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The influence of training status, age, and muscle fiber type on cycling efficiency and endurance performance

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Hopker JG, Coleman DA, Gregson HC, Jobson SA, Von der Haar T, Wiles J, Passfield L. The influence of training status, age, and muscle fiber type on cycling efficiency and endurance performance. *J Appl Physiol* 115: 723–729, 2013. First published June 27, 2013; doi:10.1152/jappphysiol.00361.2013.—The purpose of this study was to assess the influence of age, training status, and muscle fiber-type distribution on cycling efficiency. Forty men were recruited into one of four groups: young and old trained cyclists, and young and old untrained individuals. All participants completed an incremental ramp test to measure their peak O₂ uptake, maximal heart rate, and maximal minute power output; a submaximal test of cycling gross efficiency (GE) at a series of absolute and relative work rates; and, in trained participants only, a 1-h cycling time trial. Finally, all participants underwent a muscle biopsy of their right vastus lateralis muscle. At relative work rates, a general linear model found significant main effects of age and training status on GE ($P < 0.01$). The percentage of type I muscle fibers was higher in the trained groups ($P < 0.01$), with no difference between age groups. There was no relationship between fiber type and cycling efficiency at any work rate or cadence combination. Stepwise multiple regression indicated that muscle fiber type did not influence cycling performance ($P > 0.05$). Power output in the 1-h performance trial was predicted by average O₂ uptake and GE, with standardized β -coefficients of 0.94 and 0.34, respectively, although some mathematical coupling is evident. These data demonstrate that muscle fiber type does not affect cycling efficiency and was not influenced by the aging process. Cycling efficiency and the percentage of type I muscle fibers were influenced by training status, but only GE at 120 revolutions/min was seen to predict cycling performance.

gross efficiency; muscle fiber type; maximal oxygen uptake; endurance performance

CYCLING EFFICIENCY IS WIDELY held not to respond to endurance training (29, 32, 33, 35). This viewpoint was reinforced in the criticism of the case study on Lance Armstrong published in 2005 (12, 15, 30, 43). However, a careful examination of previous studies suggests that a lack of statistical power may mask meaningful differences in cycling efficiency between trained and untrained participants (e.g., 5.0–9.5%, Ref. 35). Furthermore, when comparing cycling efficiency data between trained and untrained populations from exercise tests involving relative work rates, the scaling of energy expenditure to power output can be problematic. The use of covariate-controlled

allometric models is one way of circumventing this problem (1, 3, 36).

Recently, our laboratory demonstrated that careful use of the Douglas bag method may provide a much more reliable measurement of cycling efficiency than the ubiquitous online expired gas analysis systems (21). Indeed, with sufficient statistical power, we have found a significant difference in cycling efficiency between trained and untrained populations (17). However, this difference could have been partially due to differences between the untrained and trained subjects in absolute exercise intensity when tested at the same relative intensity. Furthermore, we have found endurance training to result in significant increases in cycling efficiency (18, 19).

The influence of muscle fiber-type distribution on cycling efficiency is also controversial. Specifically, a significant positive relationship has been reported between the percentages of type I muscle fibers and cycling efficiency in some (9, 22, 32), but not all, studies (31, 37). These observations are intriguing as they may indicate the capacity for shifts in the fast myosin isoform to a more efficient isoform in endurance-trained muscle (16, 40). The muscle morphology of cyclists who have endurance trained for many years might provide an insight into this muscle fiber-type transformation and whether it influences cycling efficiency. Findings on the total cost of muscle contraction in older adults appear equivocal, with some studies (26, 27), but not all (4, 47), suggesting an influence of age. To our knowledge, only one study has directly investigated the influence of age on cycling efficiency in trained cyclists. Surprisingly, Sacchetti et al. (41) found that cycling efficiency was lower in older (mean age 66 yr) vs. younger (mean age 24 yr) competitive cyclists, regardless of cadence and power output. But this study did not take muscle biopsy samples, identify whether differences might have been accounted for by a higher cost of breathing in older trained subjects (7) due to reductions in tidal volume (24), or control for potential scaling issues highlighted above.

Finally, it has been suggested that efficiency plays an important role in determining endurance performance (25), but this has not been empirically tested. This is important, as even modest improvements in cycling efficiency have been calculated to provide a worthwhile impact on endurance cycling performance (33). There is also currently debate in the literature about the interaction and relative importance of maximum O₂ uptake ($\dot{V}O_{2\max}$), fractional utilization of $\dot{V}O_{2\max}$, and cycling efficiency on endurance exercise performance (23, 28, 45, 46). It is unclear how efficiency, $\dot{V}O_{2\max}$, and the fractional utilization of $\dot{V}O_{2\max}$ interact to determine cycling perfor-

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mance and how the aging process might influence this relationship.

