In the introductory chapter an energy flow model, used to simulate athletic performances, has been described. This energy flow model has been applied to different kinds of sports, mainly cycling and speed skating. When using these models, the efficiency of the transfer of metabolic energy production, derived from anaerobic and aerobic metabolism, to mechanical PO (forward propulsion), needs to be known. GE will differ between the different kinds of sports (cycling GE: 18.5-23.5%, speed skating GE: 15.8 ± 1.8%, 18.7 ± 1.0%), but the assumptions regarding GE, underlying the different energy flow models, are similar. The main goal of this thesis was to try to test the different assumptions regarding GE. The studies described in the first chapters (Chapters 2-6) of this thesis made use of cycling exercise, because PO can be precisely measured. Chapter 7 describes two studies, in which we tried to gain insight into one of the assumptions regarding GE, by studying speed skaters during official races. It is hypothesized that the results of Chapters 2-6 also apply to speed skating exercise.

Assumption 1 – Gross efficiency determined during submaximal exercise is constant during the day

In Chapter 2 different issues, regarding the methodology used to determine GE, were studied. Based on the results of this chapter a research protocol to determine GE was constructed. In Chapter 3 the reliability of the GE measurements, using the new protocol, was determined. It was shown that GE can be determined very reliable, the typical error was 0.59 and the coefficient of variation was 4.4%, which is in agreement with the findings of Moseley and Jeukendrup. To assess the variation in GE within the day, subjects completed six GE tests equally distributed over the 24 h of the day. A circadian rhythm in body temperature and resting VO$_2$ was found, but GE was relatively constant during the day. In conclusion, the first assumption regarding GE seems to be valid and GE can be determined independent of time of the day during follow-up experiments.

Assumption 2 – Gross efficiency is independent of the altitude above sea level at which exercise is performed

Chapter 5 describes a study in which we tested the hypothesis, that GE is lower at low to moderate altitude, due to an increased cost of VE and HR in combination with a higher RER. GE was determined at an altitude-matched similar relative exercise intensity (55% PVO$_{2\text{max}}$ or 65% PVO$_{2\text{max}}$), which resulted in a significantly lower GE at a simulated
altitude of 1,500 m than at sea level. A higher RER at altitude (0.03) can explain an absolute decrease of about 0.2% in GE. However, the remaining part of the lower GE at altitude remains unexplained, as the mean absolute decrease in GE with altitude was 0.77 ± 1.1%. It is possible that the lower GE at AL is (partly) caused by the lower absolute exercise intensity at which subjects exercised. Therefore, follow-up research is needed in which GE measurements are performed at both similar absolute and relative submaximal intensities at sea level and altitude, to make definitive conclusions about the effect of acute and chronic hypoxia on GE.

**Assumption 3 – Gross efficiency determined at submaximal exercise intensities is representative of gross efficiency at maximal and supramaximal exercise intensities**

Although, there are methods available to estimate the anaerobic energy contribution to exercise performed above VT (for example the lactate equivalent method\(^{11}\) and the MAOD method\(^{12}\) (Chapter 4A)), thus far it is difficult, if not impossible, to validate these methods. Therefore, GE can only be determined robustly during submaximal exercise below VT. However, when modeling or analyzing athletic events, it is more interesting to know what GE would be at (supra)maximal exercise intensities. In Chapter 6A a new approach to estimating GE during and immediately after high intensity exercise is introduced. In Chapter 6B the same approach was applied to time trial exercise. Using this new approach, GE is determined during submaximal exercise performed before and after high intensity exercise, based on which GE was estimated, using back-extrapolation, immediately after high intensity exercise. The results of both studies, as described in Chapter 6, suggest that GE determined at submaximal exercise intensities is not representative of GE at (supra)maximal exercise intensities. Bangsbo et al.\(^{13}\) even concluded from their study that the mechanical efficiency of the muscles is higher when high intensity exercise is performed (mainly anaerobic energy production) than during steady state submaximal exercise. So, the exact magnitude of GE during high intensity whole-body exercise remains, at this moment, unknown.

