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Bijker, K.E.; de Groot, G.; Hollander, A.P.

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K.E. Bijker · G. de Groot · A.P. Hollander

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Abstract Delta (Δ) efficiency is defined as the ratio of an increment in the external mechanical power output to the increase in metabolic power required to produce it. The purpose of the present study was to investigate whether differences in leg muscle activity between running and cycling can explain the observed difference in Δ efficiency between the two activities. A group of 11 subjects performed incremental submaximal running and cycling tests on successive days. The Δ efficiencies during running and cycling were based on five exercise stages. Electromyograph (EMG) measurements were made of three leg muscles (gastrocnemius, vastus lateralis and biceps femoris). Kendall's correlation coefficients between the mean EMG activity and the load applied were calculated for each muscle, for both running and cycling. As expected, the mean Δ efficiency during running (42%) was significantly greater than that during cycling (25%). For cycling, all muscles showed a significant correlation between mean EMG activity and the load applied. For running, however, only the gastrocnemius muscle showed a significant, but low correlation ($r=0.33$). The correlation coefficients of the vastus lateralis and biceps femoris muscles were not significantly different from 0. The results were interpreted as follows. In contrast to cycling, which includes only concentric contractions, during running up inclines eccentric muscle actions play an important role. With steeper inclines, more concentric contractions must be produced to overcome the external force, whereas the amount of eccentric muscle actions decreases. This change in the relative contribution of concentric and eccentric muscle actions, in combination with the fact

that eccentric muscle actions require much less metabolic energy than concentric contractions, can explain the difference between the running and cycling Δ efficiency.

Keywords Locomotion · Efficiency · Muscle contraction type · Electromyography

Introduction

The Δ efficiency of an activity is the ratio of an increment in the external mechanical power output to the increase in metabolic power required to produce it, and is expressed as a percentage. The Δ efficiency during running is significantly greater than that during cycling (Zacks 1973; Asmussen and Bonde-Petersen 1974; Bijker et al. 2001). Furthermore, the Δ efficiency of running is also much greater than the muscle efficiency, which is estimated to have a maximal value of 29% (Cavanagh and Kram 1985). Poole et al. (1992) compared efficiencies during cycling, using measurements of both pulmonary and leg oxygen uptake ($\dot{V}O_2$). No significant difference between these Δ efficiencies was observed and therefore Poole et al. (1992) concluded that, during cycling, processes other than those in the exercising leg muscles do not substantially contribute to the increased metabolic cost at greater power outputs. For running, changes in the metabolic energy cost of processes other than the exercising legs can only explain the great Δ efficiency if the metabolic energy cost of these processes decreases with running against greater applied loads (steeper inclines). This seems unlikely. Therefore, assuming that for cycling as well as for running the exercising legs determine the metabolic cost of the movement, the difference in the Δ efficiency between running and cycling must be due to a difference in the functioning of the exercising leg muscles.

Electromyography (EMG) can be used to study muscle activity non-invasively. Quantified EMG measurements of muscles can indicate if the muscle force is increasing or decreasing (DeLuca 1997). In addition,

K.E. Bijker (✉) · G. de Groot · A.P. Hollander
Institute for Fundamental and Clinical Human
Movement Sciences, Faculty of Human Movement Sciences,
Vrije Universiteit Amsterdam, Van der Boechorststraat 9,
1081 BT Amsterdam, The Netherlands
E-mail: k.bijker@fbw.vu.nl
Tel.: +31-20-4448459
Fax: +31-20-4448529

Komi et al. (1987) and Praagman (2001) have shown clear relationships between the mean EMG activity of concentric exercise and energy expenditure. However, for eccentric muscle actions, no relationship between mean EMG signals and applied load can be observed (Komi et al. 1987). Therefore, the estimation of mean EMG activity seems to be a good way of investigating possible differences in the actions of the leg muscles during running and cycling.

