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An analysis of performance in human locomotion

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Abstract This paper reports an analysis of the principles underlying human performances on the basis of the work initiated by Pietro Enrico di Prampero. Starting from the concept that the maximal speed that can be attained over a given distance with a given locomotion mode is directly proportional to the maximal sustainable power and inversely proportional to the energy cost of locomotion, we discuss the maximal powers (and capacities) of anaerobic (lactic and alactic) and aerobic metabolisms and the factors that limit them, and the factors affecting the energy cost of various locomotion modes. Special attention is given to the role of air resistance and frictional forces. Finally, computation of performance speed is discussed along the approach originally developed by di Prampero.

Keywords Energy cost · Maximal power ·
Maximal oxygen consumption ·
Aerobic and anaerobic metabolism

Communicated by Susan Ward.

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Introduction

When a car is driven on a highway, the car performs mechanical work. If the road is flat, the centre of mass of the car does not move vertically, and all the mechanical work is used to move along the highway as kinetic energy (external work). However, since the car does not move into empty space, energy must continuously be injected into the car to overcome aerodynamic forces and keep the speed invariant. This comes from the transformation of chemical energy into mechanical energy, via fuel oxidation in the engine. Only a fraction of chemical energy, however, can be transformed into mechanical energy, the remainder being transformed into heat: that fraction corresponds to the mechanical efficiency (η) of the engine. *Maximal power* is the maximal rate at which the chemical energy transformation occurs, *maximal capacity* the maximal quantity of chemical energy that can be made available to the car, corresponding to the volume of the fuel tank.

The maximal mechanical power is directly proportional to the maximal speed of the car through a constant F with the dimension of force. This force opposes the movement of the car and has two components: the friction of road and gearing (non-aerodynamic forces), and the air resistance (drag). At the speeds attained by cars, the latter is by far predominant. Chemical power also is directly proportional to speed, but through a constant F' which is much greater than F , being equal to the ratio of F to η . Constant F' corresponds to *fuel consumption* and indicates the amount of fuel consumed to cover a given distance. Generally, it is expressed in litre of fuel per 100 km covered. In the case of cars, fuel consumption varies with speed and among cars. For a given maximal power, the maximal speed attained is inversely proportional to F' . In the history of car manufacturing, great attention was paid to the aerodynamics of cars, in order to reduce F and thus F' .

The above principles apply to all engines. Muscles are engines, thus these principles also apply to muscle contraction and animal locomotion. However, whereas human-made engines rely on one source of energy only (gasoline, electricity or whatever), muscles rely on three substrates (glycogen, free fatty acids and phosphocreatine) intermingled in three simultaneous energetic pathways (aerobic metabolism, anaerobic lactic metabolism and anaerobic alactic metabolism). This allows animals (humans) to cover a wide spectrum of running performances, as exemplified on one side by Usain Bolt running the 100 m dash, on the other by Haile Gebreselassie running the marathon. The present knowledge of the energetics of muscular exercise is still essentially funded on the work of the great old master, Rodolfo Margaria (1901–1983) that Pietro Enrico di Prampero, the heir and continuator of Margaria's cultural tradition in the field, splendidly reviewed in 1981 (di Prampero 1981).

di Prampero was the first who comprehensively exploited the analogy between car motion and animal motion in the study of human locomotion. He was the first to express the relation of speed (v) to power (\dot{E}) in terms of energy cost (C , the human analogue of F'), as follows:

$$v = \dot{E}C^{-1}. \tag{1}$$

Starting from this concept, di Prampero analysed the energetics of running, cycling, skating, swimming and the maximal performances (records) that can be attained in each mode of locomotion (Celentano et al. 1974; di Prampero 1986; di Prampero et al. 1971, 1974, 1976, 1979, 1986; Pendergast et al. 1977, to cite only the pioneering papers). More recently, he used this knowledge to develop a quantitative model of best performances in human locomotion (di Prampero et al. 1993). His work has been highly influential, especially for younger physiologists coming from the same School. In this article, moving from Eq. 1, we discuss the concepts of maximal power and energy cost as applied to human locomotion and we analyse the concept of best performance, and in so doing track the cultural heritage of Pietro Enrico di Prampero.

Maximal metabolic power

When we deal with the maximal speed that a human can reach in any given type of locomotion, Eq. 1 can be written as follows:

$$v_{\max} = \dot{E}_{\max}C^{-1}. \tag{2}$$

Therefore, what is \dot{E}_{\max} in the case of human locomotion? Considering that three types of energy metabolisms are available to our muscles, it depends. For explosive exercise, lasting at most a few seconds, \dot{E}_{\max} is the

maximal anaerobic alactic power ($\dot{A}l_{\max}$, di Prampero 1981; Ferretti et al. 1987). For supramaximal exercise, lasting some tenths of seconds, it is the sum of maximal aerobic power (as reflected by the maximal oxygen consumption, $\dot{V}O_{2\max}$) plus the maximal anaerobic lactic power ($\dot{L}a_{\max}$, di Prampero and Ferretti 1999; Margaria et al. 1964):

$$\dot{E}_{\max} = (\dot{V}O_{2\max} + \dot{L}a_{\max}) \tag{3}$$

whence, after substitution of Eq. 3 into Eq. 2:

$$v_{\max} = (\dot{V}O_{2\max} + \dot{L}a_{\max})C^{-1}. \tag{4}$$

For prolonged exercise, relying on aerobic metabolism, \dot{E}_{\max} should correspond to $\dot{V}O_{2\max}$. Yet $\dot{V}O_{2\max}$ can be sustained only for some 8–10 min (Lacour et al. 1990; Padilla et al. 1992), although di Prampero et al (1993) assumed 14 min in their modelling of middle-distance running. For longer exercise duration, \dot{E}_{\max} is lower than $\dot{V}O_{2\max}$, and we must account for the fraction of $\dot{V}O_{2\max}$ actually sustainable over a given time (fractional utilisation of $\dot{V}O_{2\max}$, F_u). Of course, when $\dot{E}_{\max} \geq \dot{V}O_{2\max}$, then $F_u = 1$ and cancels out. On the other hand, when $\dot{E}_{\max} < \dot{V}O_{2\max}$ and $F_u < 1$, anaerobic metabolisms do not intervene as long as the metabolic steady state has been attained, after some 3 min. So we have:

