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ORIGINAL ARTICLE

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Neuromuscular factors determining 5 km running performance and running economy in well-trained athletes

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Abstract This study investigated the effects of the neuromuscular and force–velocity characteristics in distance running performance and running economy. Eighteen well-trained male distance runners performed five different tests: 20 m maximal sprint, running economy at the velocity of 4.28 m s^{-1}, 5 km time trial, maximal anaerobic running test (MART), and a treadmill test to determine VO_{2max}. The AEMG ratio was calculated by the sum average EMG (AEMG) of the five lower extremity muscles during the 5 km divided by the sum AEMG of the same muscles during the maximal 20 m sprinting. The runners' capacity to produce power above VO_{2max} (MART VO_{2gain}) was calculated by subtracting VO_{2max} from the oxygen demand of the maximal velocity in the MART (V_{MART}). Velocity of 5 km (V_{5K}) correlated with V_{MART} ($r = 0.77$, $p < 0.001$) and VO_{2max} ($r = 0.49$, $p < 0.05$). Multiple linear regression analysis showed that MART VO_{2gain} and VO_{2max} explained 73% of the variation in V_{5K}. A significant relationship also existed between running economy and MART VO_{2gain} ($r = 0.73$, $p < 0.01$). A significant correlation existed between V_{5K} and AEMG ratio during the ground contact phase at the 3 km ($r = 0.60$, $p < 0.05$) suggesting that neural input may affect distance running performance. The results of the present study support the idea that distance running performance and running economy are related to neuromuscular capacity to produce force and that the V_{MART} can be used as a determinant of distance-running performance.

Keywords Distance running performance · EMG · Ground contact time · Running economy · Stride length

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Introduction

Since the classical studies of Hill and Lupton (1923), exercise physiologists have associated the limits of human endurance performance with the ability to transport and consume oxygen during exhaustive exercise. It has been suggested that hypoxia developed in the active muscles during exercise causes fatigue and thereby limits maximal exercise performance. According to many previous studies (e.g. Costill et al. 1973; Davies and Thompson 1979; Foster et al. 1978; Joyner 1991), maximal oxygen uptake (VO_{2max}) sets the upper limit for the endurance performance. In those studies in which the subjects had similar VO_{2max} values, sub-maximal endurance (e.g. Costill et al. 1973; Farrell et al. 1978) and running economy (e.g. Conley and Krahenbuhl 1980; Morgan et al. 1989) have been shown to be related to endurance performance. Di Prampero (1986, 2003) and Bassett and Howley (1997, 2000) summarized that VO_{2max}, fractional utilization of VO_{2max}, and running economy are the major variables determining the velocity that can be maintained in distance races.

Although success in endurance sports requires high VO_{2max}, it cannot fully explain all the measured differences in endurance performance. Simultaneous strength and endurance training has been shown to improve muscle strength, running economy, and distance running performance without any changes in VO_{2max} (Johnston et al. 1997; Paavolainen et al. 1999a) suggesting that neuromuscular factors may also be important determinants of endurance running performance. This is supported by the study of Paavolainen et al. (1999c) indicating that better performance in the 10 km time trial is related to higher pre-activation of the working muscles accompanied with shorter contact times (CT) throughout the run. They presented a hypothetical model of the variables related to distance running performance. In the new model, the traditional model of endurance performance (Di Prampero 1986; Bassett and Howley 1997) was supplemented with the inclusion of factors relating to the neuromuscular capacity to produce power. Paavolainen et al. (1999a) also observed a significant relationship between the improvements in force and velocity tests, maximal anaerobic running test (MART, Rusko et al. 1993), and running economy suggesting that that the maximal velocity of the MART (V_{MART}) can be used as an indicator of neuromuscular power in endurance athletes. The V_{MART} positively correlates with the times for running distances from 400 to 5,000 m and with cross-country skiing performance (Paavolainen et al. 1999a; Rusko and Nummela 1996; Rusko et al. 1993).

An alternative explanation for the limitation of endurance performance postulates that a central nervous system integrates input from various sources during physical activity and prevents the recruitment of skeletal muscles beyond levels of intensity and duration where potential damage could occur to the heart and other vital organs (Kayser 2003; Lambert et al. 2005; Noakes 2000; Noakes et al. 2001). In accordance with this explanation, the changes in the number of skeletal muscle motor units recruited during exercise provide a more complete explanation for the impaired performance that develops during exercise and for differences in athletic performance (Noakes and St Clair Gibson 2004; St Clair Gibson and Noakes 2004).

The purpose of the present study is to investigate the importance of force and velocity characteristics determining distance running performance. A more precise aim of the study is to investigate whether the maximal velocity of the MART (V_{MART}), EMG, and stride characteristics during the 5 km are related to running economy and distance running performance.

Materials and methods

Subjects

Eighteen well-trained male distance runners participated in this study. Subjects were included if they were able to complete 10 km in under 38 min. Each subject signed an informed consent form at the beginning of the study. The study was approved by both the Ethics Committee of the University of Jyväskylä, Jyväskylä, Finland and the Ethics and Research Committee of the Faculty of Health Sciences, University of Cape Town, South Africa.

