

Corrigendum

Minetti, A. E. (2004). Passive tools for enhancing muscle-driven motion and locomotion. *J. Exp. Biol.* **207**, 1265-1272.

Unfortunately equations Ai and Aii in the first part of the Appendix to this Commentary were published incorrectly.

The correct text should read:

The speed values in Fig. 2 were obtained by estimating, for each duration (t , in s), the maximum sustainable mechanical effort (Wilkie, 1980) as:

$$W_{\text{MECH}} = A + \frac{B}{t} - \left(\frac{A \cdot \tau \left(1 - e^{-\left(\frac{t}{\tau} \right)} \right)}{t} \right), \quad (\text{Ai})$$

where A is the maximum long-term mechanical work rate (W), B is the mechanical equivalent of the available energy from anaerobic sources (J) and τ is the time constant (s) describing the inertia of the system. As developed by Wilkie, this equation is accurate for durations of 40 s to 10 min. To take into account the decay of the sustainable maximum oxygen consumption for longer exercise durations (Saltin, 1973), terms A have been multiplied by:

$$\frac{\dot{V}_{\text{O}_2}}{\dot{V}_{\text{O}_2\text{max}}} = \frac{940 - (t/60)}{1000}, \quad (\text{Aii})$$

where the first ratio represents the sustainable proportion of the total metabolic power.

The author apologises for any inconvenience this may have caused.

Commentary

Passive tools for enhancing muscle-driven motion and locomotion

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Summary

Musculo-skeletal systems and body design in general have evolved to move effectively and travel in specific environments. Humans have always aspired to reach higher power movement and to locomote safely and fast, even through unfamiliar media (air, water, snow, ice). For the last few millennia, human ingenuity has led to the invention of a variety of passive tools that help to compensate for the limitations in their body design. This Commentary discusses many of those tools, ranging from halteres used by athletes in ancient Greece, to bows, skis, fins, skates and bicycles, which are characterised by not supplying any additional mechanical energy, thus retaining the use of muscular force alone. The energy

cascade from metabolic fuel to final movement is described, with particular emphasis on the steps where some energy saving and/or power enhancement is viable. Swimming is used to illustrate the efficiency breakdown in complex locomotion, and the advantage of using fins. A novel graphical representation of world records in different types of terrestrial and aquatic locomotion is presented, which together with a suggested method for estimating their metabolic cost (energy per unit distance), will illustrate the success of the tools used.

Key words: locomotion performance, passive tool, muscle-driven motion, energy cascade, swimming, human.

Introduction

An athlete can jump as high as about 2.5 m. If a flexible pole is available, the vertical jump can reach about 6 m but if a bicycle is further added to the (sufficiently long) pole, the high jump could (hypothetically) exceed 20 m. Despite the differences in performance, the common feature is that the mechanical energy comes from forceful muscle contractions only, whose action is ‘mediated’ by passive tools. This commentary is about those tools and how they can compensate for musculo-skeletal limitations and augment motion and locomotion.

Versatility is a crucial feature in the biological world, and species can expand their habitats as long as they are comfortable with a variety of gaits and environments. Animals simultaneously capable of climbing trees, diving, running and flying probably do not exist, although some (e.g. flying squirrels, seagulls, flying fishes) display a challenging combination of those locomotion modes. Other animals, such as cheetahs and horses, favour a specialized motion and have difficulties performing well in other diverse situations.

While representing an intermediate condition between those two extremes, with a particular propensity for moving on land, humans continuously strive to improve their speed of progression in terrestrial, aquatic and aerial modes. Furthermore, humans have always been ethologically

interested in increasing their offensive power. These research processes started a few millennia ago (use of skis in Scandinavia, halteres in ancient Greece) and involved ingenious and empirical ergonomics (e.g. African bow and arrows), culminating in the last few decades with the success of human-powered flight, made possible by the combination of high-tech aeronautical engineering, exercise physiology and biomechanics.

The wide variety of invented tools, having the common feature that they do not supply any additional mechanical energy to the body, provided effective compensation for limitations in anatomical design, inadequacy of muscle performance and for the insufficient power-amplification of biological elastic structures. In the following, before discussing the different ‘augmented’ motor activities, I try to describe the path from force generation to the achieved motion, with reference to the strategies used to make such a transformation the most effective.

From muscle contraction to mechanical work via metabolic consumption

Muscles are actuators generating force. Depending on the load (and starting from rest), muscles shorten (low load),

lengthen (high load) or remain at a constant length (when load=force). While they consume metabolic substrates during all these three activities, we are mainly concerned with the shortening contraction, because it is five times more expensive than the others (Abbott et al., 1952) and is related to the production of positive work, which is necessary to initiate and sustain body movements.