$$\dot{E}_{\max} = F_u \dot{V}O_{2\max}. \tag{5}$$

Submaximal aerobic exercise has a great advantage from the experimental viewpoint, that a simple measure of oxygen consumption ($\dot{V}O_2$) is sufficient to provide an overall measure of \dot{E} . Thus, the study of aerobic exercise and the prediction of best long-distance performances have largely prevailed in the literature. It is in that context that Eq. 5 has gained large diffusion, thanks to its simplicity. It is worth mentioning, however, that Eqs. 2 and 5 rely on the assumptions that \dot{E}_{\max} and C do not vary with time during running, which is not exactly the case (Brückner et al. 1991), so that they can be considered also as nice experimental shortcuts.

It follows that \dot{E}_{\max} decreases with the total exercise duration, and thus with the distance to be covered. As a corollary, for any given subject's $\dot{V}O_{2\max}$, F_u is lower the longer the sustainable exercise time (t_{lim}). The relation of the maximal sustainable power to t_{lim} was investigated by Wilkie (1980) for an exercise duration up to 10 min, thus implying $F_u = 1$ and $\dot{L}a > 0$ (Fig. 1). In fact Wilkie applied nothing but the hyperbolic model firstly suggested by Hill (1925), further developed by Scherrer and Monod (1960), and later modified by Lloyd (1966). Starting from Wilkie's analysis, di Prampero et al (1993) calculated the overall amount of energy used to cover a given distance in a given time, and took into account not only the three energy sources for muscular exercise, but also the fact that

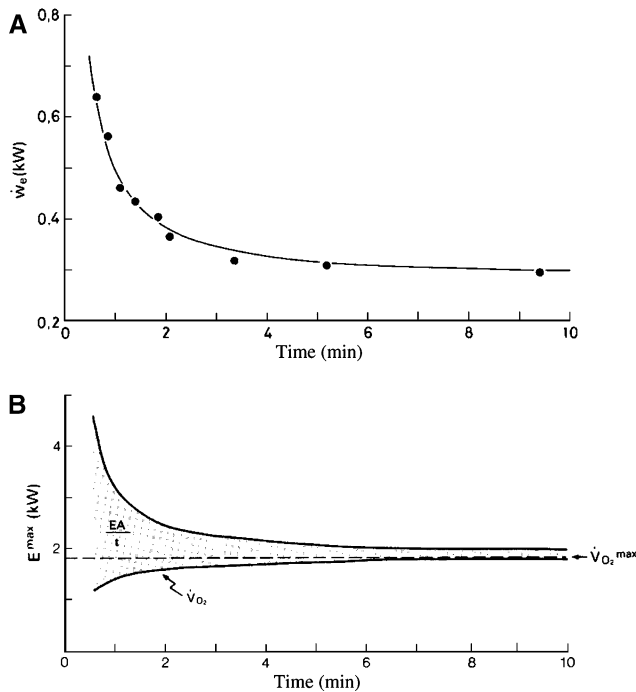


Fig. 1 **a** Maximal mechanical power sustainable on a cycle ergometer (\dot{w}_e , kW) as a function of exercise duration. The interpolating function is described by: $\dot{w}_e = 0.273 + 16t^{-1} - (0.273 t^{-1})(1 - e^{-t/\tau})$, where \dot{w}_e is in kW, t is in s and $\tau = 10$ s (from Wilkie 1980). **b** Maximal sustainable metabolic power (\dot{E}_{max} , in kW) as a function of exercise duration on cycle ergometer in a top-level athlete. The dashed horizontal line indicates the metabolic power corresponding to $\dot{V}O_{2max}$. The inferior curve describes the power actually sustained by aerobic metabolism. The superior curve represents \dot{E}_{max} , and reproduces the curve of panel **a** after accounting for the efficiency of exercise. Thus, the vertical distance between the two curves corresponds to the power contributed by anaerobic metabolism (lactic and alactic) (from di Prampero 1985b)

$\dot{V}O_{2max}$ is not reached instantaneously at the onset of exercise, but with a delay. A similar, although slightly more complex, approach was previously used by others (Péronnet and Thibault 1989) to analyse running performance and records over a wider panel of distances.

The kinetics of O_2 consumption inside contracting muscles can be conveniently described with a single-exponential equation, the time constant of which may range from 10 s (e.g. Francescato et al. 2003) to 23 s (e.g. Binzoni et al. 1992) in normal fit subjects. This allows a precise distinction of the contribution of aerobic and anaerobic alactic energy sources to energy expenditure. At first approximation, however, since the fraction of energy derived from anaerobic alactic energy sources, which are used in the exercise transient only, decreases with exercise duration, it can be neglected at least for endurance exercise, when $E_{max} < \dot{V}O_{2max}$. Moreover, in this condition, a simple measure of steady state $\dot{V}O_2$ informs on the entire metabolic power sustaining exercise, so that \dot{E}_{max} can indeed be derived from measures of $\dot{V}O_2$ only.

Maximal metabolic capacity

In contrast to power, capacity (in kJ or in L of O_2 equivalents, di Prampero 1981) deals with the quantity of available energy (tank volume, in the case of cars). Thus, the maximal capacity of a given energy metabolism corresponds to the maximal amount of energy that can be derived from the available energy metabolism.