**Assumption 4 – Gross efficiency remains constant during fatiguing exercise**

The studies described in Chapter 6 do not only provide information about GE at (supra)maximal intensities, but mainly offer insight in the change in GE during high intensity exercise. Previous research showed that efficiency decreases during submaximal endurance exercise\(^{14}\) and during high intensity knee extensor exercise.\(^{13,15}\) However, it was unknown if and how GE changes during high intensity whole-body exercise. Chapter
6 showed that GE is significantly lower after high intensity constant PO exercise (Chapter 6A) and time trial exercise (Chapter 6B), compared to before (GE before and after a 4 min constant PO trial: 18.3 ± 1.3% vs. 15.8 ± 1.7%, GE before and after a 4,000 m time trial: 22.5 ± 1.1% vs. 20.1 ± 1.4%). In addition, the decrement in GE was larger for relatively short time trials (500-4,000 m), compared to the longer time trials (15,000 m and 40,000 m). Suggested causes for the reduction in GE are a change in muscle efficiency (phosphorylative coupling efficiency × contraction coupling efficiency\(^{16}\)), recovery processes in fatigued inactive fibers in combination with an increase in respiratory and cardiac work that increases the metabolic energy cost. Although, the exact cause(s) of the decrement in GE remains to be established, it appears invalid to assume that GE stays constant during fatiguing cycling exercise.

By studying changes in kinematic characteristics of the speed skating posture/technique we tried to gain more insight in GE during competitive speed skating events. As described in the introductory chapter, it is thus far, impractical to determine GE during speed skating exercise. However, as it is thought that \(e\), the effectiveness of the push-off, is related to skating efficiency, studying \(e\) during high intensity exercise will provide us information about the validity of the fourth assumption for speed skating. The data described in Chapter 7 shows that \(e\) increases (i.e. a less effective push-off) during speed skating races (1,500 m and 5,000 m), that the increase in \(e\) is larger during 1,500 m races, compared to 5,000 m races, and that the change in \(e\) is related to the change in \(v\) (skating velocity). So, if \(e\) and GE are indeed related, Chapter 7 shows that GE decreases during speed skating races, that the decrement in GE is larger for 1,500 m races, compared to 5,000 m races, and that the change in \(e\) is significantly related to the change in \(v\) during a 5,000 m.

The results of both studies described in Chapter 6 are therefore in agreement with the results of Chapter 7A and 7B. GE decreases during cycling and speed skating events and the decrement in efficiency is larger for relatively shorter events. Passfield and Doust\(^{14}\) showed that the change in GE found between two warm-up bouts was significantly correlated with the change in PO between two 5 min performance tests (\(r = 0.73\)). In addition, in Chapter 7 it was shown that the change in \(v\) is related to the change in \(e\) during 5,000 m races. So, in conclusion, the assumption that GE remains constant during fatiguing exercise seems invalid and in addition the change in GE will influence performance outcomes.

In summary, the studies described in this thesis showed that Assumption 1, GE determined during submaximal exercise is constant during the day, is valid. Additional research is
necessary to make a definitive conclusion about Assumption 2; GE is independent of the altitude above sea level at which exercise is performed. Assumption 3, GE determined at submaximal exercise intensities is representative of GE at (supra)maximal exercise intensities, seems to be invalid. However, the exact magnitude of GE during whole-body (supra)maximal exercise remains unknown. Finally Assumption 4, GE remains constant during fatiguing exercise, is invalid.

The energy flow model adapted

Based on the studies described in Chapter 6 and 7 it can be concluded that GE declines during high intensity exercise. The current version of the energy flow model for cycling, as described in Chapter 1, and the energy flow model for speed skating make use of a constant GE during the entire exercise bout. Therefore, the original energy flow model for cycling and speed skating needs to be adapted. The constant GE, used in the current version, needs to be substituted by a declining GE over the course of a race. We propose to model the declining GE by an exponential function:

\[
GE = a \cdot e^{-b \cdot t} + GE_{\text{final}}
\]

in which \(GE_{\text{final}}\) is the GE at the end of the race, \(b\) is the rate constant, and \(a\) is the difference between GE at the start of the race (determined during submaximal exercise) and \(GE_{\text{final}}\). \(GE_{\text{final}}\) can be estimated using the back-extrapolation method described in Chapter 6A and 6B. It needs to be mentioned that the efficiency at the start of the race might be higher than the efficiency determined during submaximal exercise, as has been suggested by Bangsbo et al. However, as GE during the start of whole-body high intensity exercise is unknown, it is assumed that GE at the start of the race is similar to GE during submaximal exercise.

GE is modeled by an exponential function, because the study described in Chapter 6B showed that the rate of the decline in GE seems linear for relatively short distances (500-4,000 m), but that at 50% of the final time of the 40,000 m the final decrement in GE is almost attained. Besides, from the results of Jones et al., it can be hypothesized that the decrement in GE correlates with the decrease in muscle phosphocreatine concentration ([PCr]) and the concomitant increase in inorganic phosphate concentration during exercise. Jones et al. demonstrated that the kinetics of the muscle [PCr] response to exercise showed similarities to the \(\dot{V}O_2\) kinetics, therefore the muscle [PCr] response can be fit by an exponential function, which implies that the decrement in GE can also be represented
by an exponential function. Simulating races with the adapted version of the energy flow model, requires the use of an iterative procedure, as the exact finish time, which is needed to determine the rate of the decline in GE, is unknown before the start of the simulation.