The purpose of the present study was to investigate differences between running and cycling in the relationships between mean EMG activity of the exercising leg muscles and the external power output. Further, we investigated if such differences in muscle actions can explain the observed difference in Δ efficiency between running and cycling.

Methods

Subjects

A group of 11 healthy (7 men, 4 women) subjects participated in this study. All subjects were informed about the protocol to be used and gave written informed consent. Their [mean (SD)] age was 23.7 (4.0) years, body mass was 69.3 (7.9) kg and height was 1.79 (0.10) m.

Protocol

All subjects performed a submaximal running and cycling test on different days. After a warm up period of 10 min, the subjects started the test protocol. Each test consisted of five, 6 min-long exercise stages to ensure steady-state measurements, followed by a rest of 4 min. Heart rate values (beats per minute) were collected using a heart rate monitor (Polar Vantage). To ensure that only the aerobic energy system was involved, only those exercise trials with heart rate values less than 85% of the maximal heart rate (Snyder et al. 1994) and respiratory exchange ratios (R) values less than 0.95 were used in the calculation of Δ efficiency. Maximal heart rate was estimated as (220 minus age in years).

During the running test, the subjects ran on a treadmill at a freely chosen comfortable velocity (between 2.81 and 3.75 m·s⁻¹). Stride frequency was controlled with help of a metronome. The subjects ran up inclines between 0% and 5% in random order. The mechanical power (P_{mech}) increment between two successive inclination values was about 20 W.

The study of Marsh et al. (2000) showed that pedal cadence does not influence cycling Δ efficiency. Therefore, for practical reasons, in the present study during the cycling test all subjects cycled at a cadence of 80 r.p.m. The mean (SD) P_{mech} output during the initial cycling stage was 56.2 (8.7) W. The difference between two successive stages during cycling was about 25 W. Cycling exercise stages were also presented in random order.

Calculation of Δ efficiency

During the last 2 min of each exercise stage, the volume flow rate, O₂ and CO₂ concentrations of the expired gas were measured breath-by-breath (Oxycon Champion, Mijnhart). The R values were calculated over the same period of time. Assuming purely aerobic energy production, metabolic power (P_{met} , in watts) was calculated as (Garby and Astrup 1987):

$$P_{\text{met}} = [(4940 \cdot R + 16040)/60] \cdot \dot{V}O_2 \quad (1)$$

where $\dot{V}O_2$ is in litres per minute.

In the cycling test, the external P_{mech} was calculated from the product of crank torque and crank angular velocity. In the running test, extra external P_{mech} was calculated as:

$$P_{\text{mech}} = m_b \cdot g \cdot v \cdot \sin(\alpha) \quad (2)$$

where m_b is the mass of the subject (kilograms), g is the acceleration due to gravity and equal to 9.81 m·s⁻², v is the velocity of the treadmill (metres per second) and α is the angle of inclination (degrees).

For each subject, linear regression equations were calculated from the extra external P_{mech} and associated P_{met} data. The Δ efficiencies were calculated from the regression coefficient of the regression lines.

EMG measurements

The EMG signals from three superficial leg muscles [gastrocnemius (lateral head), vastus lateralis and biceps femoris] were recorded using Ag-AgCl surface electrodes with an inter electrode distance of approximately 2.0 cm. Before attaching the electrodes, a skin impedance below 2.5 k Ω was ensured by shaving, sanding and cleaning the skin. The EMG signals were amplified, analogue band-pass filtered (10–200 Hz) and sampled at a frequency of 1,000 Hz. During the running and cycling tests, EMG signals were recorded during the first 20 s of the 5th min of each exercise stage. Off-line, the digital EMG signals were corrected for offset, full-wave rectified and low-pass filtered (12 Hz). From the 20 s recordings, mean EMG values were calculated from ten successive running and cycling cycles.

Statistical analysis

For running as well as for cycling, for each muscle the non parametric Kendall's correlation coefficient (Siegel and Castellan 1988) was calculated between the mean EMG value and the external P_{mech} output. Differences in Δ efficiency between running and cycling were tested for significance using a Student's t -test for paired comparisons ($P = 0.05$).