The ability to generate force depends on muscle length (maximum at intermediate lengths) and on the speed at which it shortens. In particular, high contraction speeds are associated with low force produced (Hill, 1938). By multiplying the two axes of the force vs. speed relationship, we obtain the muscle mechanical power, which is maximum at about 1/3 of the maximum contraction speed. The first characteristic (force/length) does not remarkably penalize our daily activities because muscles are assembled in the body to operate near their optimal length. The second characteristic (force/speed) is more crucial, particularly when the increase in movement or locomotion speed would require muscle to contract faster. To cope with this problem, biology provides elastic structures, as tendons, working as power amplifiers or as a mechanical energy reservoir. The higher force produced by a slow contraction can be elastically stored, then the deformation energy can be released at a faster rate. The total mechanical work input is not very different from the output, whereas the output power is much higher. Examples of this mechanical power-amplification strategy are the catapult-like jumping in locusts, frogs and galagos. By contrast, tendons are used as a mechanical energy reservoir during bouncing gaits (hopping, running, trotting, galloping), where limb extensor muscles tend to operate quasi-isometrically while tendons store the energy of landing (which otherwise should be lost) and subsequently release it to assist take-off (Roberts et al., 1997; Biewener et al., 1998). This avoids fast muscle contraction and minimizes the amount of fresh energy to be provided to the system.

The next step is how muscles act across joints. Here, for the same final torque, muscles need to contract more forcefully the smaller the moment arm. Also, the simultaneous action of agonist and antagonist muscles, while stabilizing the joint and helping modulate the intended motion, implies the use of extra metabolic energy beyond the minimum that is strictly necessary to generate the same net moment.

Finally, the interaction of the body with the environment is crucial in generating motion. So-called external mechanical work can be mainly partitioned as the work necessary to accelerate and raise the body centre of mass and that needed to overcome friction and other media (terrain, air, water) forces that oppose motion. For friction to operate we need to slide with respect to the medium under consideration (it does not act, for example, between the foot and the terrain when running). Another component of the total mechanical work is the internal work, which is needed to reciprocally accelerate body segments with respect to the body centre of mass and to overcome internal friction in body tissues (Fenn, 1930). This depends on the segment inertia and on their motion pattern.

Considering locomotion, both the metabolic and mechanical

demand are expressed as costs, i.e. as energy per unit distance (e.g. ml O₂ m⁻¹ or J m⁻¹). The metabolic cost is the key index of the 'economy' of locomotion, and corresponds to the amount of fuel (litres of petrol) needed by our cars to travel a given distance (say 100 km). The proportion of the metabolic cost (or power) resulting in mechanical cost (or power) is termed 'efficiency' and, when the whole mechanical energy flux is known and the metabolism is aerobic, cannot exceed the value of 25–30% (Woledge et al., 1985). This upper limit is set by the product of the efficiency related to phosphorylation (60%) of metabolic substrates to ATP molecules and that of muscle contraction itself (from ATP molecules to force/displacement generation, equal to 50%). Although often mistakenly thought to be interchangeable concepts, efficiency and economy (the inverse of metabolic cost) are not. Schematically, economy needs efficiency, but efficiency does not imply economy. An efficient locomotion is one where most of the metabolic energy input is transformed into mechanical work, but it is possible that some of this mechanical work is not necessary for propulsion, resulting in a worse economy. If most of the mechanical work done contributes to progression, and if the mechanical work to propel ourselves is close to the minimum necessary, we also have an economical locomotion. If, for the same mechanical cost, efficiency and economy are directly related, their relationship is more deceptive when the work and metabolic energy both vary. An example is the comparison between walking and cycling at the same speed, where the same efficiency is seen together with a much lower economy of walking. This is due to the much lower mechanical work necessary in cycling.

The general term 'efficiency', as mentioned, can be envisaged as the ratio between the energy out and the energy in. While the latter is straightforward, the energy out can be chosen from the minimum amount of work necessary to move (in ideal conditions), the measured mechanical work, the external mechanical work (included the ones against air/water drag, rolling resistance and so on), etc. The first of this variety of numerators defines the so-called 'overall or performance efficiency', while the others can be used to break down this efficiency into a cascade of sub-efficiencies. Such an approach permits detection of any energy wastage occurring at the levels of muscle, appendages and associated passive tools. Depending on the type of locomotion being investigated, the efficiency cascade can be complicated by the different components of external work, internal work (including the deformation of all the body/tool parts) and the extent to which muscles are optimized for that task. Schematically, however, the overall efficiency can be considered as the product of two main components: muscle efficiency and the so-called 'transmission efficiency' (Cavagna, 1988), referring to the ability to transform net muscle force into the minimum external work necessary to move (see discussion on fin swimming, below).