In light of the limitations of past research on cycling efficiency that investigate the influence of training status, muscle fiber type, and age, there is a clear need to reevaluate previous findings. Therefore, this study sought to conduct a carefully controlled cross-sectional investigation of the influence of training status, muscle fiber type, age, and cadence on cycling efficiency. Specifically, the purposes of this study were to investigate 1) if cycling efficiency was different in trained and untrained participants; 2) if cycling efficiency was different in old and young participants; 3) if cycling cadence differentially affected efficiency in old and young, trained and untrained participants; 4) if the proportion of type I muscle fibers was different in trained and untrained, old and young participants; 5) if cycling efficiency is influenced by the proportion of type I muscle fibers; and 6) if cycling efficiency is related to endurance performance in trained cyclists. We hypothesized that cycling efficiency would be influenced by the relative proportion of type I muscle fibers in participants' vastus lateralis muscle and cycling cadence, and that both cycling efficiency and the proportion of type I muscle fibers would be higher in trained cyclists. Moreover, we hypothesized that older cyclists would have a higher cycling efficiency and proportion of type I muscle fibers. Finally, we hypothesized that cycling efficiency would be related to cycling performance in trained cyclists.

MATERIALS AND METHODS

Ethical approval. Following ethics approval by the Kent National Health Service Local Research Ethics Committee, according to the standards set by the Declaration of Helsinki, 40 male participants provided written, informed consent to participate in the study. Participants were recruited to one of four groups, depending on their age and training status; trained young cyclists (TY; $n = 10$) or untrained but physically active young men (UY; $n = 10$), age range 18–30 yr; trained older cyclists (TO; $n = 10$), or untrained but physically active older men (UO; $n = 10$), age range 50–74 yr. Young trained cyclists were recruited from local cycling clubs, and all had at least 2-yr history of competitive road or time trial cyclist, whereas old cyclists had a minimum of 10-yr training and racing history. Untrained participants were involved in regular physical activity, but not specific exercise training regimes. All participants were free of any known disease and were not taking any regular medication.

Study design and experimental procedures. All participants visited our laboratory on four occasions, separated by a minimum of 48 h. All exercise was conducted on an electromagnetically braked cycle ergometer (Schoberer Rad Messtechnik, Jülich, Germany). Before exercise testing, the position on the cycle ergometer was adjusted for each participant, and the same settings were reproduced at each subsequent visit. For untrained participants, cycling position was determined as described in Hopker et al. (17), while for trained participants their saddle height, reach, handle bar height, and crank length were replicated from their own bicycles. During all exercise tests, participants were cooled by an electric fan as required.

During the first visit, each participant performed a preliminary incremental exercise test. The test commenced at 100 W for untrained and 150 W for trained participants and increased by 20 W/min until volitional exhaustion (operationally defined as a pedal frequency of <60 revolutions/min for >5 s, despite strong verbal encouragement). For this test, respiratory gas exchange data were measured using a breath-by-breath gas analyzer (Metalyzer 3B, Cortex Biophysik, Leipzig, Germany), via a facemask covering the mouth and nose. The

participants' peak $\dot{V}O_2$ uptake ($\dot{V}O_{2\text{peak}}$) was determined as the highest average $\dot{V}O_2$ recorded over a 60-s period. Maximal minute power (MMP) was determined as the highest average power output recorded over a 60-s period.

During the second visit, all participants completed a series of 6-min submaximal cycling bouts to measure their cycling efficiency. All participants completed bouts at 100, 150, and 200 W, and at 50 and 60% MMP at their preferred cadence, and 60% MMP at 60 and 120 revolutions/min in a randomized order. Fixed cadences of 60 and 120 revolutions/min were used to assess the effect of cadence on cycling efficiency at the same relative exercise intensity. Each bout was followed by a 3-min rest period. The trained participants completed an additional bout at 250 W at their preferred cadence. Expired gases were carefully collected during the final minute of each stage in nondiffusible Mylar Douglas bags (Hans Rudolph) and analyzed (Servomex 5200, Servomex, Crowborough, UK) according to the procedures of Hopker et al. (21). Blood lactate was measured at minutes 3 and 6 (Super GL2, Dr. Müller Gerätebau, Freital) from fingertip capillary blood samples, and heart rate was measured at 1-s intervals throughout using a heart rate monitor (S810i, Polar, Kempele, Finland). After a short rest, participants completed a familiarization of the performance time trial to be conducted at visit 3 (detailed below).

On their third visit, the trained participants completed an endurance performance time trial on the cycle ergometer. During the time trial, the participants were asked to sustain the highest power output possible for 1 h. Standardized verbal encouragement was given to each participant throughout. Feedback regarding time remaining was provided in the final 10 min of the trial. After the time trial, the average power output, cadence, heart rate, and $\dot{V}O_2$ were determined.