Experimental design

The runners were required to visit the laboratory on three separate occasions over a 10-day period. On their first visit to the laboratory, the runners were given the opportunity to become familiar with the equipment and testing protocols that would be used during the trial. This familiarization was performed in an attempt to reduce error associated with subjects performing unaccustomed exercise. A personal training and racing history was also obtained from each runner. The runners were asked to maintain their regular physical activity pattern for the duration of the study and were requested not to exercise on the morning prior to their testing.

In order to measure maximal sprinting speed, running economy, distance running performance, V_{MART} and VO_{2max}, the runners ran four different running tests on a 144 m indoor track and a running test on a treadmill. The running tests were: 20 m maximal sprint with a running start of 15 m; eight laps on the track at the velocity of 4.28 m s^{-1}; 5 km time trial on the indoor track; MART on the track; and continuous and incremental exhaustive running test on the treadmill.

Day 1

Anthropometry

When the runners came to the laboratory for the second time, mass, stature, and an anthropometric assessment was conducted on each subject. Body fat content was calculated using the equation of Durnin and Womersley (1974).

Electromyographic activity measurements

Before the start of testing, each runner had bipolar EMG electrodes (Beckman miniature skin electrodes, IL, USA) placed onto the vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF), biceps femoris (BF), and gastrocnemius (GA) muscles of the right leg. The skin was shaved, rubbed with sandpaper, and cleaned with alcohol. The electrodes were positioned longitudinally on the belly of each muscle and carefully taped. All EMG data were recorded telemetrically (Biomes 2000, Glonner, Germany) during each running test on the track with a laptop computer using Labview 5.1 (National Instruments, TX, USA).

Measurements of stride parameters

In order to measure stride parameters, a photocell contact mat (Viitasalo et al. 1997) and two photocell gates connected to an electronic timer (Newtest Ltd, Oulu, Finland) were placed on the final straight of the track. During the 5 km time trial, average velocity, ground CT, and flight times (FT) were measured from a 20 m section at every other lap simultaneously with EMG from VL, VM, RF, BF, and GA. Stride frequency (strides per second) was calculated by using CT and FT as $(\mathrm{CT} + \mathrm{FT})^{-1}$. Stride length was calculated by dividing the average velocity by the stride frequency. Both EMG and stride parameter data collected during each stride were averaged for the number of strides taken along the 20 m straight during each running test. The non-smoothed EMG signals were rectified, integrated, and time normalised (Average EMG, AEMG) for the two phases of running: pre-activation (100 ms before ground contact) and total ground contact time.

Maximal 20 m sprint test

The runners performed three to five maximal 20 m sprints on the indoor track. They were able to accelerate 15 m to ensure a normal and maximal running gait throughout the 20 m. Each 20 m sprint was separated by a brief recovery period during which the runners returned to the start of the sprint course. The 20 m running time was measured using two photocell gates connected to an electronic timer (Newtest Ltd). The fastest 20 m sprint was chosen for all subsequent data analysis.

Running economy test

Before the running economy test, the runners put on the portable telemetric oxygen analyser (Cosmed K4 RQ, Rome, Italy) and the analyser was calibrated. Running economy was measured as steady-state sub-maximal oxygen uptake during eight laps (1,150 m) of sub-maximal running at the velocity of 4.28 m s^{-1}. The running velocity was regulated by small lights embedded on the inside of the track at intervals of 2.5 m. The runners were instructed to adjust their velocity to coincide with the lights which were turned on and off sequentially around the track. VO_2 was measured for every 15 s during the whole run using the Cosmed K4, and running economy was calculated as the average VO_2 (ml $kg^{-0.75}$ min^{-1}) and (ml kg^{-1} min^{-1}) of the last minute of running.

Five-km time trial

After 20 min recovery, the runners performed the 5 km time trial on the indoor track. They were instructed to run at their maximum effort and were provided verbal encouragement during the entire time trial. Times were recorded for each lap and the split times at each kilometre were given to the athletes during the time trial. The runners were asked to run the final lap as fast as possible. The signals from the EMG, photocell gates, and photocell contact mat were recorded from the 7th (948–968 m), 21st (2,964–2,984 m), 33rd (4,692–4,712 m), and last (4,980–5,000 m) lap when the runners entered the appropriate 20 m section of track. The AEMG values were calculated for all the muscles during the ground contact and 100 ms pre-activity phase. The AEMG ratios were calculated at 1 km (seventh lap), 3 km (21st lap), and 5 km (33rd and last lap) by dividing the AEMG during the 5 km time trial by the AEMG representing the best 20 m sprint.