Results

In Fig. 1 a typical example of the two regression lines and the resulting Δ efficiencies is presented. As expected,

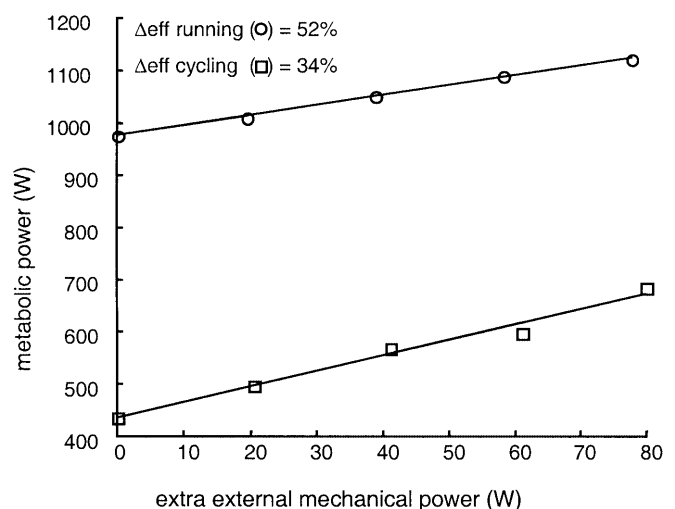


Fig. 1. Typical example of the regression lines for running and cycling, calculated from the data for the extra external mechanical power output and the metabolic power required. Both Δ efficiencies (eff) are presented in the figure

the mean (SEM) Δ efficiency during running was significantly greater than that during cycling [42% (3.2) compared to 25% (1.5), $P < 0.001$].

For cycling, all muscles showed a substantial increase in mean EMG activity with increased P_{mech} output (Fig. 2). For running however, only the gastrocnemius muscle showed an increase in mean EMG activity (Fig. 2). For the vastus lateralis muscle, the difference in increase in EMG activity between cycling and running is illustrated in Fig. 3, where raw rectified EMG data are presented for each exercise stage of the running and cycling test.

For cycling, all three leg muscles measured showed a significant relationship between mean EMG activity and the external P_{mech} output. For running however, only the correlation coefficient of the gastrocnemius muscle was significantly different from 0 (see Table 1).

Discussion

The main finding of the present study was that during running the vastus lateralis and biceps femoris muscles did not show a relationship between the mean EMG activity and the increased external P_{mech} output. For cycling, all muscles measured did show a relationship between EMG activity and external P_{mech} output.

Ericson et al. (1985), van Ingen Schenau et al. (1997) and Miura et al. (2000) concur that during cycling only concentric muscle actions are involved. Komi et al. (1987) and Shinohara et al. (1997) showed that there is a positive relationship between the EMG activity of concentric exercise and the load applied. The results of the present study therefore support the idea that during cycling concentric muscle actions dominate. Since the efficiency of concentric exercise has a maximal value of 30% (Cavanagh and Kram 1985), the Δ efficiency during cycling should not exceed this value. In the present study the mean cycling Δ efficiency was 25%. Results from previous studies (Asmussen and Bonde-Petersen 1974; Suzuki 1979; Coyle et al. 1992; Bijker et al. 2001) have also shown that the Δ efficiency of cycling is indeed less than the efficiency of concentric exercise.

Since Komi et al. (1987) did not observe a relationship between EMG activity during eccentric muscle actions and external P_{mech} output, our data for running suggest that during running up shallow inclines non-concentric muscle actions play an important role. There is little doubt that level running includes stretch-shortening cycles (Margaria 1976; Taylor 1985; van Ingen Schenau et al. 1997). During the landing phase the active muscles are stretched to decelerate body mass whereas during the push off phase the active muscles are shortening. The active stretch allows the tendons of the muscles to store elastic energy, which can be re-used during the subsequent concentric phase. As a result, the gross efficiency during running can be much greater than the muscle efficiency (van Ingen Schenau et al. 1997; Ettema 2001).