On their final visit, participants had a muscle biopsy extracted from their right vastus lateralis under local anesthetic. After administering the local anesthetic, a 1-cm incision was made one-third of the distance between the patella and anterior superior iliac spine. Conchotome forceps were used to extract tissue from participants' muscle while they rested in a supine position (13). The extracted muscle (~250–300 mg) was immediately collected in vials, removing any fatty tissue, and frozen in liquid nitrogen. Subsequently, muscle samples were stored at -80°C .

Muscle biopsy fiber-type analysis. To assess myosin heavy chain (MHC) composition, a small sample of muscle (0.005–0.01 g) was extracted from the muscle samples on a frozen metal plate before being placed into a prepared vial. Fifty microliters of sample buffer per 1 mg of muscle were inserted into the vial, in which small glass beads were then added to aid the homogenizing process. The vials were vigorously beaten in a Precellys 24 bead beater (Bertin Technologies, Aix-en-Provence, France). Samples were then spun down at 13,000 revolutions/min for 1 min to reduce foaming.

A Myosin Isoform SDS-Page stacking gel was created using the method of Mogensen et al. (32). Gels were run at 100 V for 24 h in a box of ice to keep the samples cool. MHC bands were made visible by staining with a SYPRO stain solution, before being covered with tin foil and being placed onto a Luckham 4RT Rocking Table (Luckham, West Sussex, UK) for ≥ 45 min. Following this, gels were washed in 7.5% acetic acid briefly before being scanned with a SLA-5100 fluorescence scanner (FujiFilm, Bedford, UK). The bands were then analyzed using Aida Image Analyzer software version 4.15 (Raytest Isotopenmessgeräte, Straubenhardt, Germany). The percentage of type I and type II muscle fibers was determined via the ratio of the different myosin bands visible on the gel, as described by Mogensen et al. (32).

To unambiguously confirm that the bands visible on our gels corresponded to the correct myosin isoforms, we analyzed protein identity in these bands by mass spectrometry. An additional gel was run using the same protocol as above up until the end of the electrolysis protocol. From this point, the gels were stained with Coomassie and then silver stained using the method of Shevchenko et

Table 1. Participant characteristics

Group	Age, yr	Weight, kg	$\dot{V}O_{2\text{ peak}}$, ml·kg ⁻¹ ·min ⁻¹	MMP, W	HR _{max} , beats/min
UY	22 ± 3	78.4 ± 8.8	46.7 ± 5.92	269 ± 37	192 ± 9
TY	27 ± 4	76.4 ± 8.8	56.6 ± 10.1	352 ± 25	186 ± 8
UO	58 ± 8	86.3 ± 15.0	33.7 ± 5.9	215 ± 23	171 ± 18
TO	58 ± 8	78.7 ± 13.5	47.8 ± 6.4	311 ± 69	165 ± 11

Values are means ± SD. UY, untrained young; TY, trained young; UO, untrained older; TO, trained older; $\dot{V}O_{2\text{ peak}}$, maximum O₂ uptake; MMP, maximal minute power; HR_{max}, maximum heart rate.

al. (44). The bands were then extracted from the gel before undergoing the mass spectroscopy method of Perkins et al. (38) to confirm the presence of MHC type I and II in the respective bands.

Statistical analysis. Before the biopsy visit, one participant from the TY group withdrew from the study, and his data have not been included. Between-group differences in cycling efficiency at the absolute work rates and muscle fiber-type distribution were tested for statistical significance using univariate ANOVA.

Cycling efficiency was calculated as the ratio of work done to energy expended in the final minute of the exercise bout. Work done was calculated from the power output and energy expenditure from $\dot{V}O_2$ multiplied by the caloric equivalent for the measured respiratory exchange ratio (RER) using the data of Peronnet and Massicotte (39). This index was tested against the underlying assumptions of ratios (1), including the slope of the log power output-log energy expenditure relationship being equal to 1. This assumption was found not to be upheld (95% confidence interval: 0.50–0.79), indicating that gross efficiency (GE) varied as a function of absolute power output. Accordingly, as recommended by Allison et al. (1) before analysis, we rescaled our cycling efficiency values with a log-linked allometric model, using the log of energy expenditure as a covariate in the model. Between-group differences were assessed using a generalized linear model with energy expenditure included as covariate (3). The Wald χ^2 statistic (Wald_i) was derived from this analysis. We also analyzed the “raw” data without using the rescaling method outlined above using univariate ANOVA and obtained the same statistical results. Therefore, for the purposes of this paper, only the rescaled data and results are presented.

Due to the known effect of cadence on cycling efficiency (14), cadence was included as a covariate in the analysis of trials where participants used their preferred pedaling rate.