Day 2

Incremental exhaustive treadmill test

On the next visit to the laboratory, not more than 7 days later, peak treadmill running speed (PTRS) and VO_{2max} were measured using a continuous, incremental running protocol on a horizontal, motor driven treadmill. After a brief warm up, the runners began running at 12 km h^{-1} (3.33 m s^{-1}). The speed was increased by 0.5 km h^{-1} (0.14 m s^{-1}) every 30 s thereafter (Scrimgeour et al. 1986). Oxygen consumption (Cosmed K4 RQ) and heart rate (Vantage XL Polar Electro, Finland) were measured continuously during the test. The test continued until the runner was unable to maintain the pace of the treadmill. VO_{2max} was defined as the highest oxygen consumption during the test over a 60 s period.

Maximal anaerobic running test

In the present study, the MART was done on the indoor track. The MART consisted of 10×150 m runs with a 100 s recovery period between the runs. A 5 m running start was allowed for the runners. The velocity of the first run was 4.75 m s^{-1}, and thereafter the velocity was increased by 0.41 m s^{-1} for each consecutive run. The last 150-metre run was performed at the runners' maximal effort. Each runner was guided during the first nine 150-metre runs to the desired running velocity by the pacing lights. The maximal velocity of the MART (V_{MART}) was determined as the average velocity of the fastest 150-metre run. Oxygen demand of the V_{MART} was calculated using the formula of Londeree (1986): MART $VO_{2demand}$ (ml kg^{-1} min^{-1}) = 0.205×v (m min^{-1}) + 0.109× [v (m min^{-1})/60]^2-6.1. Then the capability of the runner to produce power above VO_{2max} was calculated by: MART VO_{2gain} (ml kg^{-1} min^{-1}) = MART $VO_{2demand}$(ml kg^{-1} min^{-1})-VO_{2max} (ml kg^{-1} min^{-1}).

Data analysis

The energetic model of distance running performance was tested by calculating the 5 km running speed by the formula of Di Prampero (1986): $V_{5K} = F \times VO_{2max} \times C^{-1}$, where $F = 0.977$ for 5 km, as reported by Lacour et al. (1990), and C = [VO_2 at 4.28 m s^{-1}–3.5 (ml kg^{-1} min^{-1})] [256.8 (m min^{-1})$^{-1}$]. Pearson's product moment correlation coefficient was used to determine relationships between V_{5K}, running economy, VO_{2max}, V_{MART}, MART VO_{2gain}, and other neuromuscular variables. A stepwise multiple linear regression analysis was used to predict 5 km running speed. The independent variables were entered into the stepwise procedure to select the variables that best predicted the V_{5K}. ANOVA was used when relative EMG, running velocity, and stride characteristics were compared during the 5 km time trial. All the statistical analyses were done using SPSSWIN 13.0 (SPSS Inc., Chicago, IL, USA). Values are expressed as mean ± standard deviation or standard error. Statistical significance was accepted as $p < 0.05$.

Results

The descriptive data of the runners are shown in Table 1. The oxygen demand of the V_{MART} was 40% higher than the VO_{2max} resulting in the MART VO_{2gain} of 25.9 ± 5.6 ml kg^{-1} min^{-1}. The velocity during the 5 km time trial had a positive relationship with stride length ($r = 0.76$, $p < 0.01$) but not with stride frequency. The V_{5K} also correlated significantly with V_{MART} ($r = 0.77$, $p < 0.001$), VO_{2max} ($r = 0.55$, $p < 0.05$), and PTRS ($r = 0.61$, $p < 0.05$) but not with maximal 20 m velocity ($r = 0.42$). The V_{5K} correlated significantly with running economy only when VO_2 was expressed in ml kg$^{-0.75}$ min^{-1} ($r = -0.47$, $p < 0.05$) but not when it was expressed in ml kg^{-1} min^{-1} ($r = -0.28$). Running economy at 4.28 m s^{-1} (ml kg$^{-0.75}$ min^{-1}) correlated significantly with V_{MART} ($r = 0.52$, $p < 0.05$) and MART VO_{2gain} ($r = 0.72$, $p < 0.01$). Furthermore, a significant correlation was observed between MART VO_{2gain} and maximal 20 m velocity ($r = 0.88$, $p < 0.001$) and between V_{MART} and the velocity of the last lap in the 5 km time trial ($r = 0.54$, $p < 0.05$).

The energetic model of distance running performance was tested by calculating the V_{5K} by the formula of Di Prampero (1986), which included VO_{2max} and running economy per kg body mass, with the assumption that VO_{2rest} was 3.5 ml kg^{-1} min^{-1} and fractional utilization of VO_{2max} during the 5 km was 0.977 as reported by Lacour et al. (1990). The Pearson correlation coefficient between the calculated (4.96 ± 0.38 m s^{-1}) and measured V_{5K} (4.93 ± 0.33 m s^{-1}) was $r = 0.75$ ($p < 0.01$), and the plotted data are shown in Fig. 1.

