

The Efficiency of Muscular Exercise

Der Wirkungsgrad von Muskelarbeit

Summary

- **The efficiency η** of energy conversion is defined as the ratio between muscular power and metabolic energy expenditure. Following definitions are used: η_{gross} (muscular power/total energy expenditure), η_{net} (muscular power/(total energy expenditure–resting energy expenditure)), η_{work} (muscular power/(total energy expenditure–idling energy expenditure)), η_{delta} (Δ muscular power/ Δ energy expenditure). η_{net} of isolated muscles amounts to 30%. Because of supporting functions, lower values result in vivo during positive exercise. During negative exercise the body often stores energy (elastic, potential, kinetic) which markedly improves η if reused.
- **Measurements** are performed using ergometers (cycle ergometers, treadmill etc.) and indirect calorimetry ($\dot{V}O_2$ and $\dot{V}CO_2$). Determination of both gases is essential, because varying proportions of fat and carbohydrate oxidation influence energy turnover. For intense exercise, the anaerobic energy yield is calculated from oxygen deficit or blood lactate. Measurements have to be standardized, because movement frequency and power influence η . For comparisons η_{net} which little depends on power is preferable.
- **During sports**, values vary between 1% (arching) and 50% (running). Measurement of energy expenditure per m distance and kg of body mass is also applicable for efficiency estimation. The efficiency of complex movements can be improved by practicing, since optimized coordination reduces energy need. Aging and fatigue are therefore also influential. The mitochondrial function is probably not trainable. Clear sex differences have not been observed. An improvement of efficiency in hypoxia is improbable; a relative increase of carbohydrate metabolism reduces the need for oxygen. An increase of efficiency by nitrate consumption is under discussion.

KEY WORDS:

Energy Expenditure, Ergometry, Respiratory Quotient, Physical Training, Altitude, Nitrogen Monoxide

Introduction

The relation between muscular exercise and metabolic energy expenditure is a central topic of physiology which has been intensely investigated during the last century (reviews of older publications in (7, 27, 85)). The efficiency η of an energy transformation is defined as the relation of the exploited energy to the consumed chemical energy, usually in form of

Zusammenfassung

- **Als Wirkungsgrad η** einer Energieumwandlung bezeichnet man in der Sportphysiologie das Verhältnis zwischen mechanischer Muskelleistung und metabolischem Energieumsatz. Man unterscheidet η_{brutto} (Leistung/Gesamtenergieumsatz), η_{netto} (Leistung/(Gesamtenergieumsatz–Ruheumsatz)), η_{Arbeit} (Leistung/(Gesamtenergieumsatz–Umsatz bei Leerbewegung)), η_{delta} (Δ Leistung/ Δ Energieumsatz). η_{netto} des isolierten Muskels beträgt 30%. Aufgrund zusätzlichen Energieaufwandes für andere Zell- und Körperfunktionen erhält man in vivo bei positiver aerober Arbeit niedrigere Werte. Bei negativer Arbeit speichert der Körper oft Energie (elastisch, potentiell, kinetisch), die bei Wiederverwertung den Wirkungsgrad erhöht.
- **Die Messung** erfolgt mittels Ergometern (Drehkurbelergometer, Laufband u. a.) und indirekter Kalorimetrie ($\dot{V}O_2$ und $\dot{V}CO_2$). Wichtig ist die Bestimmung beider Gase, da wechselnde Anteile von Fett- und Kohlenhydratoxidation den Energieumsatz beeinflussen. Bei Intensivbelastung wird die anaerobe Energielieferung aus Sauerstoffdefizit oder Blutlaktatkonzentration ermittelt. Die Messungen müssen standardisiert sein, da Bewegungsfrequenz und Leistungshöhe η beeinflussen. Für Vergleiche eignet sich besonders η_{netto} , der wenig von der Leistung abhängt.
- **In der Sportpraxis** liegen die Werte zwischen 1% (Bogenschießen) und 50% (Laufen). Die Messung des Energieumsatzes je m Weg und kg Körpermasse ist ein praktikables Verfahren zur Wirkungsgradabschätzung. Der Wirkungsgrad komplexer Bewegungen kann durch Übung verbessert werden, weil wegen Koordinationsoptimierung Energie gespart wird. Alter und Ermüdung haben deshalb auch Einfluss. Dagegen scheint die mitochondriale Energielieferung nicht trainierbar zu sein. Eindeutige Geschlechtsunterschiede wurden nicht gefunden. Eine Verbesserung des Wirkungsgrades durch Hypoxie ist unwahrscheinlich, $\dot{V}O_2$ sinkt durch eine relative Zunahme des Kohlenhydratumsatzes. Eine Verbesserung des Wirkungsgrades durch Nitratgabe ist umstritten.

SCHLÜSSELWÖRTER:

Energieumsatz, Ergometrie, Respiratorischer Quotient, Training, Höhe, Stickstoffmonoxid

a decimal fraction or as percentage. In exercise physiology this corresponds to the relation between muscular exercise and energy from decomposition of nutrients or correspondingly between mechanical power and metabolic energy expenditure (85). Therefore efficiency is one decisive factor for success in many sport disciplines. >

1. CHARITÉ - UNIVERSITÄTSMEDIZIN BERLIN, Institut für Physiologie, Berlin
2. MEDIZINISCHE HOCHSCHULE HANNOVER, Institut für Sportmedizin, Hannover



Article incorporates the Creative Commons Attribution – Non Commercial License.
<https://creativecommons.org/licenses/by-nc-sa/4.0/>



QR-Code scannen und Artikel online lesen.

CORRESPONDING ADDRESS:

Univ. Prof. a. D. Dieter Böning
Institut für Physiologie
Charité - Universitätsmedizin Berlin
Charitéplatz 1, 10117 Berlin
✉: dieter.boening@charite.de

The following definitions are used (27):

- Gross efficiency (η_{gross}): power/total energy expenditure
- Net efficiency (η_{net}): power/(total energy expenditure – resting energy expenditure)
- Work efficiency (η_{work}): power/(total energy expenditure – idling energy expenditure)
- Delta efficiency (η_{delta}): Δ power/ Δ energy expenditure (difference between work rates or slope of the corresponding curve)

Efficiency in the Isolated Muscle

Net efficiency in the isolated muscle is the mathematical product of two components (54, 120):

1. Metabolic efficiency (ATP-synthesis/energy liberation from decomposition of nutrients; "phosphorylative coupling")
2. Mechanic efficiency (contractile exercise/energy liberation during ATP-splitting; "mechanical coupling")

Brooks (27) suggests the following values :

0.6 (phosphorylative coupling η) x 0.5 (mechanical coupling $\eta=0.3$ overall η)

Because of the additional cost for other cellular functions (e.g. ion pumps), friction as well as supporting functions (nervous system, circulation-ventilation, stabilizing muscles, heat dissipation etc.), η in the whole organism must be smaller. Muscular exercise of supporting activities, e.g. of the heart, is not added to the numerator.

According to Hill (64), η_{gross} is maximal in isolated muscles (frog, 0°) at approximately 45% of the isometric maximal force, while maximal power is measured at 30%. In slow and fast human muscle fibres the maximum of η_{gross} is similar in vitro, but is reached at higher velocities for the latter (61). Similarly, Kohler und Bouteillier (72) calculated that the maximum of η is scarcely influenced by the fibre types in a muscle. Apparently contrasting results during ergometry (40, 115) probably result from the fact that only one pedalling frequency was tested (60 or 80/min). A further argument against a difference is also that the metabolic efficiency for aerobic and anaerobic glucose degradation is equal (27). In animal experiments, lower η for rapid fibres were frequently calculated (review in (7)), but not if recovery metabolism after exercise is considered (8).

Types of Contraction

The type of contraction is very influential (Force-Length-Diagram, Fig. 1). During a concentric contraction, the muscle delivers exercise (positive, the sign is positive in contrast to the use in physics, because it was originally related to the energy content of the body mounting a stair (85)), η is positive. During an eccentric contraction the muscle takes up energy (negative), η is negative as well. During an isometric contraction the muscle does not deliver exercise ($\eta=0$), the inner structures, however, are partly shortened (sarcomeres) and partly distended (tendons), exercise is elastically stored. The contraction is partly concentric and partly isometric when the muscle fibres are oblique to the direction of the tendons.

Special Aspects of Negative Exercise

Part of the imported energy is lost as friction heat, part is stored in elastic structures, e.g. titin, sarcolemma, connective tissue (79, 102). Active braking (visible in the electromyogram, e.g. (97)) needs the formation of actin-myosin-bridges. However, during negative exercise, no or only little ATP is split in contrast to during positive exercise. The following hypotheses have been proposed: cleavage of the actin-myosin-connection not by

adding of ATP, but mechanically by the distending force (34); only 1 ATP for 2 actin-myosin-bridges (28); enlarged elasticity of titin after binding of Ca^{++} and actin (62, 93), resynthesis of ATP by reversion of the ATPase-effect of actomyosin. The latter hypothesis was proposed by Hill (65), because the sum of elastically-stored exercise and of heat was smaller than the added distension exercise. Ulbrich and Rüegg (117) assumed the synthesis of actomyosin-ADP as energy-rich intermediate product. The problem has not yet been solved (7, 80). In any case, the storage of negative exercise is a decisive factor for the magnitude of efficiency.

Efficiency during Exercise in Humans – Basics

For the determination of efficiency, mechanical exercise and the energy liberated by metabolism have to be measured (review of methods e.g. in (106)).

Measurement of Power

The mechanical power (work/time, unit watt) is mostly determined by the use of ergometers (e.g. cycle ergometer, treadmill). Here, however, only the work delivered to the ergometer is determined, except losses by nontangential force vectors on the pedals. Work for the movement of the center of mass, accompanying movements and stabilisation of body parts is not measured. Body posture and position on the seat exert little influence on η_{brutto} (76).