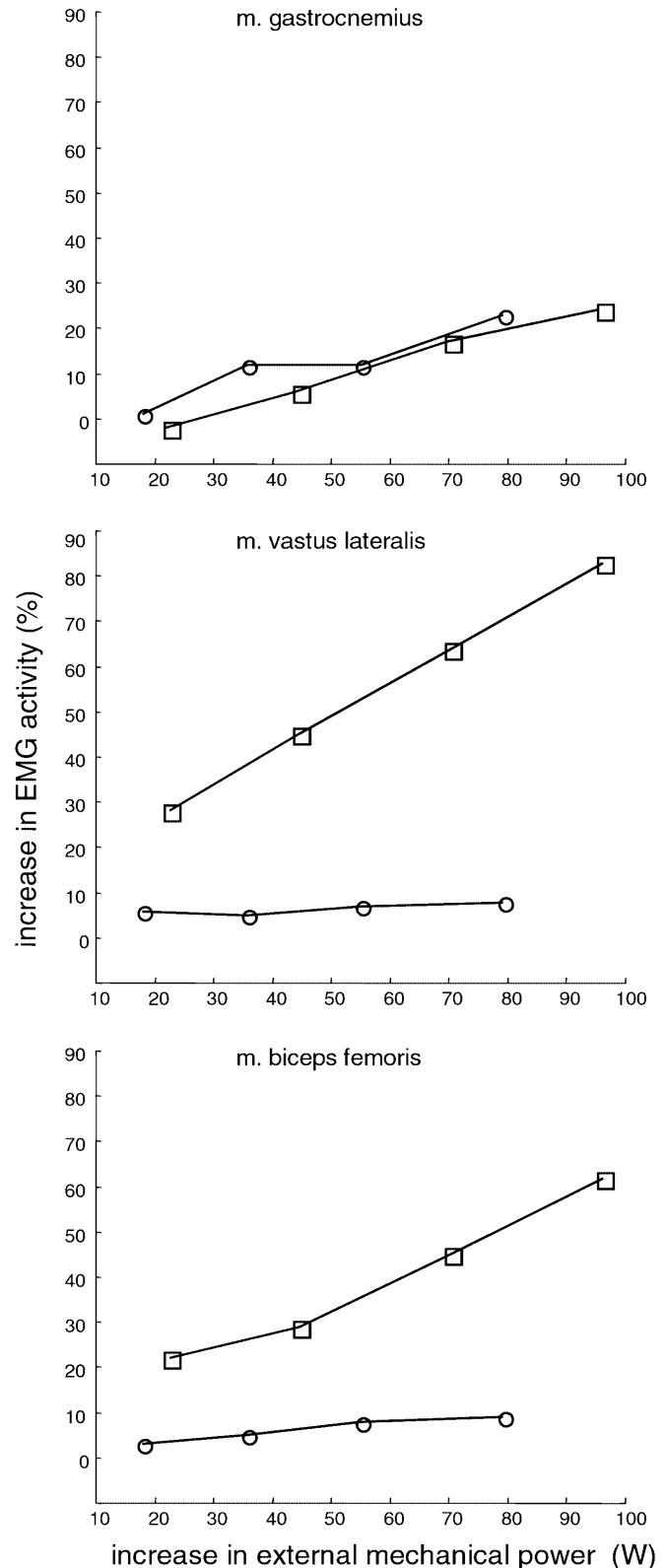


Fig. 2. Increases in mean electromyogram (EMG) activity of three leg muscles resulting from increases in external mechanical power output during running (circles) and cycling (squares). The increase in mean EMG activity is calculated as the percentage increase with respect to the exercise stage having the lowest mechanical power output