Table 1 Descriptive and performance characteristics of the runners ($n = 18$)

Variable	Mean ± SD	Min–Max
Age (years)	23.4 ± 6.6	16–34
Stature (m)	1.69 ± 0.05	1.61–1.80
Body mass (kg)	59.6 ± 4.7	50.3–67.1
Body fat (%)	10.7 ± 3.0	6.6–17.7
Training (km week^{-1})	95 ± 27	70–160[a]
V_{5K} (m s^{-1})	4.93 ± 0.33	4.30–5.30
PTRS (m s^{-1})	5.76 ± 0.33	5.28–6.53
V_{MART} (m s^{-1})	7.33 ± 0.40[a]	6.72–8.07
V_{20m} (m s^{-1})	7.72 ± 0.40[b]	7.00–8.65
MART $VO_{2demand}$ (ml kg^{-1} min^{-1})	90.0 ± 5.5[a]	81.5–100.3
VO_{2max} (ml kg^{-1} min^{-1})	64.0 ± 4.0	56.3–70.7
RE (ml kg^{-1} min^{-1})	54.3 ± 3.2[a]	49.1–60.6

Training average training volume from the last three months, VO_{2max} maximal oxygen uptake in an incremental treadmill test, *PTRS* peak treadmill running speed, V_{MART} the highest 150 m velocity in the MART, V_{5K} average velocity in a 5 km time trial, V_{20m} average velocity in a 20 m maximal speed test, *RE* oxygen uptake at the velocity of 4.28 m s^{-1}, MART $VO_{2demand}$ the oxygen demand of the V_{MART} (Londeree 1986)

[a] $n = 17$

[b] $n = 14$

The stepwise multiple regression analysis using V_{5K} as the dependent variable showed that the combination of VO_{2max} and MART VO_{2gain} were the best predictors of V_{5K} ($R^2 = 0.728$; $p < 0.001$). The linear regression formula was: $V_{5K} = 0.066$ VO_{2max} + 0.048 MART VO_{2gain}–0.549. The predicted and measured V_{5K} values are plotted in Fig. 2.

The running velocity curve during the 5 km is shown in Fig. 3. The velocity was highest during the last lap and lowest during the 32nd lap (4,424–4,568 m). The

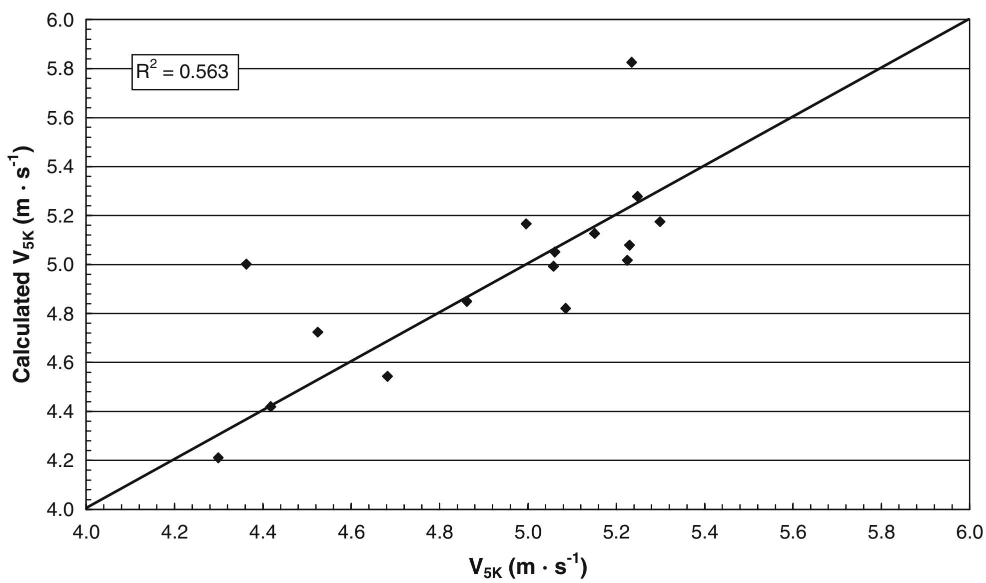

Fig. 1 Calculated (Di Prampero 1986) and measured V_{5K}. *Straight line* represents identity line