The following is valid for cycle ergometers:

$power = braking\ force \times way\ of\ 1\ revolution \times rotation\ frequency$

The relation between the rotation frequency of the braked wheel and the pedal frequency is determined by the gear ratio.

There is nearly no negative exercise but the friction in the ergometer during idling (moving the pedals without braking force) has to be considered. This is programed in electrically-braked ergometers.

On the treadmill, the calculation of work and η without additional biomechanical measurements or tethered movement is only possible with slope (Fig. 2):

$work = mass \times height = mass \times distance \times \sin \alpha$

$power = mass \times velocity \times \sin \alpha$

Without slope, external exercise is apparently zero but the center of mass moves (potential and kinetic energy). This partly elastically-stored energy serves to overcome friction on the ground, in the air and within the body.

Discipline-Specific Ergometry

If bicycles or wheelchairs are put on a treadmill and connected to a strain gauge, it is possible to measure the ground friction when idling; use of a fan allows determining air friction as part of power. It is also possible to extrapolate the power necessary against the resistances from tethered movement with varying weights. Alternatively force and rotation frequency can be measured by strain gauges and revolution counters on the bicycle.

Discipline-specific ergometers have been developed for cross-country skiing (71) and rowing, in the latter the influence of boat movements is simulated by various constructions (wind wheel, water wheel, electronically (114)). For swimmers, swimming flumes are used where power can be measured with variable flow velocities and strain gauges; another possibility is to compensate the driving power by weights on a car connected by a rope to the swimmer (tethered swimming, (122)).

Measurement of Energy Expenditure

Direct calorimetry, the most exact but also the most costly method, is rarely used. If applied with standardized conditions, the reliable routine method (108) is indirect calorimetry (measurements of oxygen uptake $\dot{V}O_2$ and carbon dioxide production excretion $\dot{V}CO_2$). Both gases must be measured because the caloric equivalent for O_2 depends on the proportion of metabolized fat and carbohydrate, respectively (19.6kJ/l and 21.1kJ/l according to Brooks (27), difference 7.7%). The caloric equivalent can be calculated using the respiratory quotient ($RQ = \dot{V}CO_2 / \dot{V}O_2$) in the expired gas. As fat ($RQ=0.7$) contains less oxygen than carbohydrate ($RQ=1.0$), a larger number of O_2 -molecules has to be inspired and metabolized for a given number of produced CO_2 -molecules. As the percentage of fat degradation decreases with increasing exercise intensity, but on the other hand increases with duration of work (81), the calculation of the caloric equivalent is a must for exact measurements. The proportion of proteins for energy supply is small especially during exercise and is therefore neglected; if necessary it may be calculated by means of nitrogen excretion in urine (51). An error might be caused if ketone bodies are consumed as ergogenic substances (38, 51); but the contribution to the energy yield can be quantified by measurement of blood concentration during work.

A different access considers the number of ATP molecules synthesized per oxygen molecule (P/O ratio). Under in vivo-conditions it amounts to 3.0-3.2 ATP per O during glucose and glycogen degradation, but only 2.8 during fat oxidation, because the produced Flavin-Adenin-Dinucleotide produced by the latter supplies only 2 ATP/O (27). Since mainly glycogen is metabolized during exercise yielding one ATP more per glucose unit, the difference in ATP production between carbohydrate- and fat metabolism amounts to at least 10%. During a diet very rich in fat, the difference increases even in untrained males because the content of decoupling proteins in the mitochondria rises (46).

An exact measurement of energy expenditure by indirect calorimetry is only possible in the steady state without rising hyperventilation (in that situation the RQ does not mirror metabolism) and without changes of phosphocreatin and lactate concentration, i.e. not earlier than 1-3min after a change in work rate and below the maximal lactate-steady state (maxLass). A moderate constant hyperventilation for respiratory compensation is not problematic, because the alveolar PCO_2 decreases only until the CO_2 -excretion again equals the metabolically-produced CO_2 -volume.

Consideration of Anaerobic Energy Sources

During very intense short exercises, the anaerobic alactic and lactic energy supply has to be considered. The alactic contribution (consumption of stored energy-rich phosphates) corresponds to the O_2 -deficit at the beginning (122) or the rapid phase of the O_2 -debt after the end of exercise (16). The lactic energy yield

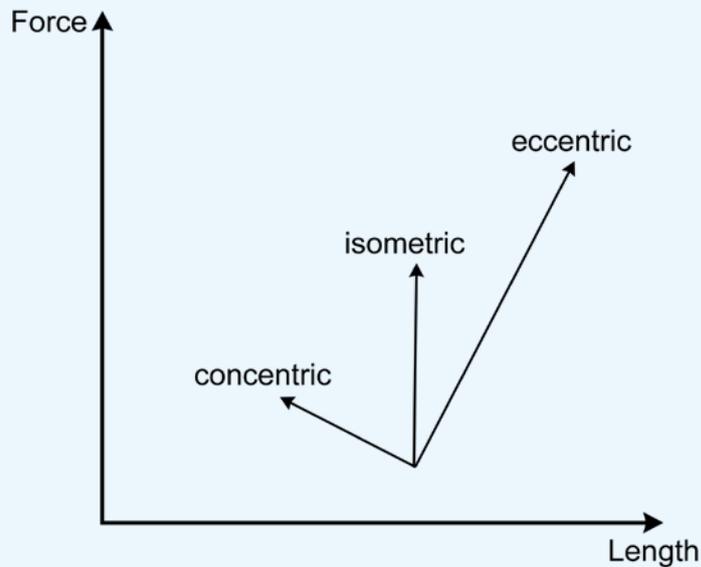


Figure 1

Types of contraction in the force-length-diagram.

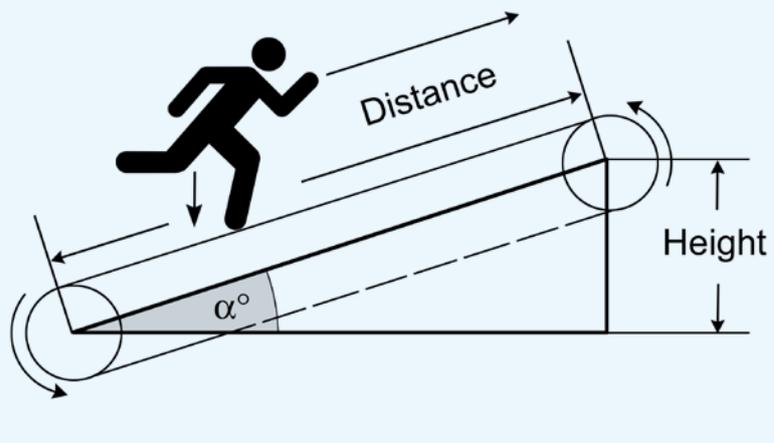


Figure 2

Treadmill. Calculation of power against gravity by use of $\sin \alpha \times \text{distance}$. From (41) with permission.

cannot be calculated from the slow phase of the O_2 -debt, because other effects like temperature regulation also contribute (53). For 1mmol/l increase of blood lactate, ca. 3ml O_2 per kg body mass and the caloric equivalent for carbohydrates is used.

Efficiency during Exercise in Humans – Application

Cycle Ergometry – Endurance Testing

Figures 3 and 4 show measurements in untrained male subjects and cyclists (25). η_{gross} increases with work rate because the percentage of resting metabolism decreases. This was also observed by other investigators (e.g. (36, 111)). In spite of this drawback it is often used. In contrast, η_{net} is less dependent on work rate. Both types of efficiency vary, however, with pedal rate, highest values are 22 and 26%, respectively, at approximately 60-70/min; similar η were measured in women (11). One cause is that the optimum of efficiency is found at >

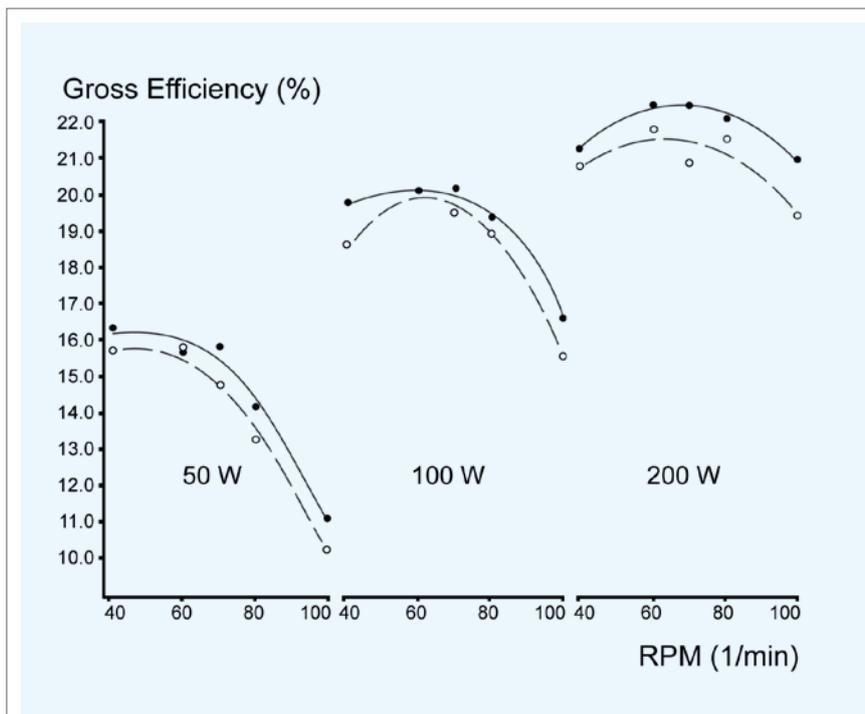


Figure 3

Gross efficiency on the cycle ergometer in dependence on pedalling frequency and status of physical fitness (open circles untrained males, filled circles trained cyclists). Mean values and quadratic regression curves. Complete data in the original paper. From (25) with permission.

medium movement velocities (e.g. (64, 72)). A further cause is that the energy cost for idling rises with frequency. On the other hand, additional muscle fibres are recruited at low frequencies because of relatively high resistive force attributing to the idling cost. The deviations, if constant pedal rate and work rate are not considered, amount to up to 12% for both η_{brutto} and η_{netto} . As the relative contribution of idling decreases with rising power, the frequency influence is reduced at 200 W.

