downhill
1	51.0	50.7	52.1
2	42.2	44.3	42.8
3	43.8	45.3	41.5
4	47.8	51.8	44.8
5	44.2	47.1	44.7
6	51.8	52.1	51.7
7	45.7	46.6	46.9
8	46.3	46.6	46.9
9	51.2	50.0	48.9
10	54.4	53.4	52.2
11	43.9	46.2	44.5
12	44.3	45.7	44.9
13	50.7	52.5	51.9
14	43.7	45.0	47.7
15	45.0	49.0	46.3
16	41.4	44.4	43.0
17	43.3	42.4	42.9
18	46.0	45.4	45.8
19	51.7	53.1	52.9
Average	46.8	48.0	47.0
SD	3.9	3.4	3.7

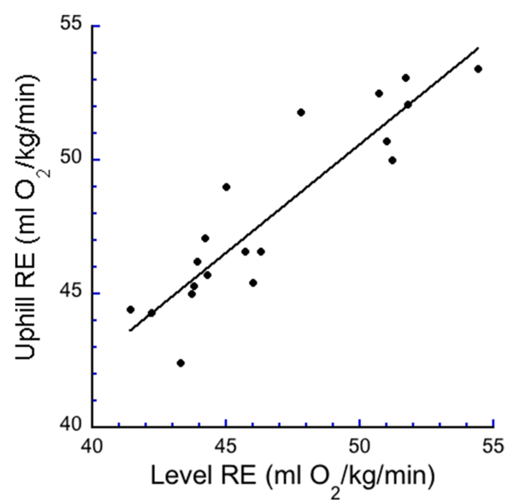

Fig. 1 Uphill running economy was strongly correlated with level running economy: $r = 0.909$, $p = 7.12\text{E}^{-8}$, $n = 19$. Linear regression equation: URE = 10.052 + (0.811 × LRE). The 95% confidence limits for r, intercept and slope were (0.775, 0.964) (1.129, 18.974) and (0.621, 1.001), respectively

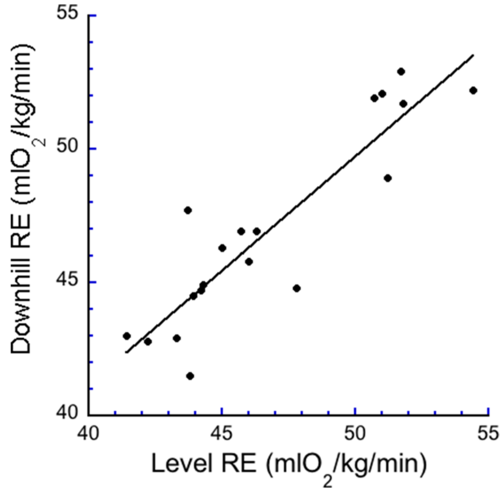

Fig. 2 Downhill running economy was strongly correlated with level running economy: $r=0.901$, $p=1.48\text{E}^{-7}$, $n=19$. Linear regression equation: DRE = 6.988 + (0.855 × LRE). The 95% confidence limits for r, intercept and slope were (0.751, 0.961) (−2.918, 16.895) and (0.644, 1.066), respectively

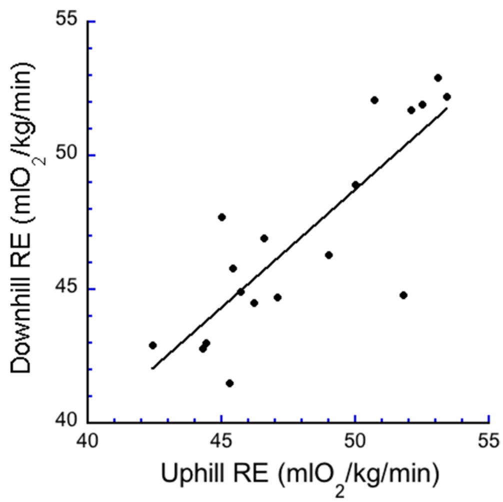

Fig. 3 Downhill running economy was strongly correlated with uphill running economy: $r=0.830$, $p=1.08\text{E}^{-5}$, $n=19$. Linear regression equation: DRE = 4.576 + (0.884 × URE). The 95% confidence limits for r, intercept and slope were (0.604, 0.932) (−10.017, 19.170) and (0.580, 1.187), respectively

cohort. Those rankings are shown in Table 3. We used the Pearson Rho method to compare the rankings and found correlation coefficients of 0.921 ($p=1.5\text{E}^{-6}$) between LRE and URE, 0.838 ($p=2.2\text{E}^{-16}$) between LRE and DRE and 0.791 ($p=7.7\text{E}^{-5}$) between DRE and URE. The three most economical rankings at each grade were dominated by the same four runners. Further, the six most economical rankings at each grade were dominated by the same six runners. At the bottom of the rankings, five runners were responsible