In summary, to improve locomotion (and motion), mechanical work should be limited to just the indispensable type and the muscle efficiency be kept close to its maximum.

Thus it is important to avoid: (1) operating muscles at too short or too long length, (2) contracting them at too high speed, (3) using joint angles with disadvantageous moment arm, (4) using co-contraction (or useless isometric force), (5) raising or lowering the overall body centre of mass too much, and (6) accelerating limbs too much with respect to the body centre of mass. Other factors to take into account include: (7) external friction should be reduced to the minimum level, (8) most of the external force should be effectively transformed into forward propulsion, and (9) mechanical energy should be stored into elastic structures for successive power-amplification purposes.

In this perspective, every passive tool collaborating to fulfil one or more of the above requirements is welcome. In the rest of this paper, numbers in bold typeface refer to the above strategies.

Where to gain more range/power

Assisted terrestrial locomotion

We began by discussing the augmented high jump (or pole vault, as it is more commonly known). In that case it is intuitive to realize that the body kinetic energy, deriving from the running speed of the athlete, is first converted into elastic energy (the deformation of the pole), and then transformed into the potential energy necessary to clear the bar. This is also true

for the normal high jump, with the difference that our tendons are not as good as the pole in storing and releasing huge amounts of elastic energy, despite roughly similar kinetic energy being available in the two cases. Thus pole vaulting uses strategy (9) to cope with biological limitations.

Long jump (in its ‘standing’ variation) is less easily investigated as an ‘augmentable’ motor act. Recent research (Minetti and Ardigó, 2002) indicated how added hand-held masses, such as the halteres used in ancient Olympic games by pentathlon athletes, can increase the jump distance by 5%. The halteres (Fig. 1), whose optimal mass for two was in the range of 7–8 kg, allow the body’s centre of mass not only to take off in an anterior and upper position, but also to land posterior to the contact point of the feet, compared to an unloaded jump. This causes the parabolic flight trajectory to be prolonged and translated forward, for the same take-off speed. Also, computer simulations and experiments have shown that the whole body, by better exploiting the shoulder rotator muscles (2) and the elastic structures along the kinematic chain (9), produces a higher mechanical power when loaded. Further enhancement of the standing long jump, which was introduced in the early modern Olympics (the record by R. C. Ewry was 3.46 m), was obtained by innovative British jumpers in the late 19th century. Joseph Darby and John Higgins, in the attempt to successfully jump over canals, developed the technique of backward-throwing the loads (dumbbells of about 3.5 kg each) during the