The maximal capacity of anaerobic alactic metabolism is set by the contracting muscle mass and by the concentration of ATP and phosphocreatine in muscles. On average, ATP concentration is 5–8 mmol kg^{-1} of wet muscle mass (di Prampero et al. 1969; Sahlin et al. 1975). Thanks to the fact that the equilibrium constant of the Lohmann’s reaction is ~ 20 (Carlson and Siger 1960), ATP concentration remains unchanged over a wide variety of situations, decreasing only when phosphocreatine concentration becomes critically low. In resting muscles, phosphocreatine concentration is about 20 mM kg^{-1} of wet muscle mass (di Prampero 1981). The overall amount of high-energy phosphates is small, insufficient to allow prolongation of exercise at \dot{A}_{max} beyond a few seconds: a very high power is inevitably coupled with a rather small capacity.

Anaerobic lactic capacity is not limited by substrate availability, but by the ability of skeletal muscles to accumulate lactate. When performing supramaximal exercise, exercise is stopped when blood lactate concentration reaches some 16–20 mM in most cases (di Prampero 1981; di Prampero and Ferretti 1999). The time necessary to reach such lactate concentration in blood, and thus exhaustion, during supramaximal exercise varies with power. At $\dot{L}a_{max}$, it is some 40 s (Margaria et al. 1964; Grassi et al. 1995). Note that the 20 mM lactate concentration is not an upper limit in blood lactate accumulation: this value is somewhat higher in power athletes (Lacour et al. 1990), has been overtaken after bicarbonate administration (Nielsen et al. 2002), and does not correspond to the maximal blood lactate concentration attained at the end of intermittent supra-maximal exercise bouts (Osnes and Hermansen 1972).

More complex is the subject of aerobic exercise capacity, because two metabolic pathways interact in determining it, differing in substrate availability. The oxidation of free fatty acids relies on a huge amount of lipids stored in the body. However, mobilisation of free fatty acids is a complex, slow phenomenon, with considerable inertia. Oxidation of intramuscular glycogen is faster, but the amount of glycogen in the body is much less than that of lipids. As a consequence, the capacity of aerobic metabolism is much less when glycogen only acts as energy source than when lipids only are used. Both pathways are simultaneously active in exercise, but the fraction of aerobic energy derived from glycogen oxidation is greater the higher the exercise intensity relative to $\dot{V}O_{2max}$ (di Prampero 1981). This implies that aerobic

Table 1 Maximal power and capacity of three main energetic pathways sustaining muscular contraction in humans, and the corresponding exhaustion time (t_{lim}) at the maximal power

Energy source	Subject	Power (W kg ⁻¹)	Capacity (kJ kg ⁻¹)	t_{lim} (s)
Anaerobic alactic	S	70–75	0.85	10
	E	45–50	0.75	15
	NA	50–55	0.75	13
Anaerobic lactic	S	40	1.5	40
	E	20	1.0	50
	NA	26	1.0	40
Aerobic	S	19	4,000–8,000	~30 min
	E	26	4,000–8,000	~25 min
	NA	16	4,000–8,000	~30 min

Data from di Prampero (1985b), di Prampero and Ferretti (1999) and Ferretti and Capelli (2008)

S sprint athlete, E endurance athlete, NA non-athlete

capacity declines with increasing metabolic power relative to $\dot{V}O_{2max}$. At powers corresponding to 85–90% of $\dot{V}O_{2max}$, all aerobic energy is provided by glycogen and glucose oxidation, and when glycogen stores are almost exhausted, exercise is stopped (Blom et al. 1986; Hermansen et al. 1967). At lower powers, not only is the rate of glycogen oxidation less, but also lipids contribute to energy production, and the more the lower is the exercise intensity.

Table 1 provides an overview of the power (in Watts) and capacity (in Joules) of each of the three main metabolic energy sources. Note that capacity is maximal when power is minimal and vice versa. $\dot{L}a_{max}$ is some 1.5 times higher than $\dot{V}O_{2max}$ in non-athletes. $\dot{V}O_{2max}$, however, is higher in endurance athletes than in non-athletes and sprint athletes, whereas $\dot{L}a_{max}$ is higher in sprint athletes than in non-athletes and endurance athletes. The same is true for $\dot{A}l_{max}$. So, endurance athletes have similar $\dot{V}O_{2max}$ and $\dot{L}a_{max}$, whereas sprint athletes have a larger difference between $\dot{L}a_{max}$ and $\dot{V}O_{2max}$ (di Prampero 1981). In fact, there is a negative relationship between maximal aerobic and anaerobic powers (Crielaard and Pirnay 1981). All maximal metabolic powers (aerobic and anaerobic) decrease with age. $\dot{L}a_{max}$ and $\dot{A}l_{max}$ are lower in subjects acclimatized to altitude (di Prampero and Ferretti 1999). $\dot{V}O_{2max}$ decreases in hypoxia (see e.g. Cerretelli and di Prampero 1987; Ferretti 1990) and can obviously be trained (Ekblom et al. 1968; Hoppeler et al. 1985). Trainable should also be $\dot{L}a_{max}$ and $\dot{A}l_{max}$, although no study has yet been carried out in support of this assertion.

The limits of power

$\dot{A}l_{max}$ is limited by the maximal rate at which ATP is re-synthesized via Lohmann's reaction. This is about one half

of the maximal rate of ATP utilisation, which, however, is maintained only over a few milliseconds, when the maximal instantaneous muscular power is developed (Ferretti et al. 1987). In turn, the maximal rate of ATP utilisation is related to the maximal muscle contraction velocity, which is set by the isoform of myosin heavy chain that is expressed in a given muscle fibre type (Bottinelli 2001). This explains why, for instance, the highest values of maximal instantaneous muscular power are found in sprint athletes, who are characterised by elevated fraction of type IIx fibres in their lower limb muscles. Similarly, we can assert that $\dot{L}a_{max}$ corresponds to the maximal rate of glycolytic activity. This corresponds to the maximal rate at which lactate is accumulated in muscle and is reflected by the maximal rate at which lactate is accumulated in blood (Margaria et al. 1964; di Prampero and Ferretti 1999).