In order to be able to use the energy flow model, the amount of mechanical power anaerobically produced \( (P_{an}) \) needs to be known. \( P_{an} \) can be determined by subtracting the aerobically produced mechanical power \( (P_{aer}) \) from the total PO delivered \( (\text{Equation 1.10})^{18,19} \). Thus far, the GE method, as has been described in Chapter 4B, assumed a constant GE during high intensity exercise. However, as it seems that GE decreases during high intensity exercise, the contribution of \( P_{aer} \) and resultantly \( P_{an} \) during exercise needs to be determined by using Equation 8.1. The relative contribution of \( P_{aer} \) will decrease and the relative contribution of \( P_{an} \) will increase when GE declines during exercise, as has been shown in Chapter 6A. Thus, the anaerobic capacity values, determined in Chapter 4B with the GE method, need to be revised, based on a declining GE during high intensity exercise. However, this would also suggest that the anaerobic capacity, determined with the MAOD method, needs to be adapted. Unfortunately, the MAOD method implies a constant efficiency,\(^{12}\) so no adaptations can be made. As, the ‘real’ anaerobic capacity cannot be determined, i.e. only indirect methods are available, it remains uncertain if the higher anaerobic capacity, derived with a declining GE, is a better representation of the ‘real’ anaerobic capacity.

**Future directions**

With the studies described in this thesis, we gained additional knowledge about the four assumptions underlying the energy flow model. Using this new information we suggested an adaptation to the current version of the energy flow model. However, further research is necessary to make definitive conclusions about **Assumption 2**: GE is independent of the altitude above sea level at which exercise is performed. Additional research is also necessary to gain more insight into the exact magnitude of whole-body GE at (supra)maximal exercise intensities (**Assumption 3**). In addition, it would be valuable if the relation between the effectiveness of the push-off and skating GE is studied. Finally, the declining GE, with the resultantly lower contribution of \( P_{aer} \) and higher contribution of \( P_{an} \) to total PO implies that the data of multiple studies, that used the GE method, may need to be revised.
Practical applications

There are several practical applications that can be deduced from the different studies presented in this thesis. First of all, it seems that there is no need to change a cyclists’ circadian rhythm before important competitive events, as GE is unaffected by time of the day (Chapter 3). This implies that a jet-lag, when crossing different time zones, will also not influence GE. It might be that in more technically demanding sports, like speed skating, different results would be found. However, thus far there are no indications that support this.

Chapter 4 shows that the 4+Y MAOD procedure and GE method resulted in the most precise estimations of the anaerobic capacity. As it is not advisable to use these methods interchangeable and because the MAOD method is more time demanding, we suggest coaches and trainers to use the GE method to determine the anaerobic capacity of their athletes. Most likely, an even better representation of the anaerobic capacity will be obtained when the decrement in GE over the course of a high intensity exercise bout is taken into account (Chapter 6).

Multiple sporting events take place at low to moderate altitude. Chapter 5 shows that GE is lower at an altitude-matched similar relative exercise intensity. As, athletes will perform their races at a certain relative exercise intensity, coaches should be aware of the lower GE. It might be that altitude acclimatization will diminish the acute effect of hypoxia on GE. However, future research is necessary to investigate this.

It has been shown that GE declines during high intensity cycling exercise (Chapter 6A, constant PO exercise; Chapter 6B, time trials) and that \( e \), which most likely reflects GE, increases (i.e. a less effective push-off and lower efficiency) during speed skating races (Chapter 7). Coaches, athletes, and scientists should collaborate, in order to evaluate if pacing strategy and/or technical adaptations can minimize the decrement in GE.

The most important message of Chapter 7 is that coaches and athletes should pay attention to achieving and maintaining a small \( e \), as the change in \( v \) is significantly related to the change in \( e \) during 5,000 m speed skating races. Besides that, the 10 fastest and 10 slowest skaters, competing in World Cup races (A and B-division) showed overall a relatively similar knee and trunk angle over the race, but significantly differed in the effectiveness of their push-off. We suggest coaches to use the presented 2-D movement registration method to analyze the kinematic characteristics of their athletes.

Finally, the suggested adaptation to the current version of the energy flow model for cycling and speed skating will make these models more representative of the real situation. The suggested adaptation will not improve the agreement between simulated finish times and finish times during official races, as it only changes the relative
contribution of $P_{ac}$ and $P_{an}$. However, more knowledge about the relative contribution of $P_{an}$ improves our understanding of the development of fatigue during races.
References