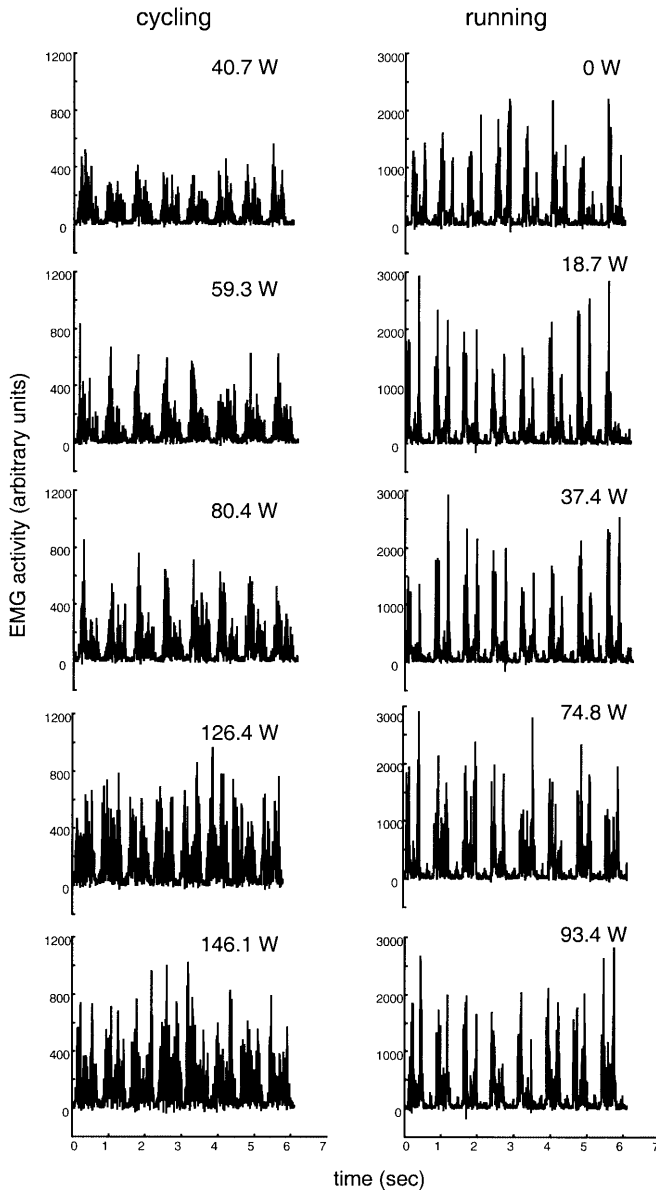


Fig. 3. A typical example of raw rectified electromyogram (EMG) data of the vastus lateralis muscle for the different exercise stages during cycling (left column) and running (right column)

Previous studies suggested that during running up inclines storage and re-use of elastic energy also takes place, which could explain the large Δ efficiencies obtained during running (Lloyd and Zacks 1972; Asmussen and Bonde-Petersen 1974). According to van Ingen Schenau (1984), however, during running up inclines, work produced by the muscles to overcome the external force is lost and can therefore not be stored. Since

muscles can only recover energy that has been previously stored, the storage and re-use of elastic energy could not explain the great running Δ efficiency. In such reasoning, however, van Ingen Schenau (1984) assumes that stretching of the muscle also implies a stretch of the contractile elements of the muscle-tendon complex. Of course, if that is the case it is difficult to explain how a muscle can contribute to external work (De Haan et al. 1989). Roberts et al. (1997), however, showed that in the gastrocnemius muscle of turkeys who ran on the level, no stretch of the contractile elements occurred. Furthermore, Kram and Taylor (1990) based their cost-of-generating-force hypothesis on the idea that during level running the contractile elements of the muscle operate isometrically. Therefore, assuming that during running on the level, as well as up inclines, in the stretching phase no stretch of the contractile elements takes place, it is likely that in both running situations (level and inclination) storage and re-utilization of elastic energy plays a role. Elastic energy storage and re-use can only explain the great Δ efficiency during running if during running up inclines the amount of elastic energy stored and re-used increases. Minetti et al. (1994), however, asserted that during running up any gradient a fixed maximal amount of elastic energy is stored and re-used. Therefore, although storage and re-use of elastic energy probably improves the economy of running up inclines, it cannot explain the great Δ efficiency during running.