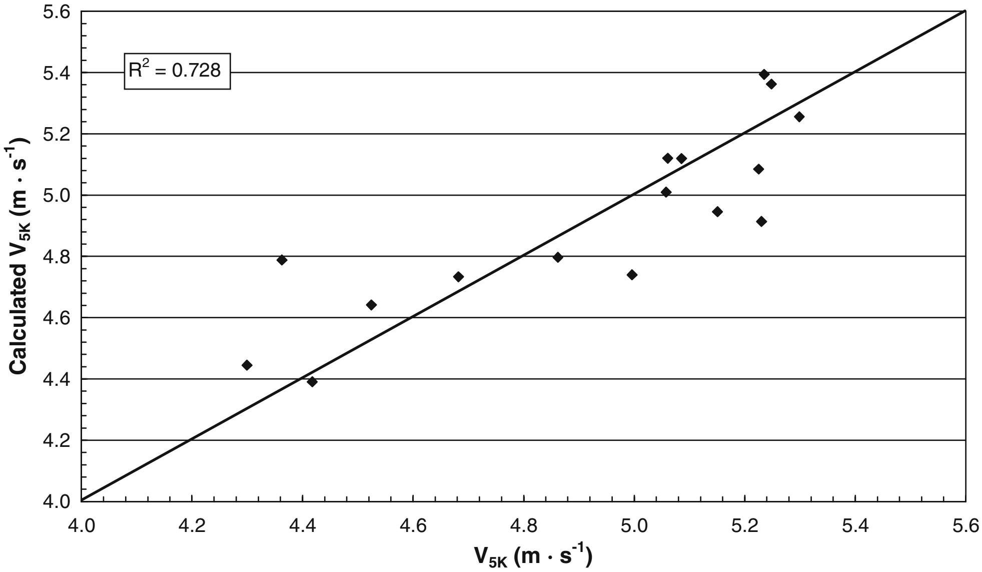

Fig. 2 Calculated (V_{5K} = 0.066 VO_{2max} + 0.048 MART VO_{2gain}–0.549) and measured V_{5K}. *Straight line* represents identity line

decrease in velocity during the 5 km was due to a decrease in stride length (from 1.62 ± 0.11 to 1.57–0.13 m, $p < 0.05$) but no significant changes could be observed in stride frequency. Although stride frequency did not change during the 5 km, ground contact time increased from 207 ± 15 to 220 ± 15 ms ($p < 0.05$) and flight time decreased from 118 ± 11 to 108 ± 10 ms ($p < 0.05$). The AEMG of all the muscles (GA, BF, VL, RF, and VM muscles) were calculated from the ground contact and pre-activity phase at the 1 km (seventh lap), 3 km (21st lap), and 5 km (33rd and last lap). The AEMG of both the ground contact and pre-activity phase decreased during the 5 km time trial (Fig. 4). Furthermore, a significant correlation existed between the V_{5K} and AEMG ratio at the 3 km (3 km/20 m max). The correlation coefficients were $r = 0.60$ for the ground contact phase and $r = 0.50$ for the pre-activity phase ($p < 0.05$).

Discussion

Traditionally, exercise physiologists have associated the limits of human endurance performance with the ability to transport and consume oxygen during exhaustive exercise. Di Prampero (1986, 2003) and Basset and Howley (1997, 2000) have summarized that distance running performance depends on the maximal metabolic power (VO_{2max}) of the subjects, on the fraction of VO_{2max} that can be sustained throughout the entire performance, and on the energy cost of the performance.

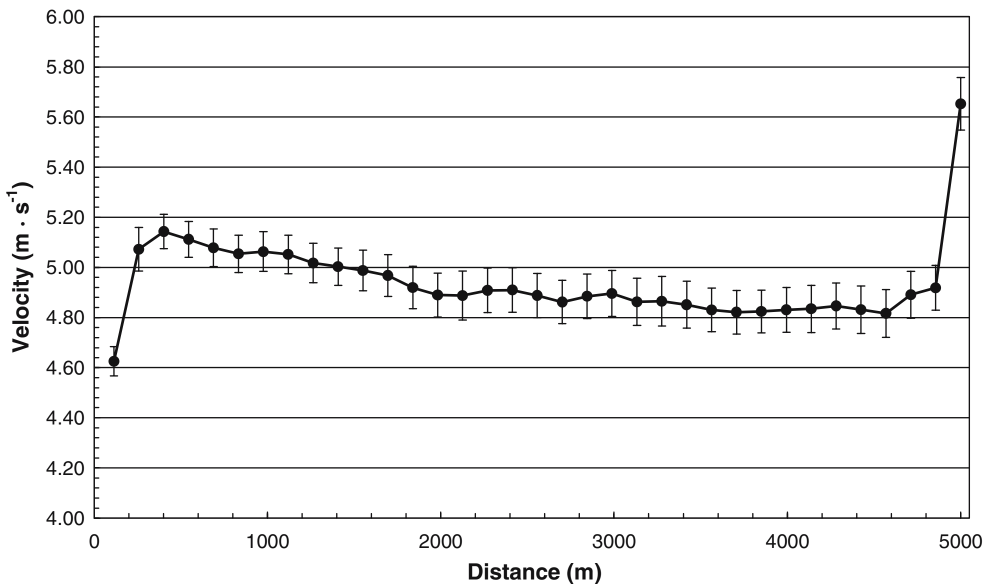

Fig. 3 The average velocity during 5 km time trial. Values are expressed as mean ± SE

