CORE

# Update and extension of the 'equivalent slope’ of speed-changing level locomotion in humans: a computational model for shuttle running 

Alberto E. Minetti ${ }^{1,2, *}$ and Gaspare Pavei ${ }^{1}$


#### Abstract

Controlled experimental protocols for metabolic cost assessment of speed-changing locomotion are quite complex to design and manage. The use of the 'equivalent slope', i.e. the gradient locomotion at constant speed metabolically equivalent to a level progression in acceleration, has proved valuable in the estimation of the metabolic cost of speed-changing gaits. However, its use with steep slopes requires extrapolation of the experimental cost versus gradient function for constant running speed, resulting in less-reliable estimates. The present study extended the model to also work with deceleration, and revised the predictive equation to enable it to be applied to much higher levels of speed change. Shuttle running at different distances (from 5+ 5 to $20+20 \mathrm{~m}$ ) was then investigated using the novel approach and software, and the predictions in terms of metabolic cost and efficiency compare well with the experimental data.


KEY WORDS: Cost of transport, Acceleration, Deceleration, Unsteady, Running

## INTRODUCTION

Unsteady locomotion in terms of both non-linear trajectory and speed changes is a common observation in the everyday life of humans and animals, as well as in sport activities of bipeds and quadrupeds. The scientific interest regarding mechanical (manoeuvrability, static and dynamic stability, performance) and metabolic sustainability of those gait changes with respect to linear/ constant speed locomotion has been met so far by only a few papers (e.g. Alexander, 2002; Wilson et al., 2018).

Moving at fluctuating speed in humans has received attention only in the last two decades. In particular, the metabolic cost and mechanics of walking and running at imposed unsteady speed were studied (Minetti et al., 2001, 2013), but only for smallintermediate accelerations/decelerations about the average speed. Interest in the metabolic implications of unsteady locomotion increased with attempts to infer the players' effort in sports such as soccer and rugby, where locomotion during the match is far from occurring at constant speed. In addition, relevant speed changes are supposed to be associated with high metabolic cost, but the experimental protocol capable of reliably measuring this came up against the problem of steady-state condition. For this reason, an

[^0]alternative had to be found, and 'the equivalent slope' concept came to hand.

The concept of 'equivalent slope' (ES) has previously been used in the physiomechanics of cycling and sprint running. In cycling, the 'rolling resistance equivalent slope, a very shallow downhill gradient at which the negative potential energy changes balance the work necessary to overcome the rolling resistance' was suggested as a handy laboratory tool to estimate tyre friction on the ground (Ardigò et al., 2003). The concept was to convert the deceleration of coasting down (on the level) into a downhill slope at which the bicycle+rider could passively remain stationary on a treadmill (thus moving at constant speed). At that gradient, gravity provides a net forward component that equates the rolling resistance effect when moving on the level. Very conveniently, the coefficient of rolling resistance corresponds to the tangent of that slope angle.

In sprint running, the ES (di Prampero et al., 2005) is an ingenious and convenient tool to infer the metabolic cost of transport of level running at (constant) acceleration by considering it an analogue of running uphill at a constant speed, for which the cost $\left(C, \mathrm{~J} \mathrm{~kg}^{-1} \mathrm{~m}^{-1}\right)$ is available in the literature (Minetti et al., 2002):

$$
\begin{equation*}
C=155.4 i^{5}-30.4 i^{4}-43.3 i^{3}+46.3 i^{2}+19.5 i+3.6 \tag{1}
\end{equation*}
$$

where $i$ is the (downhill: negative, uphill: positive) gradient (in terms of the tangent of slope angle). This equation, designed to serve as an accurate description of the measured dataset, is valid only within $-0.45<i<+0.45$, corresponding to the gradient range of metabolic experiments. As the ES for acceleration can be written as:

$$
\begin{equation*}
\mathrm{ES}=\frac{a_{\mathrm{f}}}{\boldsymbol{g}} \tag{2}
\end{equation*}
$$

where $a_{\mathrm{f}}\left(\mathrm{m} \mathrm{s}^{-2}\right)$ is forward acceleration and $\boldsymbol{g}$ is gravity, the replacement of gradient $i$ with ES in Eqn 1 is safely allowed only when $-4.41<a_{\mathrm{f}}<+4.41 \mathrm{~m} \mathrm{~s}^{-2}$. Beyond these limits, the extrapolation of $C$ can be unsafe [reliability decreases with the (squared) distance from the limit].

Recent work (P. Zamparo, G.P., A. Monte, F. Nardello, T. Otsu, N. Numazu, N. Fujii and A.E.M., unpublished) on the mechanics and energetics of shuttle running, an activity incorporating large accelerations and even larger decelerations, and the fact that sprint running also involves accelerations (up to $7 \mathrm{~m} \mathrm{~s}^{-2}$ ) well beyond the indicated limits, both encouraged us to update and further develop the previous predictive tools (di Prampero et al., 2005; Minetti et al., 2002) in order: (1) to enhance inference reliability in an extended range of accelerations and (2) to also make metabolic predictions for decelerated running.

The extension to a wider range of accelerations benefits from recent metabolic results (Giovanelli et al., 2016) of uphill, constantspeed running up to $i=+0.84$ that, according to Eqn 2, corresponds to level accelerations up to $8.24 \mathrm{~m} \mathrm{~s}^{-2}$.

The aim of the present study was to build a conceptual/ computational framework allowing us to infer the metabolic demand of accelerated/decelerated running, based either on the ES analogue (see above) or on the ultimate meaning of the cost of transport (see below), which is immediately applicable to shuttle runs in humans, but is also potentially transferable to unsteady animal locomotion.