By contrast, when we deal with the subject of $\dot{V}O_{2max}$ in terms of limitation, we have to take into account the fact that $\dot{V}O_{2max}$ is an overall integrated parameter, which relies not only on biochemical pathways, but also and mostly on O_2 flow from ambient air to mitochondria. Thus it has to do with pulmonary ventilation, gas-to-blood O_2 transfer, blood O_2 transport and peripheral O_2 diffusion and utilisation. The multifactorial models of $\dot{V}O_{2max}$ limitation are perhaps the most satisfactory tools available nowadays for discussing this subject in quantitative terms. Two models can be considered, the details of which can be found in the original publications and thus are not reported here: the one developed by Wagner (1992, 1993), and the other originally proposed by di Prampero (1985a; di Prampero and Ferretti 1990; Ferretti and di Prampero 1995; di Prampero 2003). Both models are algebraic tools that move from the O_2 conductance equation as applied to maximal exercise (Taylor and Weibel 1981). They differ under one respect: how they deal with O_2 transport by the circulation.¹

According to Wagner, blood O_2 transport is a mere convective step. As a consequence, (1) an analogous of resistances in-series is not applicable; (2) O_2 flows from alveoli to blood are supported by the difference between alveolar and mean capillary O_2 partial pressure (PO_2); (3) there is no PO_2 difference between pulmonary capillaries and peripheral capillaries; (4) mean capillary PO_2 is the driving force of O_2 diffusion into muscles. The attention is centered on diffusion, and the diffusion–perfusion interaction equations of Piiper and Scheid (1981) are used to describe O_2 transfer. So, no limitation to O_2 flow by the

¹ In 1740, Johann Sebastian Bach, starting from a clavier theme, wrote 30 celebrated variations known as the Goldberg variations. Starting from a biophysical theme (the oxygen conductance equations), physiologists were able to create and write only two variations (Wagner's and di Prampero's on oxygen flow limitation). According to some wise men, this demonstrates the inferiority of physiology to music.

circulation, described by means of the Fick equation, is included.

On the other hand, di Prampero looked at circulatory O₂ transfer as one of the numerous in-series resistances along the respiratory system. As a consequence, (1) a physiological analogue of the model of resistances in-series is applicable indeed; (2) O₂ flow from alveoli to blood is supported by the difference between alveolar and arterial PO₂; (3) the driving force of O₂ flow in blood circulation is the difference between arterial and mixed venous PO₂; (4) mixed venous PO₂ is the driving force of O₂ diffusion into muscles. Attention is centered on blood flow, which provides most of the limit to $\dot{V}O_{2\max}$.

The above differences of course have led to markedly different experimental conceptions in testing di Prampero's (Bringard et al. 2010; Esposito and Ferretti 1997; Ferretti et al. 1997a, b; but see also Brink-Elfegoun et al. 2007) and Wagner's (Knight et al. 1993; Richardson et al. 1995a, b; Schaffartzik et al. 1993) $\dot{V}O_{2\max}$ limitation models. Both models have drawbacks, but they share a great advantage with respect to other approaches proposed so far: i.e. they provide clear quantitative analysis of the limits of an integrative parameter. Unfortunately, this appears not always to be sufficiently recognized, as exemplified by the enduring mere qualitative analyses of $\dot{V}O_{2\max}$ limitation (e.g. Levine 2008).

Moreover, di Prampero's model provides a solution of the O₂ conductance equation for the specific case in which only one resistance to O₂ flow is permitted to vary. This allows a precise quantitative determination of the fraction of the $\dot{V}O_{2\max}$ limitation provided by the single resistance in question. On this basis, the conclusion was attained that circulatory O₂ flow is responsible for some 70% of the overall limitation of $\dot{V}O_{2\max}$ (di Prampero and Ferretti 1990), a figure that has however resisted robust experimental testing so far (e.g. Bringard et al. 2010).

Energy cost of human locomotion on land

As detailed analyses of the energy cost of the different types of human locomotion on land appear in several exhaustive reviews (Taylor and Heglund 1982; di Prampero 1986, 2000, 2003; Saibene and Minetti 2003), so only general principles are reported here. These principles in fact apply to all types of locomotion, whether in air or in water, but water locomotion faces specific problems that are discussed elsewhere in this issue (Zamparo 2010).

Let us recall, as already pointed out, that a body moving on land must overcome frictional forces and aerodynamic forces (air resistance or drag, see, e.g. di Prampero 1986). Drag (D) is proportional to the square of speed:

$$D = k v^2 \tag{6}$$

where constant k is proportional to air density ρ , the drag coefficient (C_x), and the projection area on the frontal plane (A):

$$k = 1/2\rho C_x A \tag{7}$$

ρ is some 800 times greater for water than for air, which largely explains the much slower speeds attained in swimming than in terrestrial locomotion. In air, it is directly proportional to barometric pressure (P_B) and inversely proportional to temperature. C_x is a non-dimensional number depending on the surface characteristics and on the geometrical shape of the moving body, as well as on the characteristics of the surrounding air flow. In the speed range of physiological relevance, it can be considered independent of fluid speed. A is the frontal surface area facing air on the direction of movement. Combining Eqs. 6 and 7 and rearranging, we have:

$$DA^{-1} = P_d = 1/2\rho C_x v^2 \tag{8}$$

where P_d is the dynamic pressure exerted on the moving body. It is noteworthy that, ceteris paribus, P_d is directly proportional to C_x . As a consequence, dynamically favourable shapes are characterised by low C_x values, with a value well below 1, such as aerodynamic contemporary cars or track bicycles used for record trials (Capelli et al. 1993; di Prampero 2000).