For untrained subjects there is a tendency for a decrease of η_{netto} beginning at 200 W; this may be explained as an effect of the increasing acidosis with hyperventilation and recruitment of supporting muscles. Considering the anaerobic metabolism (rise of blood lactate concentration by 4-6 mmol/l in this investigation) the difference is obvious.

η_{delta} and η_{work} change markedly with power and partly also with pedalling frequency (25, 63) and therefore are not recommendable for practice. For the so-called muscular efficiency, the internal work including idling is also included in the calculation; it is approximately as large as η_{netto} , but without frequency dependence (60). The reproducibility of efficiency measurements on different days is very high under standardized conditions; changes of only 0.6% for η_{netto} may be proven (94).

Cycle Ergometry – Sprint

During a 30s maximal test (Wingate Test), the calculation yielded a value of 16% for η_{netto} at approximately 700 W (16, 77). The low values probably result from very high pedalling frequency (up to 170/min) with clearly decreasing η also for rapid muscle fibres (e.g. (72)), and not optimally coordinated movements because of maximal power and exhaustion.

Treadmill Ergometry

Exercise against gravity on a treadmill without ascent (85, 89) is per definition zero and thus also η (Fig. 5). With positive slope, η_{net} reaches maximally approximately 25%, the value for stair

climbing corresponds to it. The values are similar as for cycling, because only positive work is done. During a downward move, energy expenditure decreases below the consumption for walking and running in flat terrain; η reaches a minimum of -120% at a downward slope of 5 to 10% (Fig. 6). Obviously, active braking costs nearly no energy in spite of the formation of actin-myosin bridges.

The work against air and ground friction (called external work) at 0% slope consists of raising the center of mass (force x distance) and acceleration of the body ($1/2 \text{ mass} \times \text{velocity}^2$). It can be calculated from a movement analysis using light marks and measuring ground reaction forces. A small amount of internal work (movements of limbs relative to the center of mass) is added. During "natural" movements, energy is stored during each pace. During walking, each limb functions like a pendulum which loses little energy when swinging at its natural frequency. During running, elastic energy is stored especially during landing after the flight phase in muscles, tendons, ligaments and bones (32). η_{net} rises maximally up to approximately 40% during walking, during running even to more than 50% (32, 116).

During simulated cross country skiing with rollers on a treadmill, one obtains 15-20% for η_{gross} (20, 103).

Rowing Ergometry

The η_{net} of 19% is slightly lower than during cycle ergometry (114). It is, however, typical for this cyclic movement that energy is delivered only during the rowing stroke. The preceding phase adds no or negative work; kinetic energy is elastically stored in the reversal movements.

Swimming Ergometry

In contrast to aquatic animals, man can use only a low percentage of muscular work for propulsion (inadequate body form and -surface, partly not useful movements of limbs). Additionally, buoyancy vastly compensates gravity, thereby preventing the storage of potential energy in contrast to running.

Therefore η_{gross} (related to the work of propulsion) amounts to 3 to maximally 10% (43, 98, 99, 122). Fins improve it to 15% (43). Because of the high and even rising water resistance, energy need increases more than on land nonlinearly with velocity (43). Additionally it depends on friction (properties and area of skin and bathing clothes), surface resistance (height and form of the body) and wave formation.

In females, the work of propulsion is lowered by 30%/m² body surface: the body position in water is flatter compared to males because of more fat in the lower half of the body as well as shorter legs with less muscle tissue. An increase of leg muscle mass may be a drawback. Black men are rarely successful swimmers because their leg position in water is rather oblique resulting from high bone weight (43).

Efficiency in Sports – Sports Disciplines

General

According to Sih u. Stuhmiller (112), there seems to exist a general law that the metabolic cost per unit external force per

application, e.g. the metabolic cost for one step, is relatively constant. However, in the evaluated literature solely $\dot{V}O_2$ is often taken as a basis, which increases almost linearly with speed during submaximal exercise. But the exactly calculated energy expenditure increases steeper with power than $\dot{V}O_2$ if the RER is taken into account, since the carbohydrate combustion rises in dependence on power during short exercise tests (109). Additionally, the anaerobic metabolism may increase (14).

Since it is difficult to measure power in practice (except in cycling with force-transducers and revolution counters, e.g. (119)), the energy expenditure in dependence on velocity is an acceptable indicator of efficiency (Fig. 7) and allows comparisons between different disciplines. Air resistance becomes increasingly important at high speed.

Walking and Running

With low velocities, walking is more efficient than running. The cost for the movement of the legs reaches a minimum when the stride duration corresponds to the duration of the natural oscillation of the legs. This is proportional to the length of the legs. Measurement by Cavagna et al. (33) showed that in males the minimum was close to 4 km/h. At approximately 8 km/h, one starts to run spontaneously, because the elastic energy absorbed via stretching muscles and ligaments at the end of the flight phase facilitates take-off and thus increases η . The energetic costs are influenced by biomechanical parameters (i.a. natural frequency, weight of legs, lever length, elastic properties, footwear), the quality of coordination and the ground properties (105). The success of African runners is said to be due amongst other things to biomechanical advantages (68). Hypothetical higher efficiencies of long distance runners compared to sprinters (115) are probably an artefact, since the measurements were performed on a cycle ergometer with 60 rev/min. This frequency is close to the optimum of slow fibres, which are relatively more abundant in endurance athletes. Beneke u. Taylor (17) analysed the influence of the contraction velocity on η in 100m runners and calculated that the dominance of Usain Bolt is in part a consequence of his lower stride frequency compared to his competitors. The contraction frequency is therefore close to the optimum of η and of power. But perhaps the increased force at low frequencies is even more decisive by making longer strides possible. This might explain the discrepancy to cyclists. In leg-amputated athletes with prosthesis, the energy demand for running is higher (87).

Cycling, Ice-Skating

During cycling on plane smooth surfaces, the costs of energy are by far lower than during running at the same speed in spite of a lower efficiency, because the resistance to rolling is

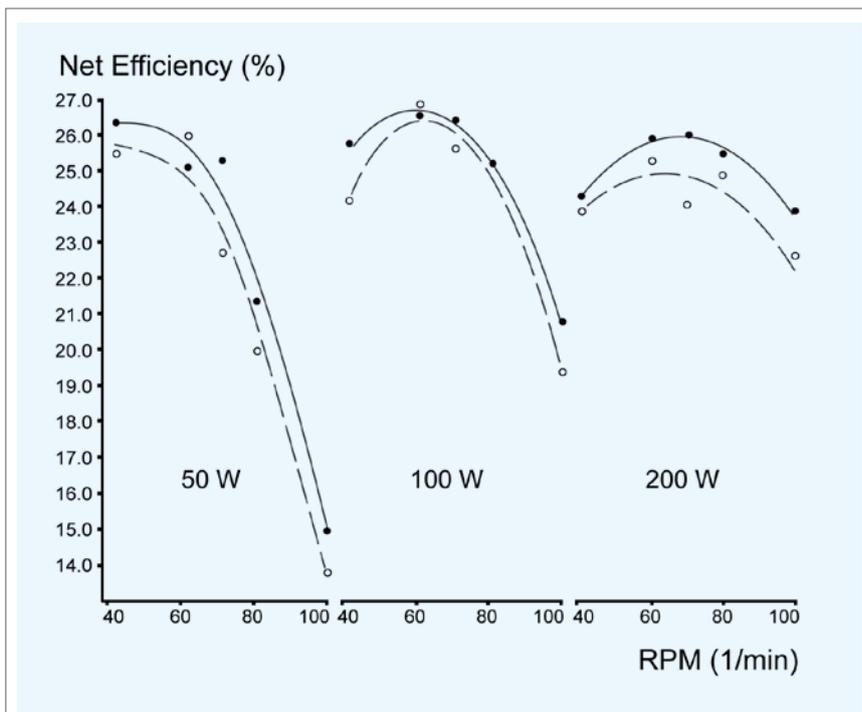


Figure 4

Net efficiency on the cycle ergometer in dependence on pedalling frequency and status of physical fitness (open circles untrained males, filled circles trained cyclists). Mean values and quadratic regression curves. Complete data in the original paper. From (25) with permission.

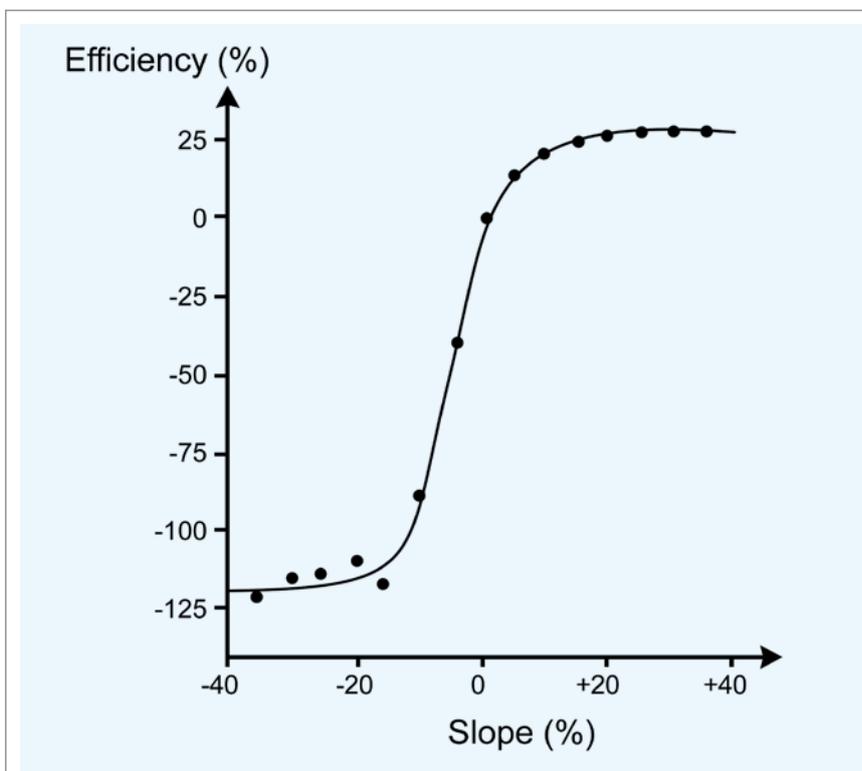


Figure 5

Efficiency during walking in dependence on the slope. The values are calculated by use of data in Figure 6. From (85) with permission.