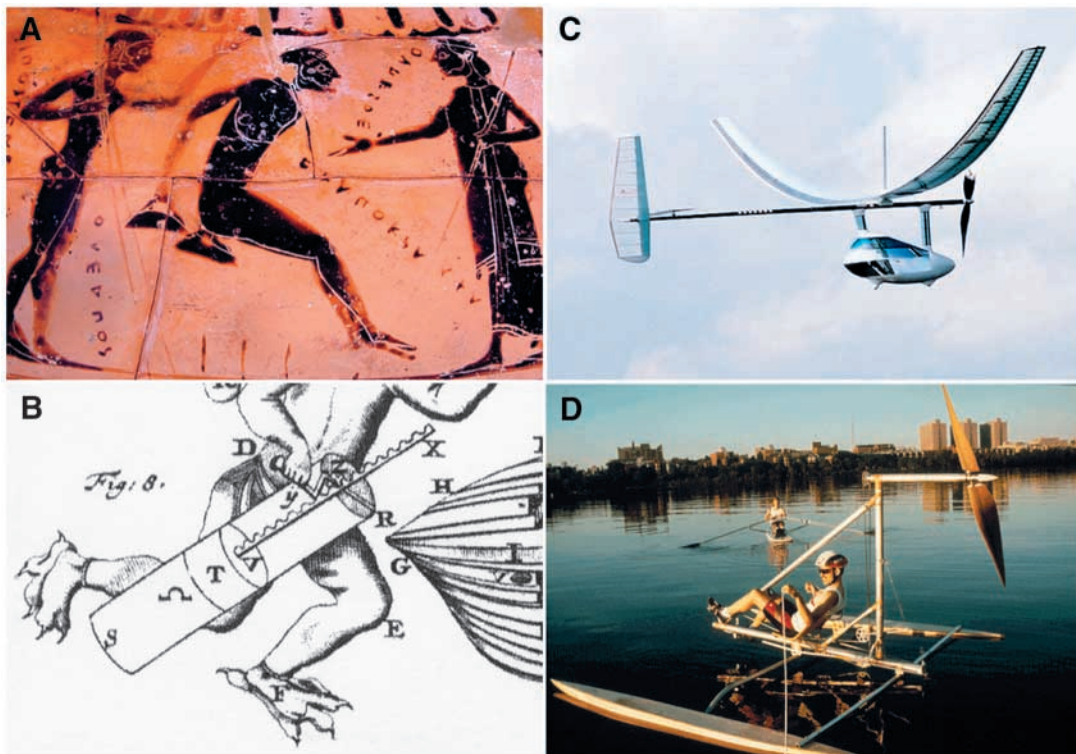


Fig. 1. (A) The hand-held masses (halteres) used to increase the long-jump distance in ancient Olympics. (B) Drawing by Giovanni Alfonso Borelli (1608–1679) published in his ‘*De Motu Animalium*’, suggesting the use of fins in swimming. (C) The human-powered aircraft from the Nihon University Aero Student Group (NASG), flying for almost 35 km at the 27th Birdman Rally (Japan) in 2003 (www.nasg.com/birdman/bm-e.html). (D) The Decavitator, a hydrofoil-based boat with a crank-operated propeller, capable of a speed of about 34 km h^{-1} on the water surface.

flight phase, obtaining additional propulsion (Darby's reported record was 4.49 m).

As far as running is concerned, there is little that can be done to improve performance substantially, although quite different from the concept of a portable passive tool, a compliant 'tuned' (9) track for athletics proved to be successful in (slightly) enhancing running speed (McMahon and Greene, 1978). The main limitations of running reside in: (i) the inverse relationship between contact time and speed, which makes the ability to store/release mechanical energy into/from the elastic structures a limiting factor, (ii) the constraint of stopping the foot with respect to the ground, which implies that (iia) the limbs need to move with respect to the body centre of mass at the same speed that the centre of mass moves with respect to the ground, largely increasing the mechanical internal work (6), and (iib) muscle contraction generates less force for propulsion (2), being directly related to the progression speed. Certain gaits can inherently circumvent these limitations. All the 'skating' techniques, using tools (in chronological sequence) such as ice-skates, cross country skis or roller-skates, demonstrate how a gait that is still bipedal can be fast. This occurs not only because of decreased friction with the

medium (7), but also because at high progression speeds the appendages push while continuing to slide on the medium, thus the contraction speed is much lower than in running (2). If in addition the vertical excursion of the body centre of mass is reduced (5) and the pendulum-like mechanism is still operating (measured in cross country skiing; Minetti et al., 2000), it is not surprising that the 'skating' gaits perform much better than running (1 h endurance record: running=20 km, roller skating=40 km; see Fig. 2). The residual limitation of skating gaits is that the upper limbs are not used, or, if they are, the poles need to stop with respect to the ground, with all the drawbacks discussed above for the lower limbs (2, 6). Further enhancement of cross-country skiing, therefore, needs to be sought in a new design of poles that would allow the pushing portion to slide. In the last few years ice-skaters have adopted an ingenious variation tool, the clapskate (Ingen Schenau, 1996), which increases speed performance by allowing the blade to be in contact with the ice for a longer time at the end of the push.

Leaving bipedal locomotion, we come to the most important invention that has revolutionised personal transportation. The bicycle (1 h endurance record=50 km)