Since D is a force, it can also be expressed as mechanical work per unit of distance, so that:

$$D = C_d \eta = k v^2 \tag{9}$$

where C_d is the fraction of the energy cost necessary to overcome air resistance. As a consequence,

$$C_d = k \eta^{-1} v^2 = k' v^2. \tag{10}$$

Because of Eq. 1, we can also write:

$$\dot{E}_d = C_d v = k' v^3 \tag{11}$$

which indicates that the metabolic power overcoming air resistance (\dot{E}_d) is directly proportional to the cube of speed. If we take into account also the metabolic power against frictional forces (\dot{E}_f), we then obtain:

$$\dot{E} = \dot{E}_d + \dot{E}_f = k' v^3 + \dot{E}_f. \tag{12}$$

A comprehensive analysis of the relationships between \dot{E} and v in several types of locomotion on flat terrain in air at sea level was carried out by di Prampero (1986) and is presented in Fig. 2. In this figure, the bold curve describes the metabolic power to be dissipated against drag. Its slope corresponds to C_d . It is constructed for a k' value of 0.774 J s² m⁻³ (di Prampero 1985b). Note that the curve is

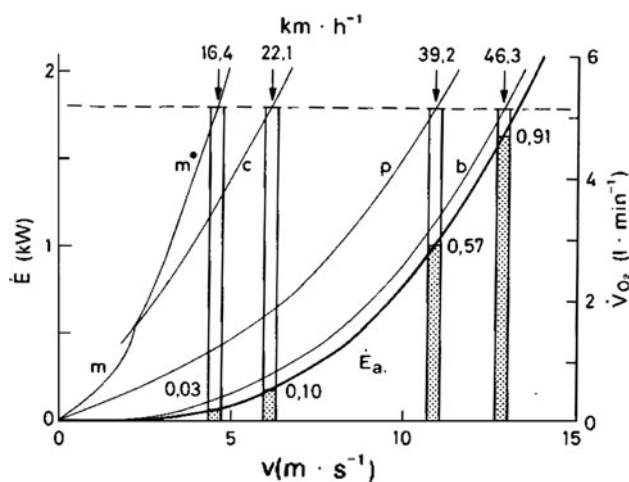


Fig. 2 The *thin curves* represent the metabolic power above resting (*left ordinate* \dot{E} , in kW, or *right ordinate* $\dot{V}O_2$, in $L \cdot \text{min}^{-1}$) as a function of speed (v , in $\text{m} \cdot \text{s}^{-1}$). They are established for a 70-kg heavy and 175-cm tall subject who moves on flat terrain at sea level ($P_B = 760 \text{ mmHg}$) on a windless day with an air temperature of 20°C (m walking, m^* competitive walking, c running, p skating, b bicycling). The *thick curve on the right* indicates the power necessary to overcome the air resistance and is constructed for a constant k' value of $0.774 \text{ J} \cdot \text{s}^2 \cdot \text{m}^{-3}$: the same curve applies to all types of human locomotion on land. The vertical distance between the *thick curve* and each of the *thin curves* represents the power necessary to overcome non-aerodynamic, frictional forces in each type of locomotion. The *horizontal dashed line on top* describes the $\dot{V}O_{2\text{max}}$ of a top endurance athlete (1.8 kW in this case). The *intersection of the dashed line with the thin curves* indicates the maximal velocity that the athlete can attain in aerobic conditions (indicated in $\text{km} \cdot \text{h}^{-1}$ on top). Below each of these intersections a histogram is drawn. The *dotted part of the histograms* indicates the fraction of \dot{E} used to overcome air resistance (from di Prampero (1985b))

flattened, and thus apparently displaced rightward and downward when k' is lowered, as when riding aerodynamic bicycles (Capelli et al. 1993); it is more curved when k' is increased, as on ancient bicycles (Minetti et al. 2001). It represents a limit that cannot be trespassed on its right side. All other curves in Fig. 2 are displaced leftward with respect to the bold curve, because in all cases metabolic power is to be used against frictional forces as well (\dot{E}_f). In Fig. 2, \dot{E}_f corresponds to the vertical distance between the bold curve and the experimental curve describing each type of locomotion. For skating and cycling, the energy cost against frictional forces (C_f) is a constant independent of speed, at least in the range $2\text{--}20 \text{ m} \cdot \text{s}^{-1}$, thus \dot{E}_f is directly proportional to speed. Of course C_f varies depending on the interaction between the terrain and the foot or device (wheel, skates, skis). In cycling, C_f depends on the width and type of the tyres, their inflation pressure and on the characteristics of the terrain, and is proportional to the overall weight of bicycle plus human (di Prampero 2000). Walking takes place in a speed range where C_d is negligible, so that $\dot{E} = \dot{E}_f$. For running and competitive walking, C_f varies linearly with speed, so that \dot{E}_f increases with v^2 .

Table 2 Parameters describing various types of human locomotion on land

Locomotion mode	k' ($\text{J} \cdot \text{s}^2 \cdot \text{m}^{-3}$)	C_x	C_f ($\text{J} \cdot \text{m}^{-1} \cdot \text{kg}^{-1}$)
Running	0.72	1.10	3.9*
Skating	0.79	0.50	1.0
Cycling, race	0.77	0.75	0.17
Cycling, traditional	1.14	1.00	0.27
Cycling, aerodynamics	0.58	0.65	0.15

Data derived from di Prampero (1985b, 2000) and Capelli et al (1993). The values refer to a subject 175 cm tall and with a 75 kg body, studied at sea level (P_B 760 mmHg, ambient temperature 20°C , relative humidity 50%). For cycling, a total mass (cyclist plus bicycle) of 85 kg was assumed

k' constant relating the energy cost to overcome aerodynamic forces to the square of speed, C_x aerodynamic (drag) coefficient, C_f energy cost against frictional forces

* indicates an average value: in fact C_f varies linearly with speed

Average values for k' , C_x and C_f are reported in Table 2 for different types of locomotion.