low and essentially only the air friction has to be overcome (42). The latter increases significantly only at high speeds. The energetic advantage compared to running disappears with slopes of 13-16% (3). Ice-skating is somewhat costlier than cycling (Fig. 7). >

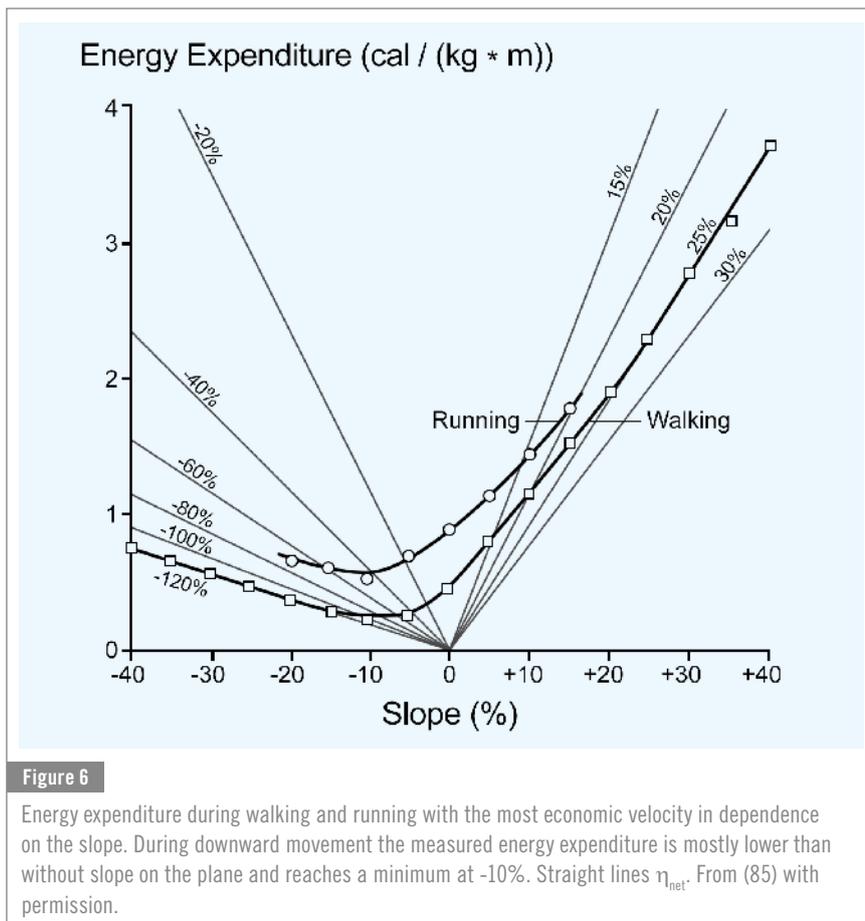


Figure 6

Energy expenditure during walking and running with the most economic velocity in dependence on the slope. During downward movement the measured energy expenditure is mostly lower than without slope on the plane and reaches a minimum at -10%. Straight lines η_{net} . From (85) with permission.

With high power, the pedalling frequency does not play any important role for η . Competitive cyclists therefore prefer high frequencies without disadvantage, because these frequencies need less muscle force with a smaller inhibition of blood flow (e.g. 90/min on long distances (82)). High frequencies are advantageous with brief intense load as well, since the power maximum of muscle fibres is at higher frequencies than the maximum of efficiency (61, 72).

In comparison to tests on ergometers, mechanical factors like cycle construction, pulling forces at the pedals and shifting of weight are not of large importance for efficiency (31).

Cross-Country Skiing

The graph for cross-country skiing is not included in Fig. 7; the position would be between ice skating and running (43). For cross-country skiers in flat territory, Niinimaa et al. (92) calculated a net efficiency of 21%, but the anaerobic metabolism was not regarded in spite of the high intensity (85% $\dot{V}O_2$ max). The cost of energy decreases in the following order: diagonal use of poles – double use of poles – skating technique (personal communication, di Prampero 2016).

Rowing

Motor activity is complex during rowing, since a majority of the muscles is used in different manners and boat, oars and man move in different directions with variable speeds. The situation is simplified on rowing ergometers, because elastic energy is stored only at the reversal points of the rowing movement. The boat, however, is a moving system with the rower as center of mass; this system stores movement energy which is dissipated by water friction (113). For propulsion on the water, η_{drag} , the ratio between driving energy and energy expenditure, is decisive; the value is 19% in a rowing shell

and 17% in a kayak (98). Since air friction is not considered, the true value is higher (detailed analysis in (43)). The utilized energy increases with increasing speed (smaller oscillations of speed and higher proportion of drive phases compared to preceding phases).

Swimming

The energy cost is dependent on the swimming style: crawl<backstroke<breaststroke<butterfly. Up to 400m, the anaerobic energy delivery is important independent of the swim style and training status (122).

Swimming technique has a large influence on efficiency. Elite swimmers need 40% less energy than college swimmers (η_{gross} 4-6%), these about 30% less than non-athletes. Remarkable, among other things, is a flatter position in the water of high-performance athletes. A detailed review dealing with the efficiency of different water sports was published by Pendergast et al. (99).

Other sport disciplines

During rhythmical movements with rapid changes between shortening and stretching (hopping, probably dancing), the efficiency increases substantially due to utilisation of negative work (34, 104). This may play a role for jumps and throws as well. Without this effect, the efficiency can drop to very low values (e.g. 1-2% in arching (21)).

Trainability and Fatigue

Essential increases are possible by improvement of coordination when performing repeated movements without high force and with moderate metabolism. Optimization of movements additionally reduces the energy need by the reduction of superfluous accompanying movements.

The more complex a movement, the larger the effect of repetition (example swimming). For runners, additional plyometric training is useful, probably because especially the use of elastic energy is improved (86). A high proportion of passive tissues (fat, bones) especially in the moved limbs increases the energy need, the frequent loss of body mass during long distance training reduces it.

When tiring, the coordination deteriorates (58); additionally there are disturbances of intramuscular homeostasis/metabolic stability visible as increases of O_2 -consumption and lactate concentration at constant power. As rapid fibres fatigue first, the optimum of η is shifted to lowered motion frequencies (1).

For simple well-learned movements (walking, running, bicycling), the training influence depends on intensity. The maxLass is transgressed earlier in untrained than trained subjects, therefore the use of rapid muscle fibres and thus anaerobic metabolism increase continuously. The necessary hyperventilation, as well as the use of supporting muscles and the increase of body temperature, cause a rise of energy need at lower work rates in untrained than trained subjects. After 4 weeks of training in previously inactive runners, a slight decrease of blood lactate concentration and energy expenditure (J/(kg*m)) was observed which then remained constant (12).

No training effect on η_{gross} and η_{net} is found below the maxLass (Fig. 3 and 4). This was also observed in a larger investigation (69 males, (91)). But in spite of such results, the trainability of efficiency is discussed again and again. For this the energy expenditure during an already well-mastered movement form should decrease. The cycle ergometer is best suited for comparison, because coordinative improvements are scarcely observed. However, comparisons have to be standardized, applying equal power and equal pedalling frequency. In older investigations (review in (25)), no or only small differences were found as long as anaerobic energy supply with lactate formation and acidosis did not play an increasing role. In more recent investigations with contrasting results, either the dependency on pedal rate was not considered (e.g. (26, 67)) or only $\dot{V}O_2$ was measured. An improved ATP-yield in the mitochondria or a reduced ATP-consumption by actin-myosin-ATPase has been discussed (reviewed e.g. in (6)). While for the latter a prolonged duration of actin-myosin-bridging is assumed, for the former an improved mitochondrial function might be conceivable (e.g. reduced leakage of H^+ across the matrix membrane).

This hypothesis is based on results of in vitro measurements. According to Divakaruni u. Brand (44), such leaks in the intact muscle are probably unimportant in vivo. Also, according to Mogensen et al. (90), Brooks (27) and Layec et al. (74), there is no proof for training-induced improvements of mitochondrial function. However, the small reduction of efficiency by fat-rich nutrition observed in untrained subjects has not been detected in endurance-trained athletes, possibly because of lower concentration of decoupling proteins (45). This is of importance for cyclists who metabolize especially fat during long-distance races (81).

Age and Sex

During childhood (43) and in advanced age (88), as well as during illness with reduced physical activity (15), a change of coordination is an important and influenceable factor; in this case resistance training is often supportive. During running, boys reach the low energy expenditure of adults only at the age of 15-16 years; during coordinatively simple, very rapid pedalling (Wingate Test), however, the efficiency is at least as high in children above 10 years as in adults (13). In contrast to the usual deterioration during aging (96), the energetic cost of running remains almost unchanged in athletes who train regularly (10). Recently, the suggestion was controversially discussed that η increases in aging subjects; the cause is thought to be an increasing proportion of slow muscle fibres with allegedly better η (95, 118). Possibly this interpretation results from mistakes in the experimental design (rapidly increasing work load in spite of steps of sufficient duration). According to Layec et al. (75), η decreases at advanced age because of massively increased ion pump activity.

A clear sex difference for η apparently does not exist (9, 52, 121). According to Aura and Komi (5), η for positive exercise is slightly higher in males, for negative exercise, however, in females; thus the values for the whole distension-shortening cyclus approach each other (38,1 and 35,5%).