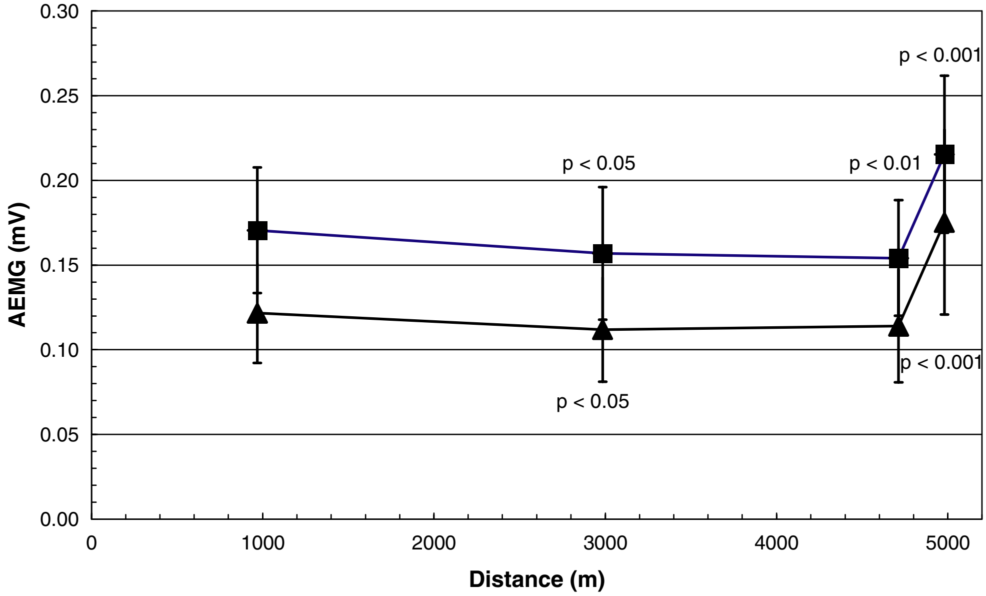

Fig. 4 The AEMG activity of five muscles of the lower extremities (BF, GA, VM, VL, and RF) during the 5 km time trial. *Squares* represent the AEMG of ground contact phase and triangle the AEMG of pre-activity phase. The comparison has been made to the values at 1 km

In the present study, the average value of the calculated (Di Prampero 1986) and the actually measured 5 km velocity were close to each other, 4.96 and 4.93 m s^{-1}, respectively. However, the equation of Di Prampero (1986) explained only 56% of the variation in the 5 km velocity. One reason for this might be that the VO_2 during the 5 km time trial was not actually measured in this study. Instead of an individual fraction, a constant fraction of 0.977 was used in the equation according to Lacour et al. (1990).

The main purpose of the present study was to test the effects of neuromuscular and force–velocity characteristics on distance running performance. In the model of Paavolainen et al. (1999a), distance running performance is influenced not only by factors related to oxygen uptake and utilization but also by factors related to muscle recruitment and force production. Paavolainen et al. (1999a) showed that the combined explosive strength and endurance training improved force, running velocity, running economy, and 5 km running performance in well-trained endurance athletes without any changes in VO_{2max}. The unsolved question is whether the improvement of the muscle force production influences running economy and thereby improves distance running performance, or the ability of neuromuscular system to produce force is an independent factor, which sets by itself an upper limit for endurance performance.

In a similar way as VO_{2max} is a measure of the safe upper limit for energy delivery (Noakes and St Clair Gibson 2004), the maximal power (e.g. V_{MART} or V_{20m}) may be a measure of the upper safe limit of the capacity of the neuromuscular system to produce power in distance runners. This is a difficult idea to prove since there is a lack of running specific tests for force production. Isometric knee extension tests and vertical jump tests, which are most commonly used, are not suitable since the activated muscles, form of muscle function, and time for force production in those tests are different from running. Therefore, in the present study, force and velocity characteristics were measured during the 5 km time trial, in the 20 m speed test and in the MART. The MART seems to be a suitable test for measuring running power above VO_{2max} since a relationship has been observed between the V_{MART} and distance running performance (Paavolainen et al. 1999a; Rusko and Nummela 1996), and V_{MART} is influenced not only by anaerobic capacity but also by the neuromuscular system's ability to produce power (Maxwell and Nimmo 1994; Nummela et al. 1996; Paavolainen et al. 1999b, 2000; Rusko et al. 1993; Rusko and Nummela 1996). In the present study, a relationship exists between V_{MART} and 20 m sprinting velocity but not between VO_{2max} and V_{MART}, suggesting that high V_{MART} is dependent on high-maximal running velocity but not high-maximal oxygen uptake.

A significant positive correlation was observed between the V_{MART} and V_{5K}, and in regression analysis, MART VO_{2gain} and VO_{2max} explained 73% of the variation in V_{5K}. In comparison, the energetic model (Di Prampero 1986) provided a predictive value of 56% in the present athletes. These results suggested that a strong relationship exists between the V_{MART} and distance running performance. This relationship cannot be explained by VO_{2max} since the V_{MART} was not related to VO_{2max}, but it can be explained by running economy since a significant relationship exists between the V_{MART} or MART VO_{2gain} and running economy. This is reasonable since running economy is included in MART $VO_{2demand}$ and hence in the MART VO_{2gain}. The formula of Londeree (1986), which was used in the calculation of MART $VO_{2demand}$, is based on a running economy of 0.205 ml kg^{-1} m^{-1}. The results of the present study suggest that the ability of neuromuscular system to produce power above VO_{2max} affects running economy. This is supported by the previous studies of Paavolainen et al. (1999a, b) in which they also observed a positive correlation between ground contact time and velocity in 5 km. This suggests that rapid force production is beneficial not only for sprint runners but also for distance runners. In the present study, 5 km running velocity was not related to ground contact times but high V_{5K} was more dependent on long strides than high-stride frequency.