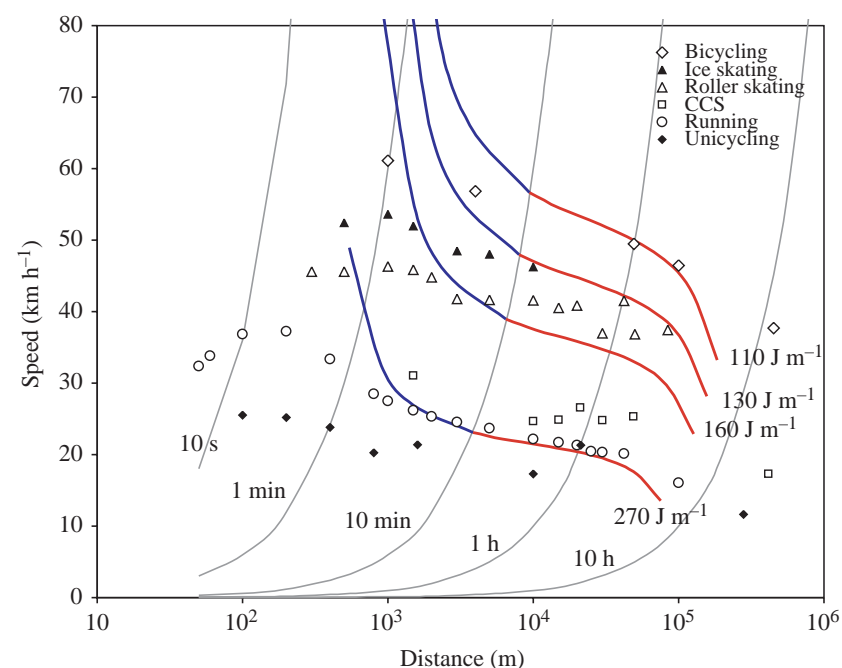


Fig. 2. The effects of passive tools in augmenting human locomotion on land. World records in terms of average speed and performance duration are represented. Vertical curves show the iso-duration relationship between the abscissa and the ordinate. From bottom to top the different locomotions (as indicated in the key) become more and more specialised, starting from running (open circles) to bipedal-like gaits (cross country ski – CCS – and ice speed skating), from hybrid legged-wheeled progressions (roller skating) to just-wheeled ones [cycling; the unicycle records shown at the bottom of the graph represent a simultaneously inefficient and uneconomic locomotion because of the lack of gears (2) and the additional balancing burden (4)]. Superimposed on the graph, are iso-metabolic cost (in J m^{-1}) curves (blue, $t < 10$ min; red, $t \geq 10$ min). For a mathematical discussion of estimation of their speed values, see Appendix.

combines three very good ideas that make it the vehicle of choice for long human-powered journeys on (regular) land: (i) the body weight is sustained by the saddle, avoiding the need for muscles to generate force for postural purposes and minimizing the vertical excursion (5) of the body centre of mass, (ii) it always allow muscles, regardless of the increased progression speed, to operate in the optimal region of the force/velocity relationship (2) by using gears, and (iii) the increased base of support associated with the two wheels avoids the need for balancing work in the sagittal plane (see how metabolically expensive is to ride a unicycle; Fig. 2) and, assisted by the speed generated, in the frontal plane. The early evolution of cycling, dating back from 1820 to 1890 (Minetti et al., 2001), was mainly addressing point (ii) by making the structure less 'shaking', while modern bicycle technology is mostly devoted to reduce the rolling resistance (7) and the main force opposing high speed progression, i.e. the aerodynamic drag (di Prampero, 2000). However, the advantages of an extraordinary tool like the bicycle can be overtaken again by walking and running when the path slope is steeper than 25% (Ardigó et al., 2003).

The world records of most of the locomotion modes described so far are plotted in Fig. 2, where the estimated metabolic cost at the different progression speeds can be appreciated (see legend to Fig. 2).