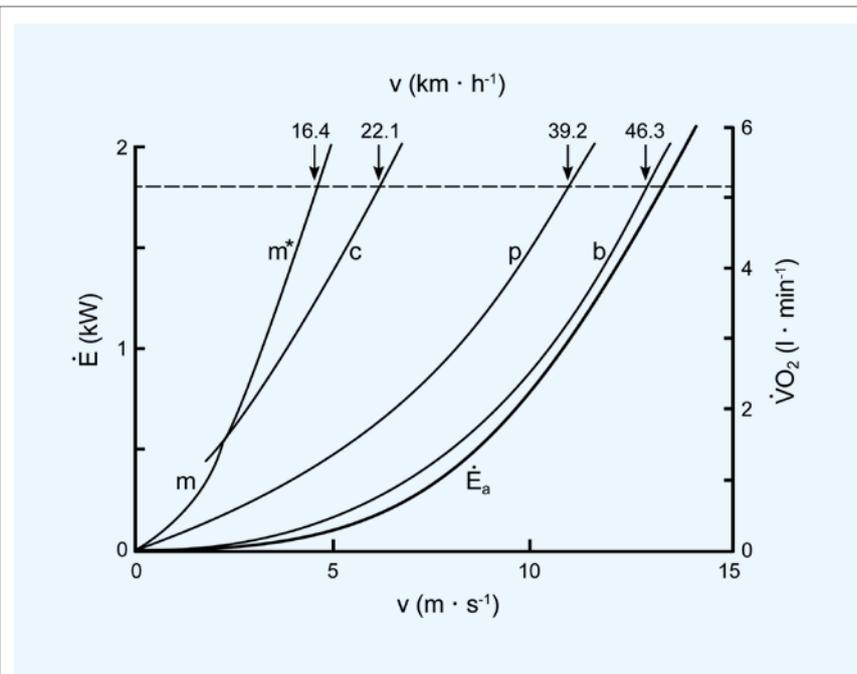


Figure 7

Net energy expenditure during walking (m), race walking (m*), running (c), ice skating (p) and cycling (b) of a hypothetical athlete (70 kg, 175 cm) in dependence on velocity v . \dot{E}_a energy expenditure against air resistance, --- $\dot{V}O_{2,max}$. From (43) with permission.

Environment

The ambient temperature has an influence because the energy needed for cooling or heating can be substantial. In a very cold environment, efficiency decreases because of dehydration of the muscles (110). Uncoupling proteins in muscle mitochondria have no influence on whole body energy turnover (47). According to He et al. (61), the efficiency increases with temperature (12-20°) in isolated human muscle fibres because the mechanical power increases more than ATP consumption. Bell u. Ferguson (11) also found a slight increase of η_{net} in vivo in young subjects, but not in elderly women when the muscle temperature was raised by 3°. The cadence with the highest efficiency (about 60-70/min in Fig. 4) increases with heating of the muscle (49).

At high altitudes, performance decreases for many sports. Records can be achieved only if the decreased air resistance plays a considerable role (throws, jumps, short run distances, but also bicycle distances between 1000 m and 50 km (42, 69)). In acute hypoxia (altitude chamber), starting from 3000 m of simulated altitude, η_{net} decreases significantly during bicycle ergometry (56). However, after acclimatization, an improved efficiency during ergometry has been claimed several times because $\dot{V}O_2$ was decreased in comparison to the lowland (e.g. (57)). Others, however, found no change in $\dot{V}O_2$ (78,83). The cause for the discrepancies is presumably an oxygen-saving decrease of fat oxidation in favor of carbohydrates by decreased β -receptor activation after some weeks at high altitudes, which reduces the oxygen need for the ATP buildup (101). That seems to be contradicted by the fact that Epo can increase fat metabolism (2, 30); however, this was examined only in normoxia and is presumably exceeded at altitude by changes of the vegetative innervation. Green et al. (59) calculated an increase of efficiency after return from 6194m of altitude. But their experimental subjects hyperventilated at least in a part of >

the performance tests, so that the raised RQ was no correct measure of the caloric equivalent; also nothing is stated about the cadence.

In addition, the assumed superior efficiency in inhabitants living at high altitudes is not ensured (reviewed in (22, 29, 35)). Lower $\dot{V}O_2$ of Tibetans could be related to lower respiratory work following from increased NO formation (48), the physique, as well as to reduced fat metabolism. If η_{net} is calculated from data (55) of Tibetans at 4700m of altitude (20-27%), the value is better than in acclimatized Chinese, but almost identical with measurements in the lowland. Hochachka et al. (66) described an improved efficiency (bicycle ergometer) in Andean natives whom they compared at sea level to lowland inhabitants, and speculated about a harmonization of the metabolism ("Fine tuning of ATP production").

An overview on in part positive and in part negative protein changes in hypoxia was published by Flueck (50). The efficiency measurements by Hochachka et al. (66), however, are probably faulty (24, 29). The net efficiency in their lowland inhabitants reaches only 10% in some cases. In Kenyans, $\dot{V}O_2$ is relatively low at both high and low altitudes, which might be related to specific features of their physique (low body mass index, long thin legs, good elastic energy storage (73, 104)). Brutsaert et al. (29), according to their own investigations in Andean inhabitants and an examination of the literature about Himalayan inhabitants, come to the conclusion that there are no efficiency improvements in these groups. To sum up, it can be stated that neither acute nor chronic hypoxia has a positive effect on η .

Efficiency and Nitrogen Monoxide

The ingestion of nitrates, e.g., from beetroot juice, often reduces $\dot{V}O_2$ for submaximal performances up to 5%, although not under all conditions (reviewed in (6, 37, 100)). Nitrates are a source of nitrogen monoxide which, among other effects, dilates blood vessels. The reduction of $\dot{V}O_2$ is interpreted as an improvement of efficiency. The same mechanisms as during training are discussed: reduced ATP consumption by lengthening of the elementary cycle of the contraction and decreased energy losses during ATP synthesis in the mitochondria. A decrease of cardiac and respiratory work resulting from NO-induced enlarged diameters of blood vessels and bronchi or a lowering of the body temperature by increased skin blood flow are also conceivable.

Unfortunately, the RQ was often not communicated or the published values are not correct. In the investigations with RQ measurements, approximately one-third of the effect might be attributed to an increased carbohydrate utilization (23). An increase of η_{net} would then amount only to about 1% absolute. The effect seems to be strongest in type II muscle fibres under hypoxic conditions, it is only rarely observed in trained individuals (4, 70). Altogether, the effect remains disputed (18, 19). Some authors (e.g. (100)) also point to the carcinogenic risk of excessive nitrate supply.

Efficiency and Doping

In this regard, there appear to be no systematic investigations. In a study on the effect of Epo in leisure-time sportsmen, the energy expenditure at 100 watts tended to increase after 13 weeks of Epo administration (84). On the contrary, Coyle (39) reported a small improvement in η_{gross} (from 21.2 to 23.1%; constant $\dot{V}O_{2,max}$) in an outstanding racing cyclist over 8 years. Meanwhile it is known that he had doped with cortisone, androstenedione, and Epo. However, the improvements were doubted (107).

Conclusions

The intramuscular net efficiency is about 30%. In case of whole body consideration, it is dependent on frequency for simple rotation movements and reaches a maximum of about 26%. Elastic energy storage often plays a considerable role, values nearly twice as high are possible during running. Moreover, the efficiency for more complicated movements can be improved substantially by practice through optimization of coordinated movements, which saves energy. On the other hand, mitochondrial energy delivery processes do not seem to be trainable.

An improvement of efficiency by stays at high altitude is not proven, apparently a relative increase of the carbohydrate turnover-rate reduces the oxygen consumption. Improvement of the efficiency by nitrate supply has also not been proven unambiguously.

Measurements of efficiency have a practical importance if the energy expenditure involved with muscle work and sports is to be examined and possibly reduced. However, many statements with regard to efficiency are not as accurate as they could be or are even doubtful because not the energy expenditure, but only $\dot{V}O_2$ was determined or because comparisons were made with different movement cadences. It is astonishing that $\dot{V}CO_2$ is not considered on a regular basis, although practically all spirometry-devices carry out the measurement. ■

Conflict of Interest

The authors have no conflict of interest.