Some practical consequences of Fig. 2 are that: (1) the fraction of C represented by C_d and C_f varies with speed and with the locomotion type; (2) because of the striking although fortuitous similarity of k' , \dot{E}_d at any given speed is similar among locomotion modes; (3) differences in v_{max} are essentially due to differences in \dot{E}_f . Particularly in cycling, \dot{E}_f is minimized by the rotational movement of the wheel and by the absence of work against gravity due to body stabilisation by the bike, so that most of \dot{E} can indeed be used to overcome air resistance. This is why cycling leads to reach the highest speeds in human locomotion.

Maximal running speed

In athletics, track competitions occur over given distances to be covered at the fastest possible speed. This speed obviously is lower the longer the distance to be covered, in agreement with the empirical model of Wilkie (1980) and following evolutions (Péronnet and Thibault 1989; di Prampero et al. 1993). Equations 4 and 5 describe the evolution of \dot{E}_{max} with time. Let us now define \dot{E}_r as the metabolic power required to run a given distance in a given time, and v_r the corresponding mean running speed. Since the distance is fixed, v_r , and thus \dot{E}_r (C in running is independent of speed), is inversely proportional to the running time. Let us now plot the relationships between \dot{E}_r and time, a quadratic hyperbola for each given running distance, and between \dot{E}_{max} and time; Wilkie's empirical model. The two curves have different concavity, so they cross on a specific point. That point indicates the sustainable metabolic power and the record time (t_{rec} , di Prampero et al. 1993, Fig. 3). In fact, at shorter times (faster speeds),

the athlete would be unable to provide all the required metabolic power, because $\dot{E}_r > \dot{E}_{max}$, whereas for longer times (slower speeds) the athlete could deliver more

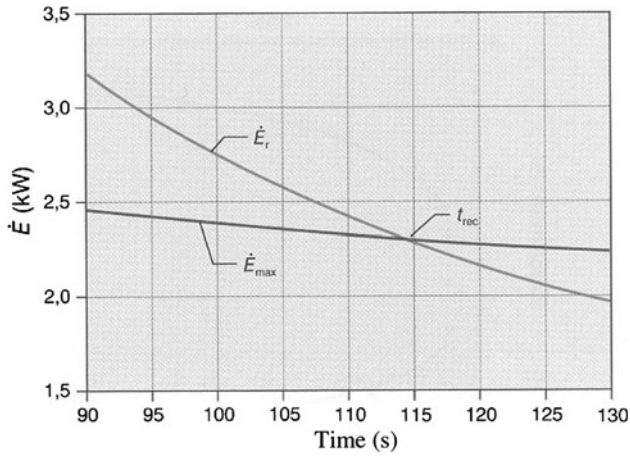


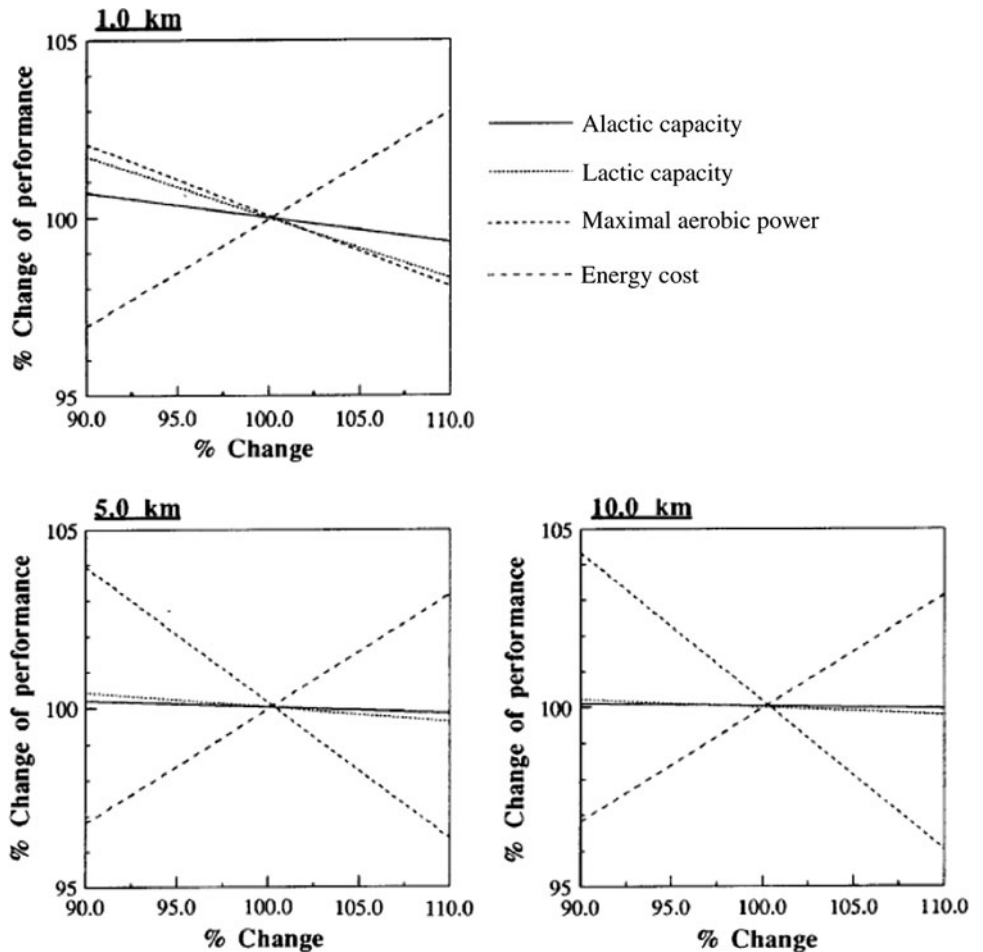
Fig. 3 Metabolic power (\dot{E} , in kW) as a function of time. The \dot{E}_r curve describes how the power required to run the 800 m distance varies with exercise time. The \dot{E}_{max} curve describes the variations of the maximal sustainable metabolic power as a function of exercise time. The best performance of the athlete at stake (t_{rec}) is indicated by the intersection of the two curves (after di Prampero et al. 1993)

metabolic power than requested to run at that speed, because $\dot{E}_r > \dot{E}_{max}$: the best performance time occurs when $\dot{E}_r = \dot{E}_{max}$. This approach, whose detailed quantitative analysis can be found elsewhere (di Prampero et al. 1993; di Prampero 2003), applies to any type of locomotion (Capelli 1999).