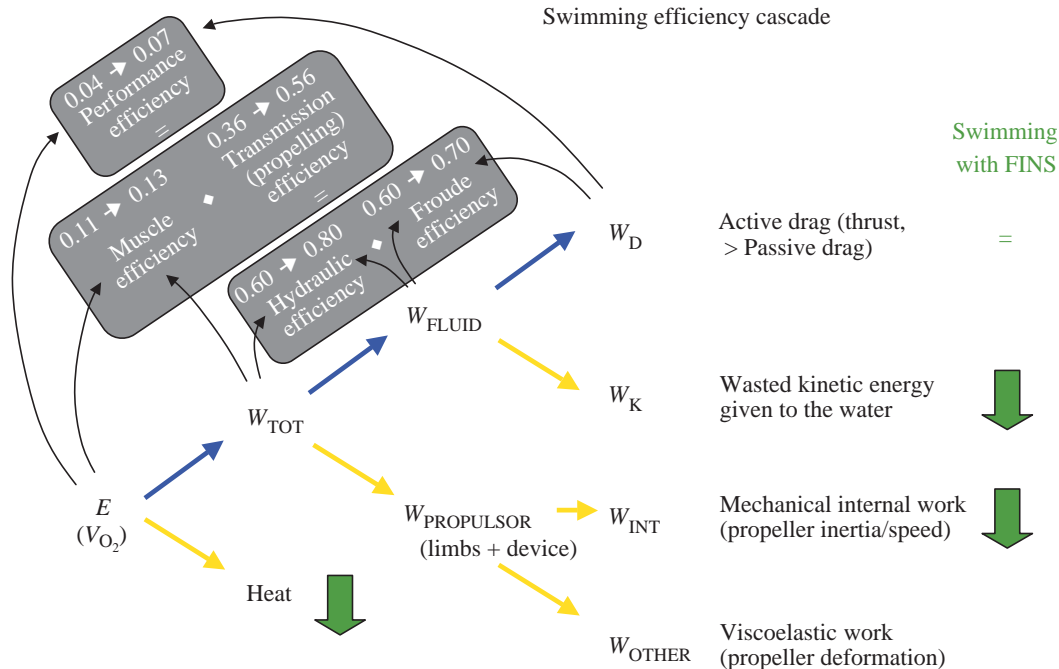


Fig. 3. Efficiency cascade for the leg kick in swimming, with and without fins (adapted from Zamparo et al., 2002). This example illustrates all the possible mechanical works (expressed as costs) to be done: W_D against water drag (which generates propulsion), W_K to uselessly accelerate water, W_{INT} to accelerate limbs, W_{OTHER} to deform propulsive structures (fins). The sum of $W_D + W_K$ is called W_{FLUID} , the sum of $W_{INT} + W_{OTHER}$ is $W_{PROPULSOR}$ and the total mechanical work is W_{TOT} (the sum of $W_{FLUID} + W_{PROPULSOR}$). E represents the metabolic cost for swimming the leg kick and, depending on the muscle efficiency value, is transformed into different proportions of work and heat. For each bifurcation (proceeding left to right and bottom to top) there is a desired transformation, marked by the blue arrow, and a side effect, marked by the yellow arrow. Thus we could say that most of W_{TOT} should be W_{FLUID} and most of W_{FLUID} should be W_D , mainly because W_D is the only indispensable work to secure propulsion (given that body shape and limbs movement). The overall efficiency, here called Performance efficiency (E_{fPE}), which is the ratio between W_D (the unavoidable work) and E , can be considered as the product of other efficiencies relating to the use (or misuse) of mechanical work along the chain. From top to bottom, the Froude efficiency (E_{fFR}) is the ratio between useful work for propulsion and the total work needed to accelerate the fluid, thus it is low when more water is uselessly accelerated. The ratio between W_{FLUID} and W_{TOT} is the Hydraulic efficiency (E_{fHY}), and is low when a lot of work is done because of dissipations or wastes in the propulsive machinery (limbs and fins). The Transmission efficiency (E_{fTR} , in swimming it should be called Propelling efficiency) is the ratio between the indispensable W_D and W_{TOT} (thus it is the product of E_{fHY} and E_{fFR}) and accounts for all the energy degradation 'outside' the involved muscles. The Muscle efficiency (E_{fMU}) is the ratio between the mechanical work and the metabolic energy expenditure (= work + heat) and accounts for the optimality of the operative range (contraction length and speed) and for the presence of co-contractions (resulting in heat with no work). As anticipated, $E_{fPE} = E_{fMU} \times E_{fTR} = E_{fMU} \times E_{fHY} \times E_{fFR}$. This analysis is crucially important, not just to better understand the energy flow in swimming, but also to appreciate the effects of passive tools, as fins, in enhancing this locomotion. While in the quoted study W_{OTHER} was not measured, the experimental W_D , W_K , W_{INT} values have been collected and the efficiency computed both for non-fins and fins conditions. The changes introduced by those passive tools have been marked with green (equal and down arrow) signs, while the change in efficiencies is numerically indicated in the schema. Finally, despite the unquestionable advantage of introducing fins in swimming the leg kick, a lot can still be done (maybe by considering a radically different design of the passive tool) to increase the efficiency and the economy of this locomotion.

Assisted aquatic locomotion

Turning to water locomotion, it does not require any biomechanical knowledge to realize that the human body is not perfectly suited to that medium. We need to move at the air–water interface, and this generates mechanically expensive bow waves, we cannot efficiently undulate our body because of lack of musculo–skeletal design and, even if we could do so, the undulating parts would not efficiently contribute to propulsion. In contrast to aquatic animals, we had to inaugurate paddling with our upper limbs to cope with the body inadequacy. While an advantage is certainly there (compared to just kick swimming), the hands and forearms did not evolve

for that task, thus the overall efficiency remains low. It is apparent, therefore, that this is a field where there is great scope for speed to be generated by passive tools. A recent study (Zamparo et al., 2002) analysed the mechanical and energetic advantage of using fins in kick swimming. The gain in speed, resulting from the application of several strategies (2, 6, 8), is particularly remarkable only if upper limbs do not contribute to propulsion, and this is the reason why fins are so effective in scuba diving. However, the efficiency cascade is not dramatically improved by fins and remains well below the standard for terrestrial locomotion (see Fig. 3 for a comprehensive analysis). A further improvement has been

achieved by using the monofin, a device mimicking the tail fluke of dolphins and simultaneously operated by the two lower limbs. Fig. 4 compares world records of monofin swimming with those of front crawl. It is apparent that, despite the use of a smaller mass of muscle (only lower limbs are active), the monofin is associated with a much better economy of energy and, thus, a higher cruising speed. Also, the analysis shows that, similarly to running (Fig. 2) and different from front crawl, the metabolic cost of swimming with this tool is almost speed-independent.