References

- (1) ANNAHEIM S, BOUTELLIER U, KOHLER G. The energetically optimal cadence decreases after prolonged cycling exercise. *Eur J Appl Physiol.* 2010; 109: 1103-1110. doi:10.1007/s00421-010-1431-9
- (2) ANNAHEIM S, JACOB M, KRAFFT A, BREYMANN C, REHM M, BOUTELLIER U. RhEPO improves time to exhaustion by non-hematopoietic factors in humans. *Eur J Appl Physiol.* 2016; 116: 623-633. doi:10.1007/s00421-015-3322-6
- (3) ARDIGO LP, SAIBENE F, MINETTI AE. The optimal locomotion on gradients: walking, running or cycling? *Eur J Appl Physiol.* 2003; 90: 365-371. doi:10.1007/s00421-003-0882-7
- (4) ARNOLD JT, OLIVER SJ, LEWIS-JONES TM, WYLIE LJ, MACDONALD JH. Beetroot juice does not enhance altitude running performance in well-trained athletes. *Appl Physiol Nutr Metab.* 2015; 40: 590-595. doi:10.1139/apnm-2014-0470
- (5) AURA O, KOMI PV. The mechanical efficiency of locomotion in men and women with special emphasis on stretch-shortening cycle exercises. *Eur J Appl Physiol Occup Physiol.* 1986; 55: 37-43. doi:10.1007/BF00422890
- (6) BAILEY SJ, VANHATALO A, WINYARD PG, JONES AM. The nitrate-nitrite-nitric oxide pathway: Its role in human exercise physiology. *Eur J Sport Sci.* 2012; 12: 309-320. doi:10.1080/17461391.2011.635705
- (7) BARCLAY CJ. Energetics of contraction. *Compr Physiol.* 2015; 5: 961-995. doi:10.1002/cphy.c140038
- (8) BARCLAY CJ, WEBER CL. Slow skeletal muscles of the mouse have greater initial efficiency than fast muscles but the same net efficiency. *J Physiol.* 2004; 559: 519-533. doi:10.1113/jphysiol.2004.069096
- (9) BEAVEN CM, WILLIS SJ, COOK CJ, HOLMBERG HC. Physiological comparison of concentric and eccentric arm cycling in males and females. *PLoS ONE.* 2014; 9: e112079. doi:10.1371/journal.pone.0112079
- (10) BECK ON, KIPP S, ROBY JM, GRABOWSKI AM, KRAM R, ORTEGA JD. Older runners retain youthful running economy despite biomechanical differences. *Med Sci Sports Exerc.* 2016; 48: 697-704. doi:10.1249/MSS.0000000000000820
- (11) BELL MP, FERGUSON RA. Interaction between muscle temperature and contraction velocity affects mechanical efficiency during moderate-intensity cycling exercise in young and older women. *J Appl Physiol* (1985) 107: 763-769, 2009.
- (12) BENEKE R, HÜTLER M. The effect of training on running economy and performance in recreational athletes. *Med Sci Sports Exerc.* 2005; 37: 1794-1799. doi:10.1249/01.mss.0000176399.67121.02
- (13) BENEKE R, HÜTLER M, LEITHÄUSER RM. Anaerobic performance and metabolism in boys and male adolescents. *Eur J Appl Physiol.* 2007; 101: 671-677. doi:10.1007/s00421-007-0546-0
- (14) BENEKE R, LEITHÄUSER RM. Energy cost of running related to running intensity and peak oxygen uptake. *Dtsch Z Sportmed.* 2017; 68: 196-202.
- (15) BENEKE R, MEYER K. Walking performance and economy in chronic heart failure patients pre and post exercise training. *Eur J Appl Physiol.* 1997; 75: 246-251. doi:10.1007/s004210050155
- (16) BENEKE R, POLLMANN C, BLEIF I, LEITHÄUSER RM, HÜTLER M. How anaerobic is the Wingate Anaerobic Test for humans? *Eur J Appl Physiol.* 2002; 87: 388-392. doi:10.1007/s00421-002-0622-4
- (17) BENEKE R, TAYLOR MJ. What gives Bolt the edge-A.V. Hill knew it already! *J Biomech.* 2010; 43: 2241-2243. doi:10.1016/j.jbiomech.2010.04.011
- (18) BESCÓS R, SUREDA A, TUR JA, PONS A. The effect of nitric-oxide-related supplements on human performance. *Sports Med.* 2012; 42: 99-117. doi:10.2165/11596860-000000000-00000
- (19) BETTERIDGE S, BESCOS R, MARTORELL M, PONS A, GARNHAM AP, STATHIS CC, AND MCCONNELL GK. No effect of acute beetroot juice ingestion on oxygen consumption, glucose kinetics, or skeletal muscle metabolism during submaximal exercise in males. *J Appl Physiol.* 2016; 120: 391-398. doi:10.1152/jappphysiol.00658.2015
- (20) BOLGER CM, SANDBAKK O, ETTEMA G, FEDEROLF P. How hinge positioning in cross-country ski bindings affect exercise efficiency, cycle characteristics and muscle coordination during submaximal roller skiing. *PLoS ONE.* 2016; 11: e0153078. doi:10.1371/journal.pone.0153078
- (21) BÖNEKER C, MAASSEN N, BÖNING D. Energieumsatz und Wirkungsgrad beim Bogenschiessen (Energy turnover and efficiency of archers). *Dtsch Z Sportmed.* 1983; 2: 44-48.
- (22) BÖNING D. Altitude and hypoxia training - effects on performance capacity and physiological functions at sea level. *Med Sport.* 2002; 6: E7-E17.
- (23) BÖNING D. „Biodoping“ mit Roter Beete? Spekulationen über einen besseren Wirkungsgrad des Muskelstoffwechsels (Biodoping with beetroot? Speculations about improved efficiency). *Dtsch Z Sportmed.* 2012; 63: 337-339. doi:10.5960/dzsm.2012.048
- (24) BÖNING D. Efficiency after altitude acclimatization. *J Appl Physiol.* 2001; 91: 1014-1015.
- (25) BÖNING D, GÖNEN Y, MAASSEN N. Relationship between work load, pedal frequency, and physical fitness. *Int J Sports Med.* 1984; 05: 92-97. doi:10.1055/s-2008-1025887
- (26) BÖNING D, PRIES AR. Pitfalls of efficiency determination in cycling ergometry. *J Appl Physiol.* 2013; 115: 1862. doi:10.1152/jappphysiol.01021.2013
- (27) BROOKS GA. Bioenergetics of exercising humans. *Compr Physiol.* 2012; 2: 537-562. doi:10.1002/cphy.c110007
- (28) BRUNELLO E, RECONDITI M, ELANGOVAN R, LINARI M, SUN YB, NARAYANAN T, PANINE P, PIAZZESI G, IRVING M, LOMBARDI V. Skeletal muscle resists stretch by rapid binding of the second motor domain of myosin to actin. *Proc Natl Acad Sci USA.* 2007; 104: 20114-20119. doi:10.1073/pnas.0707626104
- (29) BRUTSAERT TD, HAAS JD, SPIELVOGEL H. Absence of work efficiency differences during cycle ergometry exercise in Bolivian Aymara. *High Alt Med Biol.* 2004; 5: 41-59. doi:10.1089/152702904322963681
- (30) CAILLAUD C, CONNES P, BEN SAAD H, MERCIER J. Erythropoietin enhances whole body lipid oxidation during prolonged exercise in humans. *J Physiol Biochem.* 2015; 71: 9-16. doi:10.1007/s13105-014-0374-8
- (31) CASTRONOVO AM, CONFORTO S, SCHMID M, BIBBO D, D'ALESSIO T. How to assess performance in cycling: the multivariate nature of influencing factors and related indicators. *Front Physiol* 4 Art. 116: 1-10, 2013.
- (32) CAVAGNA GA, KANEKO M. Mechanical work and efficiency in level walking and running. *J Physiol.* 1977; 268: 467-481. doi:10.1113/jphysiol.1977.sp011866
- (33) CAVAGNA GA, THYS H, ZAMBONI A. The sources of external work in level walking and running. *J Physiol.* 1976; 262: 639-657. doi:10.1113/jphysiol.1976.sp011613
- (34) CAVANAGH PR, KRAM R. Mechanical and muscular factors affecting the efficiency of human movement. *Med Sci Sports Exerc.* 1985; 17: 326-331. doi:10.1249/00005768-198506000-00005
- (35) CERRETELLI P, GELFI C. Energy metabolism in hypoxia: reinterpreting some features of muscle physiology on molecular grounds. *Eur J Appl Physiol.* 2011; 111: 421-432. doi:10.1007/s00421-010-1399-5
- (36) CHAVAREN J, CALBET JAL. Cycling efficiency and pedalling frequency in road cyclists. *Eur J Appl Physiol.* 1999; 80: 555-563. doi:10.1007/s004210050634
- (37) CLEMENTS WT, LEE SR, BLOOMER RJ. Nitrate ingestion: a review of the health and physical performance effects. *Nutrients.* 2014; 6: 5224-5264. doi:10.3390/nu6115224
- (38) COX PJ, KIRK T, ASHMORE T, WILLERTON K, EVANS R, SMITH A, MURRAY AJ, STUBBS B, WEST J, MCLURE SW, KING MT, DODD MS, HOLLOWAY C, NEUBAUER S, DRAWER S, VEECH RL, GRIFFIN JL, AND CLARKE K. Nutritional ketosis alters fuel preference and thereby endurance performance in athletes. *Cell Metab.* 2016; 24: 256-268. doi:10.1016/j.cmet.2016.07.010
- (39) COYLE EF. Improved muscular efficiency displayed as Tour de France champion matures. *J Appl Physiol.* 2005; 98: 2191-2196. doi:10.1152/jappphysiol.00216.2005
- (40) COYLE EF, SIDOSSIS LS, HOROWITZ JF, BELTZ JD. Cycling efficiency is related to the percentage of type I muscle fibers. *Med Sci Sports Exerc.* 1992; 24: 782-788. doi:10.1249/00005768-199207000-00008
- (41) DE MARÉES H. Sportphysiologie. Hellenthal: Sportverlag Strauss, 2003, p. 800.