Pearson's product moment correlation coefficient was used to assess relations between muscle fiber type and cycling efficiency at different work rates, and between cycling efficiency and performance trial power output in the trained groups. Where data at relative exercise intensities was included in the correlation analysis, covariate corrected data (adjusted for energy expenditure as outlined above) were used.

For the assessment of performance power output, an independent *t*-test was used to ascertain if there were differences between the two trained groups that completed the 1-h trials. The covariate-controlled analysis was then used again with work rate as the covariate to assess

differences in the other responses during the 1-h performance trial. The determinants of 1-h time-trial performance were examined using stepwise multiple linear regression. Multicollinearity diagnostics were examined for strong interrelationships between the predictors in the model. Variables considered for inclusion in the regression were $\dot{V}O_{2\text{ peak}}$, MMP, muscle fiber type, cycling efficiency, and age as an independent variable in the analysis. The criteria of $P < 0.05$ for inclusion and $P > 0.1$ for removal was used. Data are presented as means ± SD, unless stated otherwise.

RESULTS

Maximal variables. Analysis of variance of the MMP data collected during the maximal test revealed a significant main effect of training status (see Table 1; $P < 0.01$), and of age ($P < 0.01$), but no significant interaction ($P = 0.66$). Differences between the groups were also evident for $\dot{V}O_{2\text{ peak}}$, with significant main effects for training status (see Table 1; $P < 0.01$) and age ($P = 0.01$). Again there was no interaction effect ($P = 0.32$). Maximum heart rate demonstrated a significant main effect for age (see Table 1: younger age group = 22 ± 17 beats/min, $P < 0.01$), but not training status ($P = 0.14$).

Training status, age, and cycling efficiency. Mean values for cycling efficiency in each of the groups are shown in Table 2. At a work rate of 100 W, cycling efficiency was not significantly different between groups. There was a significant interaction between training status and age for cycling efficiency at 150 W [$F_{(1,33)} = 4.39$, $P = 0.046$]. The untrained participants did not meet the criteria for achieving a valid efficiency measure at 200 W (i.e., RER < 1.0) and so were excluded from this analysis. Consequently, only trained participants were considered at this work rate. Using an independent samples *t*-test, TY cyclists possessed a significantly higher cycling efficiency than TO cyclists (+1.4%; $t = -3.66$, $P < 0.01$).

Regardless of the group, cycling efficiency was significantly affected by exercise intensity, being 0.9 ± 1.2% higher at 60% MMP vs. 50% MMP ($P < 0.01$). At the relative work rates of 50% and 60% MMP, no interaction was evident for GE, but there was a significant effect of training status (50% MMP: Wald_i = 38.98, $P < 0.01$; 60% MMP: Wald_i = 14.10, $P < 0.01$) and age (50% MMP: Wald_i = 31.61, $P < 0.01$; 60% MMP: Wald_i = 4.56, $P = 0.03$). See Table 2. At 60% MMP, 60 revolutions/min, a significant main effect for training status was found (Wald_i = 29.83, $P < 0.01$), but not for age or an interaction. At 60% MMP, 120 revolutions/min, some untrained participants (5 UO and 5 UY) were excluded from the analysis due to their RER value being >1.0. During this trial, a significant main effect was evident for training status (Wald_i = 10.46, $P < 0.01$), but not for age (Wald_i = 0.47, $P = 0.49$); there was also no statistically significant interaction (Wald_i = 3.13, $P < 0.08$). See Table 2.

Table 2. Cycling efficiency values for the different groups calculated from submaximal steady-state work bouts

Group	100 W	150 W	200 W	50% MMP	60% MMP	60% MMP, 60 rev/min	60% MMP, 120 rev/min
UY	16.1 ± 2.1	17.9 ± 1.3		17.3 ± 1.2	17.6 ± 1.3	18.9 ± 1.2	13.8 ± 1.4
TY	17.5 ± 1.8	19.9 ± 0.9	21.1 ± 0.7	20.8 ± 1.2	21.3 ± 1.3	21.6 ± 1.2	17.5 ± 1.3
UO	16.8 ± 1.8	18.8 ± 2.4		15.9 ± 1.3	17.0 ± 1.5	17.9 ± 1.2	14.6 ± 1.7
TO	17.8 ± 3.4	18.2 ± 1.0	19.3 ± 0.7	18.1 ± 1.2	19.4 ± 1.3	20.9 ± 1.1	15.5 ± 1.2

Values are means ± SD in %; $n = 10$ (TO, UO, UY) and $n = 9$ (TY). UO and UY groups were excluded from the 200-W trial, as the majority of participants' data showed respiratory exchange ratio values >1.0.