Assisted launching

It is beyond the aims of this Commentary to propose a fully comprehensive list of passive tools, but it is necessary to briefly mention launching devices. In contrast to the dumbbell-assisted long-jump where masses were thrown (backward) to enhance the human body performance, we are here referring to activities whose goal focuses on the forward thrown object, as in racket sports and archery. Both categories try to remedy the inherent limitation of the musculo-skeletal system by introducing limb-lengthening (e.g. the tool named 'cesta' in the 'pelota vasca', the golf club and the cricket/baseball bat) and elastic tools (badminton and tennis rackets, for example) capable of storing and releasing elastic energy (2, 9) with power-amplifying effects. Archery is probably the most ancient passively augmented human activity (African arrows date back to 25 000 BCE, Chinese crossbow to 1500 BCE). From hunting to war making, the technical evolution of spear/stone/arrow throwing has allowed man to continuously increase the distance thrown and the degree of precision. Modern commercial crossbows, manually loaded tools where the elastic energy of their limb deformation is held by a catch mechanism, are capable of releasing the arrow at about 360 km h^{-1} , for a distance range ($=v^2 g^{-1}$) of about 1 km. The actual record distance for the foot bow (a crossbow where both upper and lower limbs are involved in loading) is 1.8 km (corresponding to a release speed of at least 480 km h^{-1} and an estimated distance on the Moon of 10.8 km). The traditional bow and its modern evolution, the compound bow (H. W. Allen, 1969), deserve a special mention for their technological simplicity and ingenuity. In both tools the mechanical work needed to bend their elastic limbs (9) is slowly done (2) by muscles (back/shoulder) stronger than the ones involved in forward hand throwing. One of the drawbacks of traditional bows, i.e. that the isometric force needed to sustain the tension increases with the distance drawn backward, making the aiming phase with strong bows quite stressful, has been very recently (1969) attenuated by the compound bow. Such an invention consists of a normal bow with limbs, having asymmetrical cams located at the

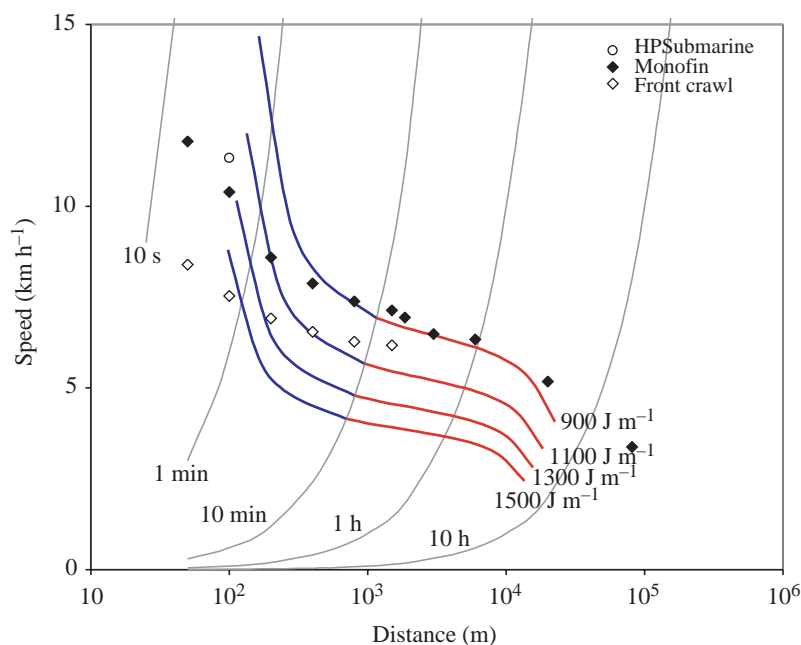


Fig. 4. The effects of passive tools in augmenting human locomotion in water. World records in terms of average speed and performance duration are here represented for front crawl and monofin swimming. Iso-duration and iso-cost curves are as in Fig. 2 and Appendix. The cost of front crawl well matches the data published elsewhere (di Prampero, 1986), showing an increase with speed, while the cost of monofin swimming seems to be speed independent in a wide range of speeds/durations.

ends, which act as pulleys for the string. The variable moment arm generated at the limb ends results in a higher tension, and thus a greater storage of elastic energy at mid-draw, but enables the aiming phase (end-draw) to start by sustaining a fraction (the so-called 'let-off' of, say, 40%) of the 'normal' isometric tension. Since the total energy stored in the bow is represented by the area below the force vs. length curve, a higher power amplification and a better precision (due to a more relaxed aiming) are expected. The distance record for a compound bow is today about 1.4 km. All of the quoted records can be regarded as feats if we consider that hand-throwing an arrow, as some colleagues and I recently experienced in the field, results in a maximal distance of about 21 m.