Any voluntary high-intensity exercise such as a 5 km time trial is not possible without a conscious decision first to begin the exercise and second to stop the effort (Kayser 2003). Running at higher velocity always needs an increase in spatial and temporal recruitment of motor units (St Clair Gibson and Noakes 2004). This was also shown in the results of the present study since both running velocity and EMG activity of lower extremities decreased during the 5 km time trial (Fig. 4). The running velocity curve of the 5 km (Fig. 3) represents typical pace judgement in the time trial. In the beginning of the run (approximately 0.5 km), the runners overestimated their running abilities and the pace was gradually decreased during the first 2 km and thereafter the velocity remained fairly constant until the final lap, at which point the velocity increased significantly.

An interesting finding of the present study was the relationship between relative EMG-activity at the 3 km and V_{5K}. This suggests that the runners who could keep their level of muscle recruitment at high level at the critical phase of the time trial perform better than the runners whose level of muscle recruitment decreased remarkably during the 5 km. As reviewed by Kayser (2003), central command in the motor cortex is perceived as a sense of effort, and exercise is volitionally terminated when the sense of effort and other sensations such as muscle pain become more intense than is tolerable (St Clair Gibson and Noakes 2004). Indeed it is these sensations, which appear to cause the termination of, or ‘‘limit’’ the exercise performance (Lambert et al. 2005; St Clair Gibson and Noakes 2004). This suggests that based on the sense of effort and the past experience of running, each runner has developed the capacity to anticipate the proper velocity for the 5 km time trial already during the first steps of the run as also in other all-out efforts (Ansley et al. 2004a, b). It might also explain why the last lap was run faster than the previous ones for each runner, although one might expect the presence of some peripheral muscle ‘‘fatigue’’ that would have been more severe at the end of the 5 km than at the beginning of the run. The AEMG and running velocity of all the runners increased during the final lap suggesting that, in spite of accumulated muscle fatigue, the runners were able to increase their muscle recruitment and running velocity remarkably. The velocity of the final lap was related to the V_{MART} but not to the VO_{2max} or running economy suggesting that neuromuscular capacity to produce power is more decisive than oxygen utilization in distance running race during the final lap. Even though the decisive role of the central nervous system in distance running performance is obvious and logical and supported by these findings, the notion that it limits exercise to prevent jeopardizing the integrity of the organism remains unproven as yet (Lambert et al. 2005; Noakes and St Clair Gibson 2004).

Collectively, these findings add further support for the interpretation of the results of the training study (Paavolainen et al. 1999a) in which combined endurance and explosive type strength training improved skeletal muscle force–velocity characteristics and running economy. It is likely that sprint type training improves motor unit recruitment and synchronization, illustrated by force production and efficiency of running. In a recent study, trained cyclists performed sprint training bi-weekly for 4 weeks (Creer et al. 2004). The EMG data showed that sprint stimulus was sufficient to improve motor unit recruitment and synchronization. The authors suggested that the synchronization of motor units results in force potentiation, which improves efficiency and coordination. These authors also suggested that the improved efficiency, due to neural alterations, may have delayed the onset of fatigue.

In addition, the results of the present study support further the idea that distance running performance and running economy are related to neuromuscular capacity to produce force and that the V_{MART} can be used as a determinant of distance running performance. These results further support the hypothesis that the neural control and the ability of the neuromuscular system to produce force and power provide additional information to the energetic model of distance running performance as presented by Di Prampero (1986, 2003) and Bassett and Howley (1997, 2000).

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References

Ansley L, Robson P, St Clair Gibson A, Noakes TD (2004a) Anticipatory pacing strategies during supramaximal exercise lasting longer than 30 s. Med Sci Sports Exerc 36:309–314

Ansley L, Schabort E, St Clair Gibson A, Lambert MI, Noakes TD (2004b) Regulation of pacing strategies during successive 4-km time trials. Med Sci Sports Exerc 36:1819–1825

Bassett DR, Howley ET (1997) Maximal oxygen uptake: classical versus contemporary viewpoints. Med Sci Sports Exerc 29:591–603

Bassett DR, Howley ET (2000) Limiting factors for maximum oxygen uptake and determinants of endurance performance. Med Sci Sports Exerc 32:70–84

Conley DL, Krahenbuhl GS (1980) Running economy and distance running performance of highly trained athletes. Med Sci Sports Exerc 12:357–360

Costill DL, Thomason H, Roberts E (1973) Fractional utilization of the aerobic capacity during distance running. Med Sci Sports Exerc 5:248–252