Table 3. Mean oxygen cost and ventilation values for participant groups at work rates of 100 and 150 W

Group	$\dot{V}O_2$ 100 W	$\dot{V}O_2$ 150 W	$\dot{V}E$ 100 W	$\dot{V}E$ 150 W
UY	1.78 ± 0.24	2.35 ± 0.20	43.7 ± 8.2	56.0 ± 7.6
TY	1.59 ± 0.19	2.08 ± 0.18	35.7 ± 4.2	44.6 ± 6.2
UO	1.72 ± 0.25	2.28 ± 0.32	52.1 ± 4.8	72.4 ± 15.0
TO	1.59 ± 0.27	2.26 ± 0.19	40.1 ± 7.1	54.0 ± 8.6

Values are means ± SD in l/min. $\dot{V}O_2$, O₂ uptake; $\dot{V}E$, minute ventilation.

At fixed work rates, there were significant differences in minute ventilation ($\dot{V}E$)/ $\dot{V}O_2$ for both training status and age; however, there was no significant interaction ($P > 0.05$). Table 3 shows submaximal $\dot{V}O_2$ and $\dot{V}E$ data at the work rates of 100 W and 150 W. At 100 W, the trained participants ventilated 3.6 ± 9 liters less per 1,000 ml of oxygen consumed compared with the untrained group ($F = 5.59$, $P = 0.02$). At 150 W, the same comparison yielded a reduction of 5.2 ± 9 liters less per 1,000 ml of oxygen consumed for the trained participants compared with the untrained participants ($F = 14.18$, $P < 0.01$). This equated to lower $\dot{V}E$ of ~10 and ~15 liters at 100 W and 150 W for the trained participants compared with the untrained participants ($P < 0.05$ in both cases). At 100 W, the young cyclists ventilated 4.2 ± 8 liters less per 1,000 ml of oxygen consumed compared with the older group ($F = 7.64$, $P = 0.01$), and 5.2 ± 8 liters less per 1,000 ml of oxygen consumed at 150 W ($F = 14.46$, $P < 0.01$). This equated to a lower $\dot{V}E$ of ~6.5 and ~13 liters at 100 W and 150 W for the young participants compared with the older group ($P < 0.05$ in both cases). The relationship between $\dot{V}E$ and GE was statistically significant at 100 W ($r = 0.35$, $P = 0.048$) and at 150 W ($r = 0.42$, $P = 0.02$) with $\dot{V}E$ explaining between ~12 and ~18% of the variance in GE.

Training status, age, and percentage muscle fiber-type distribution. The proportion of type I muscle fibers in the vastus lateralis muscle was significantly higher in the trained groups ($P < 0.01$; Fig. 1). There was no significant effect of age on muscle fiber-type distribution.

Relations between age, cycling efficiency, endurance performance time trial, and percentage muscle fiber-type distribution. Cycling performance was only assessed in the trained group due to difficulties in ensuring an appropriate pacing strategy for the untrained group. One-hour endurance performance power output was not significantly different between the older and

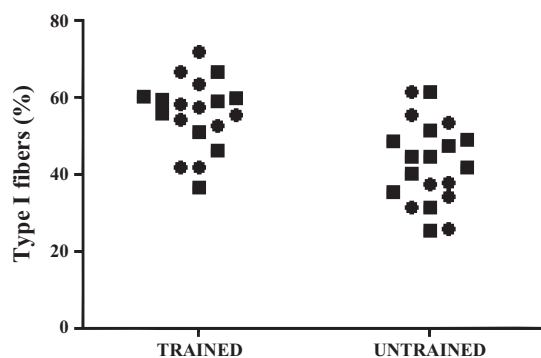


Fig. 1. Mean proportion of type I muscle fiber distribution (●, young group; ■, old group). Differences exist between trained ($n = 19$) and untrained groups ($n = 20$) ($P < 0.01$).

young groups (TY = 239 ± 34 vs. TO = 209 ± 52 W, $P = 0.15$). Endurance performance correlated with cycling efficiency at 60% MMP at 120 revolutions/min, regardless of age ($r = 0.57$, $P < 0.01$, Fig. 2A). Moreover, cycling efficiency during the endurance performance time trial (mean relative exercise intensity = 69.5% MMP) was positively correlated to cycling efficiency at 60% MMP at 120 revolutions/min ($r = 0.65$, $P < 0.01$, Fig. 2B). Mean cycling efficiency during the endurance performance trial was significantly higher compared with the 60% MMP at 120 revolutions/min trial (19.6 ± 1.2 vs. 16.6 ± 1.5%, $P < 0.01$). When accounting for mean endurance performance power output as a covariate, TO cyclists had a significantly lower efficiency than TY during the time trial (18.7 ± 0.9 vs. 20.2 ± 1.3% for TO and TY; $P < 0.01$). The work rate corrected data indicated that $\dot{V}O_2$ (3.31 ± 0.18 vs. 3.11 ± 0.18; $P < 0.05$) and not RER (0.929 ± 0.05 vs. 0.927 ± 0.05; $P = 0.94$) accounted for the differences in endurance performance efficiency for TO and TY, respectively.