Table 3 Individual rankings submaximal oxygen uptake; smaller rank = lower oxygen uptake

Participant	Level	Uphill	Downhill
1	17	15	14
2	2	2	2
3	1	5	5
4	7	13	15
5	6	7	11
6	15	18	16
7	12	9	9
8	11	12	10
9	14	16	13
10	18	19	19
11	5	6	8
12	8	8	7
13	16	14	17
14	13	4	4
15	10	10	12
16	4	1	3
17	3	3	1
18	9	11	6
19	19	17	18

for the three least economical runs at each of the grades. In other words, on a numerical ranking basis, the most and least economical runners on the level were generally the most and least economical runners both uphill and downhill.

Discussion

We reject our three null hypotheses. We found strong correlations among LRE, URE and DRE. Relative inter-individual differences in RE were largely unchanged at the different grade and speed combinations. We believe that the strong correlations between LRE, URE and DRE are due to the participants having roughly equal training/practice exposure to level, uphill and downhill terrain and thus equal skill and/or physiological adaptations.

Our findings are consistent with Gregor and Costill (1973) who measured $\dot{V}O_2$ submax in ten runners at grades of 0%, +6%, and −6%, while treadmill speed was held constant at 214 m/min. We re-analyzed their data and found correlations of 0.89 between LRE and URE, 0.83 between LRE and DRE, and 0.88 between DRE and URE. However, the aerobic intensity in their study varied widely across the three running tasks, from 30.1 to 53.3 ml/kg/min which equates to 44.3–78.5% of $\dot{V}O_2$ max. Such a broad range of exercise intensities involves substantially different metabolic fuel mixtures. In contrast, the three running tasks in the present study were well-matched with only a small difference between the level and uphill conditions; 68.6 ± 5.60 vs. 70.3 ± 5.04% of $\dot{V}O_2$ max ($p = 0.012$).

More recently, Balducci et al. have investigated similar questions. Balducci et al. (2016) compared the RE of 10 elite endurance mountain runners on a level treadmill and with the treadmill inclined to 12.5 and 25%. They reported that URE was not significantly correlated with LRE ($r = 0.10$ for 12.5% and 0.09 for 25% inclines). Of note, the LRE was remarkably homogenous, with only a 12% inter-individual range. Moreover, one subject who exhibited the ninth worst LRE was the most economical subject up both the 12.5 and 25% inclines and that subject's data substantially reduced the strength of the correlation. Subsequently, Balducci et al. (2017) compared LRE and URE for a larger ($n = 24$) and more heterogeneous group of experienced mountain runners (inter-individual LRE range was ~ 24%). Their analysis revealed a strong ($r = 0.84$) and significant ($p < 0.001$) correlation between LRE and URE. The results of Balducci et al. (2017), Gregor and Costill (1973) and the present study are all consistent.

The mean LRE at a speed of 238 m/min in our study of was 46.8 ml/kg/min which is consistent with previous studies (Boileau et al. 1982; Bransford and Howley 1977; Davies and Thompson 1979). The inter-individual range for LRE in our participants, 27.8%, is also similar to those reported in other studies (Daniels et al. 1977; Farrell et al. 1979). The ranges for URE and DRE in our study were 23% and 24%, respectively. Those are similar to the 19.9% and 19.6% reported by Gregor and Costill (1973).

Given the differences in impact forces reported for level, uphill and downhill running (Gottschall and Kram 2005; Hamill et al. 1984) and the relationship between ventilation and shock attenuation (Daley et al. 2013; Frederick et al. 1984), we explored if there were differences in the ventilation during each of the three conditions tested. We compared the ventilatory equivalent (VEQ = $\dot{V}_E/\dot{V}O_2$) between the three grade–speed combinations (Table 4). $\dot{V}_E$ is the volume of air expired per minute. Indeed, VEQ was greater during DR when compared with LR ($p = 6.4E^{-4}$) and UR ($p = 7.1E^{-4}$). It may be that the greater $\dot{V}_E$ during DR was due to a visceral piston effect (Daley et al. 2013).