Other augmented activities

For sake of brevity, we conclude by mentioning those activities where multiple tools (thus multiple power enhancing and energy saving strategies) have been simultaneously adopted, as for instance, in roller/ice skate racket sports (hockey), aerofoil-bicycle-propeller for human powered flight (Gossamer Condor, web.mit.edu/invent/www/ima/maccready_intro.html), hydrofoil-bicycle-propeller for speed record of human powered boat (Decavitator, lancet.mit.edu/decavitator/), bicycle and propeller inhuman powered submarines (www.isrsubrace.org), armchair+bicycle in recumbent bikes, etc.

Conclusions and perspectives

While humans occasionally show interest in designing dissipative activities (beach volley, beach soccer, beach tennis, retro-running, unicycle, water-polo, etc.), most effort is still directed towards enhancing body motion and locomotion by better exploiting muscles, our biological actuators. Some challenges that seemed inconceivable only a few decades ago are today feasible and locomotion performance is increased despite the invariant feature, i.e. the maximum metabolic power the human machinery makes available. This has resulted from the interdisciplinary effort of mechanical engineers, exercise physiologists and biomechanists, together with the technological advancement in material science. The analysis of progression economy and efficiency cascade reveals the activities where research is most likely to enhance performance further. It is thought that the field of biomimetics, where solutions adopted in animal evolution of biological structures are introduced in the human domain, will provide a substantial contribution to such a direction in the near future.

Appendix

The speed values in Fig. 2 were obtained by estimating, for each duration (t , in s), the maximum sustainable mechanical effort (Wilkie, 1980) as:

$$\dot{W}_{\text{MECH}} = A + \frac{B}{t} - \left(\frac{A \left(1 - e^{-\left(\frac{t}{\tau} \right)} \right)}{t} \right), \quad (\text{Ai})$$

where A is the maximum long-term mechanical work (W), B is the mechanical equivalent of the available energy from anaerobic sources (J) and τ is the time constant (s) describing the inertia of the system. As developed by Wilkie, this equation is accurate for durations of 40 s to 10 min. To take into account the decay of the sustainable maximum oxygen consumption for longer exercise durations (Saltin, 1973), terms A have been multiplied by:

$$\frac{\dot{V}_{\text{O}_2}}{\dot{V}_{\text{O}_2\text{max}}} = \frac{940 - 60t}{1000}, \quad (\text{Aii})$$

where the first ratio represents the sustainable proportion of the total metabolic power. With this inclusion, the duration range for accurate speed predictions extends from 40 s to several hours. To calculate iso-cost curves the following equation was used:

$$\dot{s} = \frac{3.6}{C} \left(\frac{\dot{W}_{\text{MECH}}}{Ef} - \dot{W}_{\text{BASMET}} \right), \quad (\text{Aiii})$$

where \dot{s} (km h^{-1}) is the progression speed, Ef is the efficiency of muscle contraction (0.25; Woledge et al., 1985), \dot{W}_{BASMET} is the basal metabolic power (W) and C is expressed as J m^{-1} . For the following simulations we assumed that $A=450$ W, $B=21$ kJ, $\tau=10$ s and $\dot{W}_{\text{BASMET}}=80$ W to approximate the athletes' profile. While the first two equations are always

operating simultaneously, the curves have been coloured to represent the main influencing effect: blue (Wilkie, 1980) for $t < 10$ -min and red (Saltin, 1973) for $t \geq 10$ min.

The lower iso-cost curve [$C=270$ J m^{-1} or 3.6 J (kg m)^{-1} for $\text{mass}=75$ kg] is very well matched to the world records of running. This comes at no surprise since we know that running cost is speed independent and very close to that value. The curve is much higher than the experimental points for short performance duration, where the acceleration in the starting phase requires extra energy and penalizes the average speed (this is supposed to happen in all activities where a standing start is imposed). To draw other iso-cost curves for higher C values can help to estimate the average metabolic cost in short distance sprint race [e.g. for 400 m sprint running, the cost is approximately 400 J m^{-1} or 5.3 J (kg m)^{-1} , corresponding to +48% if compared to normal steady state speed].

In Fig 2, running represents the most expensive form of terrestrial locomotion (except for unicycle), while a progression towards more economical modes is apparent. Hybrid forms (legged + wheels or + skates) imply a 40–50% energy saving, while the bicycle (point mass + wheels) gives a 60% advantage. This increases the average speed and the range (in 1 h humans can run 20 km, rollerskate 40 km and cycle 50 km).

Many thanks to Luca Ardigo and Federico Formenti for helping to search for world records of the illustrated modes of locomotion.

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