The percentage of type I muscle fibers was not significantly related to cycling efficiency at any work rate or cadence

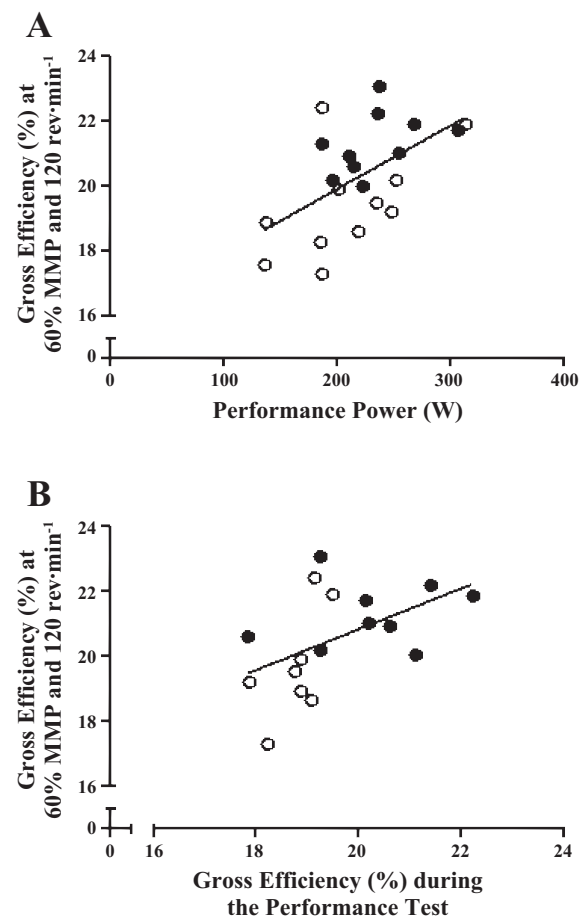


Fig. 2. A: correlation between cycling efficiency at 60% maximal minute power (MMP) at 120 revolutions/min and mean performance power output during a 1-h performance time trials (●, trained young, $n = 10$; ○, trained old, $n = 10$). B: correlation between cycling efficiency at 60% MMP at 120 revolutions/min and cycling efficiency calculated from the 1-h performance time trial. Mean power output from all participants = 69.5% MMP. ●, Trained young, $n = 9$; ○, trained old, $n = 8$. All participants included in the analysis had a respiratory exchange ratio <1.0 throughout the time trial.

combination. Muscle fiber type was not significantly related to cycling performance ($P > 0.05$), or the prediction of cycling efficiency during the performance test. In exploring the performance data set, stepwise multiple regression indicated that muscle fiber type did not significantly predict any performance-related marker in the conducted analysis ($P > 0.05$). The performance power output was predicted by the amount of oxygen consumed and the conversion into work (performance $\dot{V}O_2$ and GE) ($r = 0.998$) with standardized β -coefficients of 0.94 and 0.34, respectively. Based on the mean data collected in this study, this regression analysis indicates that an improvement in cycling efficiency of 1% with no changes in $\dot{V}O_2$ would result in a performance power gain of ~ 12 W. In terms of other parameters assessed and associated with performance independently, only age significantly added to the prediction for parameters in the model where MMP was included (standardized β -coefficients of 1.21 for MMP and 0.45 for age).

DISCUSSION

This study demonstrates that differences in cycling efficiency are evident between trained and untrained individuals, regardless of age. Furthermore, differences in cycling efficiency are also evident between old and young participants, regardless of training status. Contrary to our hypotheses, the findings of the present study demonstrate that, although the percentage of type I muscle fibers in the vastus lateralis muscle was significantly different between trained and untrained individuals, it was not related to cycling efficiency and could not account for differences in efficiency between the two groups. Furthermore, the aging process did not influence muscle fiber-type distribution. Finally, we found cycling efficiency was significantly related to cycling endurance performance.

Influence of training status and age on cycling efficiency. Changes in running economy with training and advancing age are well reported in the literature (see Ref. 47 for review). Considerably less is known about changes in cycling efficiency, but the key messages now appear to be similar. In agreement with our previous studies (17, 18, 19), the data from the present study demonstrate that cycling efficiency is higher in trained cyclists, and that this influence is independent of age. This finding is in contrast to some previous research where a lack of statistical power from insufficient participant numbers, less reliable methods of measurement, and use of relative work rates may confound the findings (29, 32, 34, 35). In the present study, Douglas bags were used to measure energy expenditure, and data were rescaled as a function of the absolute power output. Thus direct comparisons were possible between trained and untrained individuals cycling at the same relative, but different absolute, power outputs. Where absolute work rates have previously been used to investigate differences in cycling efficiency between trained and untrained participants, power outputs have often also been very low for trained cyclists (29, 32, 35). Even though cross-sectional in nature, the results of this study are supportive of previous findings that endurance training increases cycling efficiency using longitudinal study designs over short-term (19), single (18), or multiple (42) cycling seasons.