It is also noteworthy that, the shorter the distance, the greater is the role played by acceleration at running start. di Prampero et al (2005) have considered acceleration in sprint running analogous to running uphill at constant speed, with slope proportional to acceleration. This implies a further increase in C with respect to running at constant speed on the level, so that the Wilkie's relation between \dot{E}_{max} and time, for time shorter than 5 min, deviates upward.

An improvement of t_{rec} is attained when the \dot{E}_{max} curve is shifted upward. This can be achieved either by increasing $\dot{V}O_{2max}$ and/or maximal anaerobic power and capacity, or by reducing C . Capelli (1999) investigated the quantitative role of these variables in determining t_{rec} (Fig. 4). He computed the percent changes in t_{rec} induced by given percent changes in each of the variables at stake. Figure 4 shows that (1) C is the main physiological determinant of performance; (2) the role of aerobic power increases with

Fig. 4 Percent improvement or deterioration of record time as a function of percent variations of aerobic power, anaerobic lactic capacity, anaerobic alactic capacity and energy cost of running on the three indicated distances (after Capelli 1999)



the distance covered, and thus with the performance time; (3) the role of anaerobic capacity decreases with the distance covered, becoming negligible in running at distances above 5 km. Note that, whereas C is barely modifiable in running, it can undergo remarkable reductions in cycling, when aerodynamic bicycles are used. Moreover, remarkable reductions of C can be obtained in swimming through improvement of the swimming technique and through the improvement of floating by means of contemporary buoyant suits (Chatard and Wilson 2008).

The effects of altitude

Barometric pressure is the pressure exerted on the Earth surface by the air column above it. Thus, its value depends on the height of the air column, so that P_B decreases with altitude. Because of Dalton's law, and because the composition of dry air is constant around the Earth, with 20.94% O_2 , the decrease in P_B entails a decrease in the inspired PO_2 (PiO_2). In fact the decrease in PiO_2 is even larger than that in P_B , because the water vapour pressure to be subtracted to obtain dry air at body temperature (conventionally 37°C) is invariant (47 mmHg) and independent of the overall pressure. For example, whereas at sea level ($P_B = 760$ mmHg) PiO_2 equals 149 mmHg, on top of Mount Everest ($P_B = 253$ mmHg, one third of that at sea level) PiO_2 is 43 mmHg (less than one third of that at sea level) (West et al. 1983). The reduction of P_B , and thus of PiO_2 , is the cause of the reduction of $\dot{V}O_{2max}$ at altitude (Cerretelli and Margaria 1961; Cerretelli 1980; Ferretti 1990). On the other hand, the decrease in P_B is accompanied by a proportional decrease in ρ , which is only partially corrected for by the concomitant decrease in ambient temperature. What is the final effect on v_{max} of these two effects of P_B , which act in opposite directions, since the former reduces \dot{E}_{max} whereas the latter reduces C_d ? It depends on (1) the type of locomotion; (2) the exercise intensity; and (3) the intrinsic characteristics of the effects of altitude on $\dot{V}O_{2max}$.

Concerning the first item, Fig. 2 clearly shows that the fraction of C represented by C_d increases with the speed. Thus the role of C_d in establishing v_{max} is minimal in running, nil in walking, and maximal in cycling. As a consequence, v_{max} in endurance running at altitude is affected essentially by the decrease in $\dot{V}O_{2max}$. This explains for instance the results obtained at the Olympic Games in Mexico City (2,200 m above sea level), when all runners competing at distances from 5 km and above had significant reductions in performances. Noteworthy at this purpose is the progressive decrease in the average speed on the marathon with altitude, which parallels that in $\dot{V}O_{2max}$ (Roi et al. 1999). Of course, when exercise intensity goes up, v_{max} also increases, so that the relative role of C_d in determining v_{max} becomes higher.

So the effects of ρ reduction become more and more evident, whereas the shorter duration of supramaximal exercise reduces the impact of the $\dot{V}O_{2max}$ reduction. This explains why at the Olympic Games in Mexico world records were established in all running events shorter than 800 m.

Cycling is the locomotion mode in which most influential is the effect of C_d on v_{max} , and thus in which most efficient is the reduction of ρ in counterbalancing the negative effects of the $\dot{V}O_{2max}$ decrease on performance. Because of the non-linearity of the $\dot{V}O_{2max}$ decrease at altitude, due to the effects of the O_2 equilibrium curve on $\dot{V}O_{2max}$ in hypoxia (Ferretti et al. 1997b), at relatively low altitudes the beneficial effects of ρ reduction on C_d prevail on the negative effects of $\dot{V}O_{2max}$ reduction on \dot{E}_{max} in determining long-lasting aerobic performance. Thus, as altitude is increased, v_{max} firstly increases to reach a peak, and then it decreases (di Prampero et al. 1979; Capelli and di Prampero 1995). The decrease in v_{max} takes place as soon as the athlete operates on the linear part of the oxygen equilibrium curve, where the decline of $\dot{V}O_{2max}$ becomes more important than that of ρ . Based on the classical relationship between $\dot{V}O_{2max}$ and altitude, di Prampero et al. (1979) estimated that the optimal altitude for best performances in 1 h track cycling was about 3,600 m above sea level (Fig. 5). Incidentally there is a velodrome at such altitude, in La Paz, Bolivia, but all 1 h record attempts in La