- (42) **DI PRAMPERO PE.** Cycling on Earth, in space, on the Moon. *Eur J Appl Physiol.* 2000; 82: 345-360. doi:10.1007/s004210000220
- (43) **DI PRAMPERO PE.** The energy cost of human locomotion on land and in water. *Int J Sports Med.* 1986; 07: 55-72. doi:10.1055/s-2008-1025736
- (44) **DIVAKARUNI AS, BRAND MD.** The regulation and physiology of mitochondrial proton leak. *Physiology (Bethesda).* 2011; 26: 192-205. doi:10.1152/physiol.00046.2010
- (45) **EDWARDS LM, HOLLOWAY CJ, MURRAY AJ, KNIGHT NS, CARTER EE, KEMP GJ, THOMPSON CH, TYLER DJ, NEUBAUER S, ROBBINS PA, CLARKE K.** Endurance exercise training blunts the deleterious effect of high-fat feeding on whole body efficiency. *Am J Physiol Regul Integr Comp Physiol.* 2011; 301: R320-R326. doi:10.1152/ajpregu.00850.2010
- (46) **EDWARDS LM, MURRAY AJ, HOLLOWAY CJ, CARTER EE, KEMP GJ, CODREANU I, BROOKER H, TYLER DJ, ROBBINS PA, AND CLARKE K.** Short-term consumption of a high-fat diet impairs whole-body efficiency and cognitive function in sedentary men. *FASEB J.* 2011; 25: 1088-1096. doi:10.1096/fj.10-171983
- (47) **ERLANSO-ALBERTSSON C.** The role of uncoupling proteins in the regulation of metabolism. *Acta Physiol Scand.* 2003; 178: 405-412. doi:10.1046/j.1365-201X.2003.01159.x
- (48) **ERZURUM SC, GHOSH S, JANOCHA AJ, XU W, BAUER S, BRYAN NS, TEJERO J, HEMANN C, HILLE R, STUEHR DJ, FEELISCH M, AND BEALL C.** Higher blood flow and circulating NO products offset high-altitude hypoxia among Tibetans. *Proc Natl Acad Sci USA.* 2007; 104: 17593-17598. doi:10.1073/pnas.0707462104
- (49) **FERGUSON RA, BALL D, SARGEANT AJ.** Effect of muscle temperature on rate of oxygen uptake during exercise in humans at different contraction frequencies. *J Exp Biol.* 2002; 205: 981-987.
- (50) **FLUECK M.** Plasticity of the muscle proteome to exercise at altitude. *High Alt Med Biol.* 2009; 10: 183-193. doi:10.1089/ham.2008.1104
- (51) **FRAYN KN.** Calculation of substrate oxidation rates in vivo from gaseous exchange. *J Appl Physiol.* 1983; 55: 628-634.
- (52) **FREYSCHUSS U.** Comparison between arm and leg exercise in women and men. *Scand J Clin Lab Invest.* 1975; 35: 795-800. doi:10.1080/00365517509095812
- (53) **GAESSER GA, BROOKS GA.** Metabolic bases of excess post-exercise oxygen consumption: a review. *Med Sci Sports Exerc.* 1984; 16: 29-43. doi:10.1249/00005768-198401000-00008
- (54) **GAESSER GA, BROOKS GA.** Muscular efficiency during steady-rate exercise: effects of speed and work rate. *J Appl Physiol.* 1975; 38: 1132-1139.
- (55) **GE RL, CHEN QH, WANG LH, GEN D, YANG P, KUBO K, FUJIMOTO K, MATSUZAWA Y, YOSHIMURA K, TAKEOKA M, AND TOBAYASHI T.** Higher exercise performance and lower $\dot{V}O_{2max}$ in Tibetan than Han residents at 4,700 m altitude. *J Appl Physiol.* 1994; 77: 684-691.
- (56) **GOLEC L, DEBINSKI W.** Work efficiency and the coefficient of recovery effectiveness in hypoxia. *Biol Sport.* 1993; 10: 115-118.
- (57) **GORE CJ, CLARK SA, SAUNDERS PU.** Nonhematological mechanisms of improved sea-level performance after hypoxic exposure. *Med Sci Sports Exerc.* 2007; 39: 1600-1609. doi:10.1249/mss.0b013e3180de49d3
- (58) **GRASSI B, ROSSITER HB, ZOLADZ JA.** Skeletal muscle fatigue and decreased efficiency: two sides of the same coin? *Exerc Sport Sci Rev.* 2015; 43: 75-83. doi:10.1249/JES.00000000000000043
- (59) **GREEN HJ, ROY B, GRANT S, HUGHSON R, BURNETT M, OTTO C, PIPE A, MCKENZIE D, AND JOHNSON M.** Increases in submaximal cycling efficiency mediated by altitude acclimatization. *J Appl Physiol.* 2000; 89: 1189-1197.
- (60) **HANSEN EA, SJOGAARD G.** Relationship between efficiency and pedal rate in cycling: significance of internal power and muscle fiber type composition. *Scand J Med Sci Sports.* 2007; 17: 408-414.
- (61) **HE ZH, BOTTINELLI R, PELLEGRINO MA, FERENCZI MA, REGGIANI C.** ATP consumption and efficiency of human single muscle fibers with different myosin isoform composition. *Biophys J.* 2000; 79: 945-961. doi:10.1016/S0006-3495(00)76349-1
- (62) **HERZOG W, POWERS K, JOHNSTON K, DUVALL M.** A new paradigm for muscle contraction. *Front Phys.* 2015; 6: 174. doi:10.3389/fphys.2015.00174
- (63) **HESSER CM, LINNARSSON D, BJURSTEDT H.** Cardiorespiratory and metabolic responses to positive, negative and minimum-load dynamic leg exercise. *Respir Physiol.* 1977; 30: 51-67. doi:10.1016/0034-5687(77)90021-4
- (64) **HILL AV.** The efficiency of mechanical power development during muscular shortening and its relation to load. *Proc R Soc Lond B Biol Sci.* 1964; 159: 319-324. doi:10.1098/rspb.1964.0005
- (65) **HILL AV.** Production and absorption of work by muscle. *Science.* 1960; 131: 897-903. doi:10.1126/science.131.3404.897
- (66) **HOCHACHKA PW, STANLEY C, MATHESON GO, MCKENZIE DC, ALLEN PS, PARKHOUSE WS.** Metabolic and work efficiencies during exercise in Andean natives. *J Appl Physiol.* 1991; 70: 1720-1730.
- (67) **HOPKER JG, COLEMAN DA, GREGSON HC, JOBSON SA, VON DER HT, WILES J, PASSFIELD L.** The influence of training status, age, and muscle fibre type on cycling efficiency and endurance performance. *J Appl Physiol.* 2013; 115: 723-729. doi:10.1152/jappphysiol.00361.2013
- (68) **HUNTER GR, MCCARTHY JP, BAMMAN MM, LARSON-MEYER DE, FISHER G, NEWCOMER BR.** Exercise economy in African American and European American women. *Eur J Appl Physiol.* 2011; 111: 1863-1869. doi:10.1007/s00421-010-1816-9
- (69) **JOKL E, JOKL P, SEATON DC.** Effect of altitude upon 1968 Olympic Games running performance. *Int J Biometr.* 1969; 13: 309-311. doi:10.1007/BF01553038
- (70) **JONES AM, FERGUSON SK, BAILEY SJ, VANHATALO A, POOLE DC.** Fiber type-specific effects of dietary nitrate. *Exerc Sport Sci Rev.* 2016; 44: 53-60. doi:10.1249/JES.0000000000000074
- (71) **KEHLER AL, HAJKOVA E, HOLMBERG HC, KRAM R.** Forces and mechanical energy fluctuations during diagonal stride roller skiing; running on wheels? *J Exp Biol.* 2014; 217: 3779-3785. doi:10.1242/jeb.107714
- (72) **KOHLER G, BOUTELLIER U.** The generalized force-velocity relationship explains why the preferred pedalling rate of cyclists exceeds the most efficient one. *Eur J Appl Physiol.* 2005; 94: 188-195. doi:10.1007/s00421-004-1283-2
- (73) **LARSEN HB, SHEEL AW.** The Kenyan runners. *Scand J Med Sci Sports.* 2015; 25: 110-118. doi:10.1111/sms.12573
- (74) **LAYEC G, BRINGARD A, LE FUR Y, MICALLEF JP, VILMEN C, PERREY S, COZZONE PJ, AND BENDAHAN D.** Mitochondrial coupling and contractile efficiency in humans with high and low $\dot{V}O_2$ peaks. *Med Sci Sports Exerc.* 2016; 48: 811-821. doi:10.1249/MSS.0000000000000858
- (75) **LAYEC G, HART CR, TRINITY JD, LE FUR Y, JEONG EK, RICHARDSON RS.** Skeletal muscle work efficiency with age: the role of non-contractile processes. *Clin Sci (Lond).* 2015; 128: 213-223. doi:10.1042/CS20140274
- (76) **LEIRDAL S, ETTEMA G.** The relationship between cadence, pedalling technique and gross efficiency in cycling. *Eur J Appl Physiol.* 2011; 111: 2885-2893. doi:10.1007/s00421-011-1914-3
- (77) **LEITHÄUSER RM, BÖNING D, HÜTLER M, BENEKE R.** Enhancement on Wingate anaerobic test performance with hyperventilation. *Int J Sports Physiol Perform.* 2016; 11: 627-634. doi:10.1123/ijspp.2015-0001
- (78) **LEVETT DZ, FERNANDEZ BO, RILEY HL, MARTIN DS, MITCHELL K, LECKSTROM CA, INCE C, WHIPP BJ, MYTHEN MG, MONTGOMERY HE, GROCOTT MP, FEELISCH M; CAUDWELL EXTREME EVEREST RESEARCH GROUP.** The role of nitrogen oxides in human adaptation to hypoxia. *Sci Rep.* 2011; 1: 109. doi:10.1038/srep00109
- (79) **LICHTWARK GA, BARCLAY CJ.** A compliant tendon increases fatigue resistance and net efficiency during fatiguing cyclic contractions of mouse soleus muscle. *Acta Physiol (Oxf).* 2012; 204: 533-543. doi:10.1111/j.1748-1716.2011.02361.x
- (80) **LOISELLE DS, TRAN K, CRAMPIN EJ, CURTIN NA.** Why has reversal of the actin-myosin cross-bridge cycle not been observed experimentally? *J Appl Physiol.* 2010; 108: 1465-1471. doi:10.1152/jappphysiol.01198.2009
- (81) **LUCIA A, HOYOS J, CHICHARRO JL.** Physiology of professional road cycling. *Sports Med.* 2001; 31: 325-337. doi:10.2165/00007256-200131050-00004
- (82) **LUCIA A, HOYOS J, CHICHARRO JL.** Preferred pedalling cadence in professional cycling. *Med Sci Sports Exerc.* 2001; 33: 1361-1366. doi:10.1097/00005768-200108000-00018