Creer AR, Ricard MD, Conlee RK, Hoyt GL, Parcell AC (2004) Neural, metabolic and performance adaptations to four weeks of high intensity sprint-interval training in trained cyclists. Int J Sports Med 25:92–98

Davies CTM, Thompson MW (1979) Aerobic performance of female marathon and male ultramarathon athletes. Eur J Appl Physiol 41:233–245

Di Prampero PE (1986) The energy cost of human locomotion on land and water. Int J Sports Med 7:55–72

Di Prampero PE (2003) Factors limiting maximal performance in humans. Eur J Appl Physiol 90:420–429

Durnin JV, Womersley J (1974) Body fat assessed from total body density and its estimation from skinfold thickness: measurements on 481 men and women aged from 16 to 72 years. Br J Nutr 32:77–97

Farrell PA, Wilmore JH, Coyle EF, Billing JE, Costill DL (1978) Plasma lactate accumulation and distance running performance. Med Sci Sports 11:338–344

Foster C, Costill DL, Daniels JT, Fink WJ (1978) Skeletal muscle enzyme activity, fibre composition and VO_{2max} in relation to distance running performance. Eur J Appl Physiol 39:73–80

Hill AV, Lupton H (1923) Muscular exercise, lactic acid and the supply and utilization of oxygen. Q J Med 16:135–171

Johnston RE, Quinn TJ, Kertzer R, Vroman NB (1997) Strength training in female distance runners: impact on running economy. J Strength Cond Res 11:224–229

Joyner MJ (1991) Modeling: optimal marathon performance on the basis of physiological factors. J Appl Physiol 70:683–687

Kayser B (2003) Exercise starts and ends in the brain. Eur J Appl Physiol 90:411–419

Lacour JR, Padilla-Magunacelaya S, Barthélémy JC, Dormois D (1990) The energetics of middle-distance running. Eur J Appl Physiol 60:38–43

Lambert EV, St Clair Gibson A, Noakes TD (2005) Complex systems model of fatigue: integrative homeostatic control of peripheral physiological systems during exercise in humans. Br J Sports Med 39:52–62

Londeree BR (1986) The use of laboratory test results with long distance runners. Sports Med 3:201–213

Maxwell NS, Nimmo MA (1994) Anaerobic capacity in humans: validation of a maximal anaerobic running test against the maximal accumulated oxygen deficit. Clin Sci (Suppl Biochem Exerc) 87:15–16

Morgan DW, Martin PE, Krahenbuhl GS (1989) Factors affecting running economy. Sports Med 7:310–330

Noakes TD (2000) Physiological models to understand exercise fatigue and the adaptations that predict or enhance athletic performance. Scan J Med Sci Sports 10:123–145

Noakes TD, Peltonen JE, Rusko HK (2001) Evidence that a central governor regulates exercise performance during acute hypoxia and hyperoxia. J Exp Biol 204:3225–3234

Noakes TD, St Clair Gibson A (2004) Logical limitations to the catastrophe models of fatigue during exercise in humans. Br J Sports Med 38:648–649

Nummela A, Mero A, Stray-Gundersen J, Rusko H (1996) Important determinants of anaerobic running performance in male athletes and non-athletes. Int J Sports Med 17(Suppl 2):S91–S96

Paavolainen L, Häkkinen K, Hämäläinen I, Nummela A, Rusko H (1999a) Explosive strength-training improves 5-km running time by improving running economy and muscle power. J Appl Physiol 86:1527–1533

Paavolainen LM, Nummela AT, Rusko HK (1999b) Neuromuscular characteristics and muscle power as determinants of 5-km running performance. Med Sci Sports Exerc 31:124–130

Paavolainen L, Nummela A, Rusko K, Häkkinen K (1999c) Neuromuscular characteristics and fatigue during 10-km running. Int J Sports Med 20:1–6

Paavolainen LM, Nummela AT, Rusko HK (2000) Muscle power factors and VO_{2max} as determinants of horizontal and uphill running performance. Scand J Sci Sports 10:286–291

Rusko H, Nummela A (1996) Measurement of maximal and submaximal anaerobic power. Int J Sports Med 17(Suppl 2):S89–S130

Rusko H, Nummela A, Mero A (1993) A new method for the evaluation of anaerobic running power in athletes. Eur J Appl Physiol 66:97–101

Scrimgeour AG, Noakes TD, Adams B, Myburgh KH (1986) The influence of weekly training distance on fractional utilization of maximum aerobic capacity in marathon and ultramarathon runners. Eur J Appl Physiol 55:202–209

St Clair Gibson A, Noakes TD (2004) Evidence for complex system integration and dynamic neural regulation of skeletal muscle recruitment during exercise in humans. Br J Sports Med 38:797–806

Viitasalo JT, Luhtanen P, Mononen HV, Norvapalo K, Paavolainen L, Salonen M (1997) Photocell contact mat: a new instrument to measure contact and flight times in running. J Appl Biomech 13:254–266