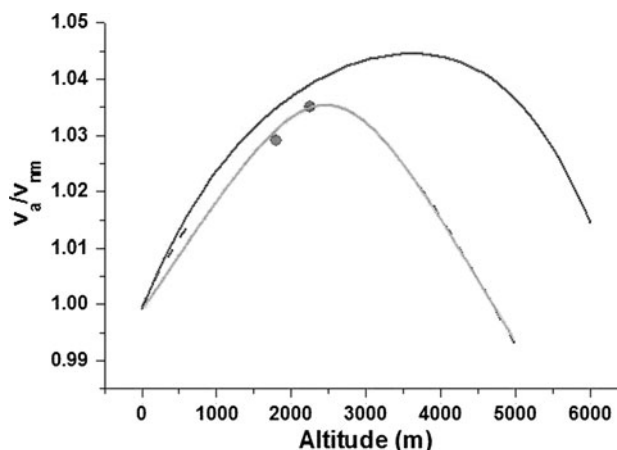
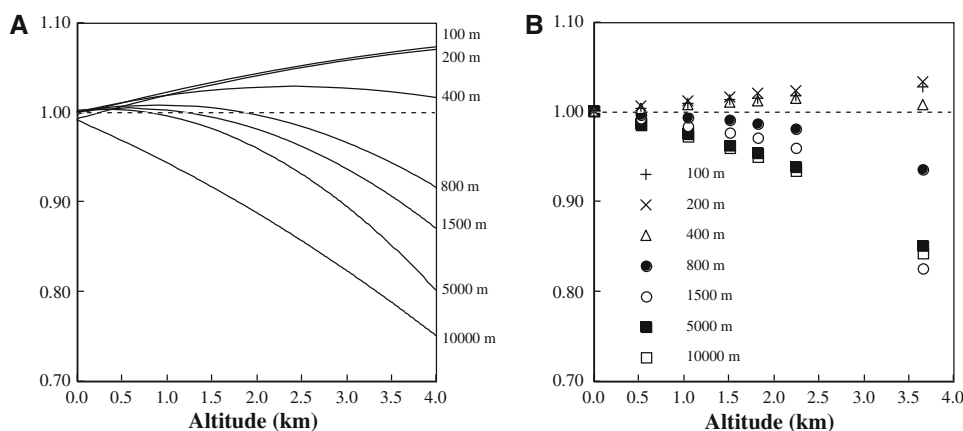


Fig. 5 Evolution of the maximal cycling speed at altitude. Speed is expressed relative to the maximal speed at sea level, set equal to 1 ($v_{rec}^{alt}/v_{rec}^{sl}$, ordinate). The *top curve* represents the predictions made after di Prampero et al. (1979), based on the classical description of the $\dot{V}O_{2max}$ decrease at altitude. The *lower curve* modifies the previous prediction by accounting for the fact that athletes undergo greater $\dot{V}O_{2max}$ decrease than non-athletes (Ferretti et al. 1997b), because of the “Dempsey” effect (Dempsey et al. 1984). The two experimental points refer to the actual performances of the two athletes (*right* Francesco Moser from Italy, *left* Jeannie Longo from France) who in the eighties established world records of 1 h unaccompanied cycling on track at sea level and at altitude with equivalent bicycles (after Ferretti and Capelli 2008)

Fig. 6 Relative changes in record speed with respect to that at sea level ($v_{\text{rec}}^{\text{alt}}/v_{\text{rec}}^{\text{sl}}$) as a function of altitude in various athletics distances, from 100 m to 10 km. **a** Results of theoretical analysis. **b** Experimental data points derived from world record tables before 1991, for records established at altitudes comprised between sea level and 3,600 m. Data after Péronnet et al (1991)



Paz have to date failed. Moreover, the two athletes who established 1 h records at sea level and at altitude with similar bikes attained lesser performances at altitude than predicted. The discrepancy between prediction and actual performance may rely on the “Dempsey” effect (Dempsey et al. 1984; Dempsey and Wagner 1999). In fact when endurance athletes with high $\dot{V}O_{2\text{max}}$ values perform maximal exercise at sea level, they typically undergo desaturation of arterial blood, so that they operate closer to the steep part of the O_2 equilibrium curve. As a consequence, when they are exposed to hypoxia, they undergo a greater $\dot{V}O_{2\text{max}}$ decrease than those who do not desaturate (e.g. non-athletes), since the decline of $\dot{V}O_{2\text{max}}$ in hypoxia is a mirror image of the O_2 equilibrium curve (Ferretti et al. 1997b). If the greater decrease in $\dot{V}O_{2\text{max}}$ in athletes than in non-athletes is accounted for in predicting the maximal cycling performance at altitude, a closer correspondence between prediction and performance is observed (see Fig. 5).

Similar approaches to the investigation of maximal performance at altitude can be applied to any type of locomotion. However, the benefits of ρ reduction, and thus the positive effect of altitude on v_{max} , become less evident as \dot{E}_f is increased. The effects of altitude on performance in running different distances were modelled by Péronnet et al (1991) and their results are reported in Fig. 6. It appears that, at least with aerobic exercise (e.g. 5 and 10 km events), there is an almost immediate decrease in v_{max} at altitude. However, the benefits of altitude on performance become more and more evident, as long as the distance is shortened, the speed is increased and anaerobic energy sources prevail.

Conclusions

The analytical approach of di Prampero et al (1993) to the study of best performances in human locomotion is perhaps

the best quantitative tool available nowadays for our understanding of human performance. In practice, it implies that performance can be improved as far as we succeed in improving v_{max} , which, according to Eq. 1 in its various specific versions, can be achieved essentially along two ways: (1) increasing \dot{E}_{max} ; (2) decreasing C . The physiological determinants of both have been discussed in this article. Sudden decreases in C have provided the most dramatic changes in performance, as occurred in cycling, for example when aerodynamic bicycles were introduced, or more recently in swimming with contemporary buoyant suits. Also, the evolution of track elasticity has contributed to improving performance in running.

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