In comparison to trained young individuals, considerably less research has focused on the cycling efficiency of older individuals, either trained or untrained. In contrast to previous studies that have suggested that cycling economy and effi-

ciency might be higher in older age (26, 27, 51, 52), our results demonstrate that cycling efficiency is lower. This finding appears regardless of training status and at the same relative work rates (50 and 60% MMP; see Table 2). Moreover, our data also show that, in the trained groups, younger cyclists have a higher cycling efficiency at both absolute and relative work rates.

As cycling cadence has previously been shown to affect cycling efficiency (14), we sought to investigate whether, at the same relative exercise intensity, the cadence-efficiency relationship was affected by aging and training status by testing participants at 60 and 120 revolutions/min. Our data demonstrate that, at both cadences, trained cyclists had a higher cycling efficiency than untrained individuals. However, interestingly, age was not shown to be an influencing factor in the cadence-efficiency relationship. These findings are largely in agreement with the only other published study investigating the effect of age on cycling efficiency (41). Sacchetti et al. (41) showed that a young trained cyclist group (24 ± 5.3 yr) had a significantly higher efficiency than their older counterparts (65.6 ± 2.8 yr) across a range of cadences (40–120 revolutions/min). Subsequently, in the current study cycling efficiency was found to be higher in younger participants with preferred cycling cadence used as a covariate in the analysis. However, when cycling at the same fixed cadence (60 or 120 revolutions/min), the influence of age disappears, and training status appears to account for differences between the groups. However, in the present study, five UO and five UY participant data sets were excluded from the analysis due to their RER being >1.0 , and so this might have influenced our ability to discern significant differences between the groups. Additionally, Sacchetti et al. only used relative work rates and did not appear to take account of possible scaling inaccuracies within their data (3). Therefore, it is difficult to determine whether their findings were simply a result of the higher absolute power outputs sustained by the younger cyclists.

It is possible that, due to the length of the cycling efficiency trials in the present study (63 min for untrained groups, 72 min for trained groups), there might have been an upward drift of $\dot{V}O_2$ over time that differentially affected the groups. However, we attempted to mitigate the effect of the $\dot{V}O_2$ slow component by randomizing the order of the power outputs within the efficiency trials and allowing a 3-min recovery period between work bouts.

Interestingly, regardless of which group participants were in, the oxygen cost of breathing was seen to only account for a small fraction of the variance in GE (12 and 18% at 100 and 150 W, respectively). In support of previous research, the present study demonstrates that the oxygen cost of breathing is higher in older individuals (7). To calculate the impact of the work of breathing on the differences in efficiency we have demonstrated between group, we consulted the work of Vella et al. (50), who report the oxygen cost of ventilation to be between 2.14 and 2.74 ml/l at relative ventilation rates of 35–50% of maximal ventilation. Consequently, if it was assumed that all participants in the present study were cycling at a fixed work rate of 150 W, had an identical RER, and the measured $\dot{V}O_2$ responses were adjusted for the elevated ventilation recorded, these adjustments would account for ~ 0.2 – 0.3% of GE units. In this example, the alterations to the $\dot{V}O_2$ would reduce the difference in GE between the older and

younger group to 0.1%, and 0.9% between trained and untrained participants. Therefore, the additional oxygen cost of ventilation with age has the potential to account for a considerable amount of the observed differences in cycling efficiency between old and young groups in this study.