- (83) **LUNDBY C, CALBET JA, SANDER M, VAN HG, MAZZEO RS, STRAY-GUNDERSEN J, STAGER JM, CHAPMAN RF, SALTIN B, LEVINE BD.** Exercise economy does not change after acclimatization to moderate to very high altitude. *Scand J Med Sci Sports.* 2007; 17: 281-291.
- (84) **LUNDBY C, ROBACH P, BOUSHEL R, THOMSEN JJ, RASMUSSEN P, KOSKOLOU M, AND CALBET JA.** Does recombinant human Epo increase exercise capacity by means other than augmenting oxygen transport? *J Appl Physiol.* 2008; 105: 581-587. doi:10.1152/jappphysiol.90484.2008
- (85) **MARGARIA R.** Biomechanics and energetics of muscular exercise. Oxford: Clarendon Press, 1976.
- (86) **MCBRIDE JM, SNYDER JG.** Mechanical efficiency and force-time curve variation during repetitive jumping in trained and untrained jumpers. *Eur J Appl Physiol.* 2012; 112: 3469-3477. doi:10.1007/s00421-012-2327-7
- (87) **MENGLKOCH LJ, KAHLE JT, HIGHSMITH MJ.** Energy costs and performance of transtibial amputees and non-amputees during walking and running. *Int J Sports Med.* 2014; 35: 1223-1228. doi:10.1055/s-0034-1382056
- (88) **MIAN OS, THOM JM, ARDIGO LP, NARICI MV, MINETTI AE.** Metabolic cost, mechanical work, and efficiency during walking in young and older men. *Acta Physiol (Oxf).* 2006; 186: 127-139. doi:10.1111/j.1748-1716.2006.01522.x
- (89) **MINETTI AE, MOIA C, ROI GS, SUSTA D, FERRETTI G.** Energy cost of walking and running at extreme uphill and downhill slopes. *J Appl Physiol.* 2002; 93: 1039-1046. doi:10.1152/jappphysiol.01177.2001
- (90) **MOGENSEN M, BAGGER M, PEDERSEN PK, FERNSTROM M, SAHLIN K.** Cycling efficiency in humans is related to low UCP3 content and to type I fibres but not to mitochondrial efficiency. *J Physiol.* 2006; 571: 669-681. doi:10.1113/jphysiol.2005.101691
- (91) **MOSELEY L, ACHTEN J, MARTIN JC, JEUKENDRUP AE.** No differences in cycling efficiency between world-class and recreational cyclists. *Int J Sports Med.* 2004; 25: 374-379. doi:10.1055/s-2004-815848
- (92) **NIINIMAA V, SHEPHARD RJ, DYON M.** Determinations of performance and mechanical efficiency in nordic skiing. *Br J Sports Med.* 1979; 13: 62-65. doi:10.1136/bjism.13.2.62
- (93) **NISHIKAWA K.** Eccentric contraction: unraveling mechanisms of force enhancement and energy conservation. *J Exp Biol.* 2016; 219: 189-196. doi:10.1242/jeb.124057
- (94) **NOORDHOF DA, DE KONING JJ, VAN ERP T, VAN KEIMPEMA B, DE RIDDER D, OTTER R, AND FOSTER C.** The between and within day variation in gross efficiency. *Eur J Appl Physiol.* 2010; 109: 1209-1218. doi:10.1007/s00421-010-1497-4
- (95) **ORTEGA JD.** Counterpoint: skeletal muscle mechanical efficiency does not increase with age. *J Appl Physiol.* 2013; 114: 1109-1111. doi:10.1152/jappphysiol.01438.2012a
- (96) **ORTEGA JD, FARLEY CT.** Effects of aging on mechanical efficiency and muscle activation during level and uphill walking. *J Electromyogr Kinesiol.* 2015; 25: 193-198. doi:10.1016/j.jelekin.2014.09.003
- (97) **PENAILILLO L, BLAZEVICH AJ, NOSAKA K.** Factors contributing to lower metabolic demand of eccentric than concentric cycling. *J Appl Physiol (1985)* jap 00536 02016, 2017.
- (98) **PENDERGAST D, ZAMPARO P, DI PRAMPERO PE, CAPELLI C, CERRETELLI P, TERMIN A, CRAIG A, JR, BUSHNELL D, PASCHKE D, AND MOLLENDORF J.** Energy balance of human locomotion in water. *Eur J Appl Physiol.* 2003; 90: 377-386. doi:10.1007/s00421-003-0919-y
- (99) **PENDERGAST DR, MOON RE, KRASNEY JJ, HELD HE, ZAMPARO P.** Human Physiology in an Aquatic Environment. *Compr Physiol.* 2015; 5: 1705-1750. doi:10.1002/cphy.c140018
- (100) **POORTMANS JR, GUALANO B, CARPENTIER A.** Nitrate supplementation and human exercise performance: too much of a good thing? *Curr Opin Clin Nutr Metab Care.* 2015; 18: 599-604.
- (101) **ROBERTS AC, REEVES JT, BUTTERFIELD GE, MAZZEO RS, SUTTON JR, WOLFEL EE, AND BROOKS GA.** Altitude and beta-blockade augment glucose utilization during submaximal exercise. *J Appl Physiol.* 1996; 80: 605-615.
- (102) **ROBERTS TJ.** Contribution of elastic tissues to the mechanics and energetics of muscle function during movement. *J Exp Biol.* 2016; 219: 266-275. doi:10.1242/jeb.124446
- (103) **SANDBAKK O, ETTEMA G, LEIRDAL S, JAKOBSEN V, HOLMBERG HC.** Analysis of a sprint ski race and associated laboratory determinants of world-class performance. *Eur J Appl Physiol.* 2011; 111: 947-957. doi:10.1007/s00421-010-1719-9
- (104) **SANO K, ISHIKAWA M, NOBUE A, DANNO Y, AKIYAMA M, ODA T, ITO A, HOFFREN M, NICOL C, LOCATELLI E, AND KOMI PV.** Muscle-tendon interaction and EMG profiles of world class endurance runners during hopping. *Eur J Appl Physiol.* 2013; 113: 1395-1403. doi:10.1007/s00421-012-2559-6
- (105) **SAUNDERS PU, PYNE DB, TELFORD RD, HAWLEY JA.** Factors affecting running economy in trained distance runners. *Sports Med.* 2001; 34: 465-485.
- (106) **SCHARHAG-ROSENBERGER F, SCHOMMER K.** Die Spiroergometrie in der Sportmedizin. *Dtsch Z Sportmed.* 2013; 64: 362-366. doi:10.5960/dzsm.2013.105
- (107) **SCHUMACHER YO, VOGT S, ROECKER K, SCHMID A, COYLE EF.** Scientific considerations for physiological evaluations of elite athletes. *J Appl Physiol (1985)* 99: 1630-1631; author reply 1631-1632, 2005.
- (108) **SCHUTZ Y.** On problems of calculating energy expenditure and substrate utilization from respiratory exchange data. *Z Ernahrungswiss.* 1997; 36: 255-262. doi:10.1007/BF01617794
- (109) **SHAW AJ, INGHAM SA, FOLLAND JP.** The valid measurement of running economy in runners. *Med Sci Sports Exerc.* 2014; 46: 1968-1973. doi:10.1249/MSS.0000000000000311
- (110) **SHEPHARD RJ.** Metabolic adaptations to exercise in the cold. An update. *Sports Med.* 1993; 16: 266-289. doi:10.2165/00007256-199316040-00005
- (111) **SIDOSSIS LS, HOROWITZ JF, COYLE EF.** Load and velocity of contraction influence gross and delta mechanical efficiency. *Int J Sports Med.* 1992; 13: 407-411. doi:10.1055/s-2007-1021289
- (112) **SIH BL, STUHMLER JH.** The metabolic cost of force generation. *Med Sci Sports Exerc.* 2003; 35: 623-629. doi:10.1249/01.MSS.0000058435.67376.49
- (113) **STEINACKER JM.** Performance physiology, performance analysis, training management. In: *Manual for Rowing Technique - Technique, Performance and Planning*, edited by Altenburg D, Mattes K, Steinacker JM. Wiebelsheim: Limpert; 2012: 21-52.
- (114) **STEINACKER JM, MARX TR, MARX U, LORMES W.** Oxygen consumption and metabolic strain in rowing ergometer exercise. *Eur J Appl Physiol Occup Physiol.* 1986; 55: 240-247. doi:10.1007/BF02343794
- (115) **STUART MK, HOWLEY ET, GLADDEN LB, COX RH.** Efficiency of trained subjects differing in maximal oxygen uptake and type of training. *J Appl Physiol.* 1981; 50: 444-449.
- (116) **TABOGA P, LAZZER S, FESSEHATSION R, AGOSTI F, SARTORIO A, DI PRAMPERO PE.** Energetics and mechanics of running men: the influence of body mass. *Eur J Appl Physiol.* 2012; 112: 4027-4033. doi:10.1007/s00421-012-2389-6
- (117) **ULBRICH M, RUEGG JC.** Is the chemomechanical energy transformation reversible? *Pflugers Arch.* 1976; 363: 219-222. doi:10.1007/BF00594604
- (118) **VENTURELLI M, RICHARDSON RS.** Point: skeletal muscle mechanical efficiency does increase with age. *J Appl Physiol.* 2013; 114: 1108-1109. doi:10.1152/jappphysiol.01438.2012
- (119) **VOGT S, SCHUMACHER YO, ROECKER K, DICKHUTH HH, SCHOBBERER U, SCHMID A, AND HEINRICH L.** Power Output during the Tour de France. *Int J Sports Med.* 2007; 28: 756-761. doi:10.1055/s-2007-964982
- (120) **WHIPP BJ, WASSERMAN K.** Efficiency of muscular work. *J Appl Physiol.* 1969; 26: 644-648.
- (121) **YASUDA N, GASKILL SE, RUBY BC.** No gender-specific differences in mechanical efficiency during arm or leg exercise relative to ventilatory threshold. *Scand J Med Sci Sports.* 2008; 18: 205-212. doi:10.1111/j.1600-0838.2007.00637.x
- (122) **ZAMPARO P, CAPELLI C, PENDERGAST D.** Energetics of swimming: a historical perspective. *Eur J Appl Physiol.* 2011; 111: 367-378. doi:10.1007/s00421-010-1433-7