As stated above, stretch-shortening cycles include both eccentric and concentric muscle actions. During running up inclines, the amount of concentric contractions has to increase to overcome the external force (i.e. gravity) whereas the contribution of eccentric muscle decreases (Minetti et al. 1994; Taylor 1994), but will still be substantial. It is well known that the metabolic cost of eccentric muscle actions is much less than that of concentric contractions (Asmussen 1953; Bigland-Ritchie and Woods 1976; Rall 1985). As Minetti et al. (1993) showed, a change in the relative contribution of concentric and eccentric muscle actions, combined with the difference in metabolic costs between both muscle actions will lead to very small increases in the metabolic cost for running up shallow inclines. Consequently, for running up shallow inclines, as used in the present study, the Δ efficiency will be much greater than the concentric muscle efficiency. During running up steep inclines, concentric contractions will probably dominate, just as they do during cycling. As a result, the Δ efficiency during running up steep inclines should be much less than the Δ efficiency during running up shallow inclines. It would be interesting to test this hypothesis in further research.

Table 1. Kendall's correlation coefficients between mean electromyogram (EMG) values and external P_{mech}

	Gastrocnemius muscle	Vastus lateralis muscle	Biceps femoris muscle
Cycling	0.55 ^a	0.92 ^a	0.64 ^a
Running	0.33 ^a	0.02	0.06

^aCorrelation coefficient is significantly different from 0

The gastrocnemius muscle has a large compliant Achilles tendon, which seems to be ideal for stretching. Therefore, at first sight it seems strange that this muscle shows a significant relationship between the mean EMG activity and the load applied during running up shallow inclines, suggesting that concentric contractions play an important role. Hof and van den Berg (1983) showed that there is a difference between ankle plantar flexor and knee extensor muscles in their contribution of eccentric and concentric muscle actions during level running. Whereas, during level running, for the knee extensors the contribution of eccentric muscle actions was substantial, for the ankle plantar flexors concentric contractions already played a prominent role. Consequently, during running up inclines, where more concentric contractions must be produced, the gastrocnemius muscle (which is an ankle plantar flexor) will show a much better relationship between EMG activity and the load applied than the vastus lateralis muscle (knee extensor).

In our explanation of the great Δ efficiency of running, as well as a constant amount of elastic energy stored and re-used, we have also assumed that the amount of internal P_{mech} produced remained constant during running up shallow inclines. Minetti et al. (1994), indeed, showed that for the range of inclines that was used in the present study, the amount of internal P_{mech} produced remained nearly constant and would therefore not influence the Δ efficiency during running. Another assumption we made was that the average vertical ground reaction force will not change substantially during running up shallow inclines. Since the metabolic cost of running seems to be directly proportional to the average vertical ground reaction force (Kram 2000) a change in this force would influence the Δ efficiency. However, the inclines used in the present study were so small that the change in the average vertical ground reaction force, and consequently also in the metabolic cost of supporting the mass of the body, would have been negligible and would not have influenced the Δ efficiency during running.

In conclusion, the present study showed a difference between running and cycling in the relationship between the mean EMG activity of leg muscles and the load applied. This difference can be used to explain the observed difference in Δ efficiency between the two types of locomotion. For cycling, the high correlation coefficients confirm the theory that concentric contractions are the main muscle actions. For running, the lack of a relationship between EMG activity and the load applied suggests that during running up shallow inclines, eccentric muscle actions also play an important role. A change in the relative contributions of concentric and eccentric muscle actions, combined with the large difference in metabolic cost between both muscle action types can explain the great Δ efficiency during running.

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