Muscle fiber-type distribution, aging, and cycling efficiency. Muscle fiber type has been suggested to play a key role in determining both cycling efficiency and cycling performance (9, 22). Moreover, it has previously been suggested that the physiological adaptation responsible for improvements in cycling efficiency with training could be a shift in muscle fiber-type distribution toward the more efficient type I muscle isoform (12). However, the present study found no relationship between the percentage of type I muscle fibers and cycling efficiency. Thus the findings of the present study contradict the work and longstanding view of Coyle et al. (9) and Horowitz et al. (22), who reported a strong correlation between cycling efficiency and the percentage of type I muscle fibers ($r \sim 0.75$; $P < 0.001$). While the mean percentage of type I fibers and cycling efficiency values between the trained individuals in the present study and that of Coyle et al. (9) are similar (%type I: 55 vs. 56%; GE: 19.8 vs. 20.6%, for the present study vs. Coyle et al.), conclusions drawn from the two studies are very different. On closer inspection of the work of Coyle et al., the equation relating cycling efficiency and muscle fiber type suggests that the maximal cycling efficiency that could be achieved (on the basis of the vastus lateralis muscle possessing 100% slow-twitch fibers) is 23.7%. In contrast, in the present study, we have one cyclist with an efficiency of 23.7%, but only a 60% type I muscle fiber composition. Furthermore, using the equation of Coyle et al. (9), data on a multiple Grand Tour winning cyclist (12) suggest the percentage of type I muscle fibers increased from 62.4% to an improbable 90.3% to correspond to the increase in cycling efficiency reported. In contrast, even though we established a significant difference in muscle fiber type based on training status, we did not find an interaction effect between fiber type, age, and training status. This suggests that age does not appear to influence muscle fiber type, whether an untrained or a trained individual is considered. This finding is consistent with the previous work of Coggan et al. (8) and Trappe et al. (48), who, in cross-sectional and longitudinal studies, found similar muscle fiber distributions in younger and older athletes. In the present study, there is no difference between our two trained groups, even though the shortest training period in the TO group was at least 10 yr compared with 2 yr in the TY group. Therefore, it seems likely that an endurance training stimulus has minimal effect on muscle fiber-type distribution. Our findings also suggest that cycling efficiency is determined by factors other than the percentage of type I fibers. The precise mechanisms for this remain to be determined, but appear to be affected by training status. Thus, in the present study, even though the TO cyclists have a lower cycling efficiency than the TY, they still exhibit a higher cycling efficiency than either untrained group at 50 and 60% MMP.

Determinants of endurance exercise performance. Using Coyle's endurance performance model (10, 11, 25) as a framework, we sought to assess which of the physiological variables of $\dot{V}O_{2\text{ peak}}$, MMP, cycling efficiency, or muscle fiber type contribute most to endurance cycling performance with specific reference to the performance model presented by Joyner and Coyle (25). The mean relative exercise intensity sustained during the endurance performance trial was 69% MMP. Mea-

sured cycling efficiency during the endurance performance trial was significantly lower than, but correlated with, steady-state cycling efficiency measured at 60% MMP at 120 revolutions/min ($r = 0.65$, $P < 0.01$). It is important to note that the correlation was only observed at the high cadence of 120 revolutions/min and was not seen when considering cycling efficiency at preferred cadence. Horowitz et al. (22) identified a significant difference between two groups for both cycling efficiency and percentage of type I muscle fibers. Moreover, Horowitz et al. also reported that the group with the greater efficiency maintained a 10% higher average power output during their endurance performance trial for the same $\dot{V}O_2$. In the present study, no difference in muscle fiber-type distribution between the groups ($P > 0.05$), or the prediction of cycling efficiency during the endurance performance test was found, contradicting the endurance performance model of Joyner and Coyle (25).

Joyner and Coyle (25) suggest a link between fiber type, cycling efficiency, and endurance performance power output. In the present study, a stepwise multiple linear regression found that muscle fiber type did not predict cycling efficiency, or endurance performance ($P > 0.05$). But performance power output was predicted by the amount of oxygen consumed and the conversion into work (endurance performance $\dot{V}O_2$ and cycling efficiency) as outlined by the model of Joyner and Coyle (25) ($r = 0.998$), with standardized β -coefficients of 0.94 and 0.34, respectively. Caution needs to be exercised in the interpretation of this data though, as mathematical coupling is evident. Differences in cycling efficiency between the groups of trained participants (18.7 ± 0.9 vs. $20.2 \pm 1.3\%$ for TO and TY) suggest that, for the same performance power output, the TO group would need to consume $\sim 6.5\%$ more oxygen to match the TY participants in this study.

Conclusion. Differences in cycling efficiency with age are apparent, but the reasons for this are unknown. Fiber-type distribution is not related to cycling efficiency and does not appear to be markedly influenced by age or training status. Older trained individuals appear to have smaller age-related declines in both maximal and submaximal exercise responses. Specifically, compared with reductions seen in untrained individuals, the trained cyclists in this study were able to somewhat preserve their $\dot{V}O_{2\text{ peak}}$, maximal minute power output, and cycling efficiency. The present study adds further support to the notion of the importance of incorporating endurance exercise into a physically active lifestyle during later life to maintain the capacity of numerous physiological systems.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: J.G.H., D.A.C., S.A.J., and L.P. conception and design of research; J.G.H., D.A.C., H.C.G., and T.V.d.H. performed experiments; J.G.H., D.A.C., H.C.G., and T.V.d.H. analyzed data; J.G.H., D.A.C., T.V.d.H., and J.W. interpreted results of experiments; J.G.H. and D.A.C. prepared figures; J.G.H. drafted manuscript; J.G.H., D.A.C., H.C.G., S.A.J., T.V.d.H., J.W., and L.P. edited and revised manuscript; J.G.H., D.A.C., H.C.G., S.A.J., T.V.d.H., J.W., and L.P. approved final version of manuscript.

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