Our experiment was motivated by previous research by Daniels et al. (1984) who found only weak correlations between economy in five different exercise modes. They concluded that economy is not an intrinsic general physiological trait within an individual but varies depending on the mode of exercise being performed. Given the numerous differences in the biomechanics of running on the level, uphill and downhill (Vernillo et al. 2017a), we considered them to be different modes of exercise and hence we expected to not find strong correlations between LRE, URE and DRE. Clearly, our data refute our expectations. Within the group

Table 4 Volumetric flow rate of expired air ($\dot{V}_E$) and ventilatory equivalent: VEQ = $\dot{V}_E/\dot{V}O_2$

Participant	$\dot{V}_E$ (l/min)			VEQ		
	Level	Uphill	Downhill	Level	Uphill	Downhill
1	62.0	60.0	70.9	18.2	17.7	20.4
2	44.3	50.3	50.6	16.5	17.7	18.6
3	68.9	69.7	67.8	23.8	23.3	24.7
4	75.8	85.0	74.7	19.6	20.3	20.6
5	57.7	59.8	65.4	16.6	16.2	18.7
6	77.4	72.9	72.9	25.3	23.8	23.9
7	55.2	55.6	59.3	18.4	18.2	19.3
8	81.3	81.5	83.2	24.5	24.4	24.7
9	74.0	75.8	75.1	22.1	23.2	23.5
10	66.9	63.1	64.5	19.3	18.5	19.3
11	46.7	49.0	47.7	21.3	21.2	21.4
12	56.7	47.3	59.2	19.3	15.6	19.9
13	81.4	82.7	89.1	21.0	20.6	22.5
14	55.7	49.8	65.6	17.3	15.1	18.7
15	83.0	88.8	93.0	26.5	26.6	29.5
16	51.4	52.4	57.3	18.9	18.0	20.3
17	52.0	55.4	51.3	16.2	17.6	16.0
18	80.7	76.2	82.4	22.1	21.1	22.7
19	57.2	56.4	64.7	18.2	17.4	20.1
Average	64.6	64.8	68.1*	20.3	19.8	21.3*
SD	12.8	13.7	12.8	3.1	3.3	3.1

*Significantly different from level running, $p < 0.05$

of trained runners that we studied, those who were the most economical runners on the level were also generally the most economical uphill and downhill runners. Those who were the least economical runners on the level were also generally the least economical when running uphill and downhill. Within our sample, RE during level, uphill and downhill running was not mode-specific.

Some evidence supports the idea that good running economy is a skill. Jensen et al. (1999) compared track runners and orienteers. The two groups had equal RE on a level smooth surface but on a rough and hilly course, the orienteers had substantially better RE than the track runners. Even among world-class orienteers, individuals vary considerably in the ratio of their level vs. uphill running maximal performance on a treadmill (Lauenstein et al. 2013). That suggests that the athletes varied in their LRE/URE ratio but economy was not measured in that study. A recent study from our laboratory (Swinnen et al. 2018) found that trained runners have better RE than aerobically trained triathletes and trained cyclists. The conclusion of that study was that running is an acquired or practiced skill and greater skill results in better RE.

The present study could not distinguish if level, uphill and downhill running are distinct skills in terms of RE because all of the participants regularly ran on a variety of terrain. It would be interesting to compare the LRE, URE and DRE of runners who habitually only run on level ground to runners who consistently train on both level and hilly/mountainous terrain. We can imagine that those who train extensively on uphill and downhill terrain might have better URE and DRE than runners who have no or limited experience with hills, but for now we lack such specific data.

Based only on our RE data, we have no reason to suggest that athletes need to prioritize the inclusion of uphill- and downhill-specific training so as to optimize their overall running performance. Uphill-specific running training improves LRE (Barnes et al. 2013), but we are not aware of any study showing improvements in URE in response to specific uphill running training. Moreover, RE is not the only factor affecting performance. Giovanelli et al. (2016) found that maximal leg muscle power production predicted finishing time in an uphill marathon race and suggested that uphill-specific training could enhance performance. There is substantial evidence that downhill running experience reduces the delayed onset muscle soreness that occurs after prolonged downhill running (see review by Eston et al. 1995). Mountain ultramarathons that include substantial downhill running incur dramatic and protracted leg strength deficits (Millet et al. 2011) and may or may not impair RE (Vernillo et al. 2017b). Future studies should test for any improvements in URE, DRE, performance and recovery in response to uphill- and downhill-specific training interventions. Overall, runners planning to compete on courses with substantial uphill and downhill portions would be wise to prepare with both uphill-specific and downhill-specific training sessions.

In conclusion, we find that RE is generalizable between level, uphill and downhill grades. Differences in RE between individuals probably reflect differences in both intrinsic physiological properties and skill. Our data did not reveal any individuals who were particularly economical at one specific grade. Economical runners are economical runners regardless of the grade.

Author contributions TJB and RK conceived and designed the experiment. TJB conducted the experiments. TJB and ALRO processed the data and performed statistical analysis. TJB, ALRO and RK wrote and edited the manuscript. All authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent Informed consent was obtained from all individual participants included in the study.

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