## MATERIALS AND METHODS

## Mathematical model

When pooling previous and recent results (Minetti et al., 2002; Giovanelli et al., 2016; see Fig. 1), the whole dataset confirms the trend of an oblique asymptote at very steep gradients. This suggests that the uphill part $(i>0)$ of the phenomenon should be modelled as a combined equation composed of an oblique line (asymptote) summed to a decreasing exponential. The result, obtained by using a graphical/statistical package (Grapher, Apple Computers Inc., USA) with the uphill data only, is:

$$
\begin{equation*}
C_{\mathrm{PG}}=39.5 i+3.6 e^{-4 i} \tag{3}
\end{equation*}
$$

where $C_{\mathrm{PG}}$ is the cost of positive gradient (running).


Fig. 1. Metabolic cost of running ( $C$ ) versus gradient ( $\boldsymbol{i}$ ). Open circles are data from Minetti et al. (2002): the positive gradient is in red, the negative gradient is in blue. Solid black circles are data from Giovanelli et al. (2016). The thin black line through the circles represents the curve for Eqns 3 and 4 (see Materials and Methods, 'Mathematical model'), whereas the linear (asymptotic) component of Eqns 3 and 4 is presented as a straight black line starting from the origin.

Although there are no new data in the literature, to our knowledge, about the metabolic cost of downhill running at $i<-0.45$, the visual inspection of Fig. 1 suggests that the trend shown by the oblique asymptote indicated by the existing data (Minetti et al., 2002) is reliable. By following the same approach as that leading to Eqn 3 (the only difference is that here we need an increasing exponential), a new fitting of (just) the downhill data is obtained as:

$$
\begin{equation*}
C_{\mathrm{NG}}=-8.34 i+3.6 e^{13 i} \tag{4}
\end{equation*}
$$

where $C_{\mathrm{NG}}$ is the cost of negative gradient (running). Regression coefficients in Eqns 3 and 4 have been slightly adjusted to reduce the number of digits and to ensure continuity between the two curves (at $i=0$ ).

The accuracy of the newly proposed equation(s) for $C$ has been tested by computing the ratio, in the range $-0.45 \leq i \leq+0.45$, between Eqns 4 and 3 with the negative and positive gradient branches of Eqn 1, respectively, resulting in an average value of 0.9993 . Curves for Eqns 3 and 4 are also plotted in Fig. 1.

The present mathematical approach (Eqns 4 and 3) to data fitting is more modellistic than descriptive (Eqn 1), and it comes from a suggestion about the efficiency of locomotion introduced in the first half of the last century (Margaria, 1938). In synthesis, there has to be a minimum cost ( $C_{\text {min }}, \mathrm{J} \mathrm{kg}^{-1} \mathrm{~m}^{-1}$ ) for gradient running (and walking), which relates to coping with the inevitable work to sustain overall positive (uphill) and negative (downhill) changes in potential energy of the body ( $W_{\text {vert }}, \mathrm{J} \mathrm{kg}^{-1} \mathrm{~m}_{\text {vert }}{ }^{-1}$, where $\mathrm{m}_{\text {vert }}$ is the vertical metres travelled).

By following the formula of Minetti et al. (2002):

$$
\begin{equation*}
C_{\min }=\frac{W_{\mathrm{vert}}}{\mathrm{eff}}=\frac{\boldsymbol{g}}{\mathrm{eff}} \sin (\operatorname{atan} i) \tag{5}
\end{equation*}
$$

where eff refers to the efficiency of converting metabolic into mechanical energy. Depending on the sign of $i$, maximum eff value for positive work $(0.25, i>0)$ and for negative work $(-1.25, i<0)$ done by muscle force is used. This, together with the approximation $i=\sin (\operatorname{atan} i)$ (see below), results in:

$$
C_{\min }=39.2 i(\text { uphill gradient })
$$

and

$$
\begin{equation*}
C_{\min }=-7.85 i(\text { downhill gradient }) \tag{6}
\end{equation*}
$$

the coefficients of which closely resemble the linear components of Eqns 3 and 4 where, in accordance with muscle physiology (Woledge et al., 1985), the absolute ratio between negative and positive efficiencies (and, consequently, between slopes of the linear parts of $C$ curves) is close to 5 [from Eqns 3 and 4, $\operatorname{abs}(39.5 /-8.34)=4.7]$.

The linear components of Eqns 3 and 4 are plotted in Fig. 1 as straight lines.

The concept of ES of accelerated running has been introduced together with 'equivalent mass' (EM; di Prampero et al., 2005). EM, expressed as a fraction of the actual body mass, is a value greater than 1 to take into account the amount of the accelerating (or decelerating) vector in the analogous gradient (at ES) running at constant speed, and can be rewritten as:

$$
\begin{equation*}
\mathrm{EM}=\left(\mathrm{ES}^{2}+1\right)^{0.5} \tag{7}
\end{equation*}
$$

In the original paper, the metabolic cost of accelerated running ( $C_{\mathrm{AR}}, \mathrm{J} \mathrm{kg}^{-1} \mathrm{~m}^{-1}$ ) was computed by using equivalent versions of the present Eqns 2 and 7, in combination with Eqn 1, where gradient
$i$ was replaced by ES, as:

$$
\begin{align*}
C_{\mathrm{AR}} & =\left(55.4 \mathrm{ES}^{5}-30.4 \mathrm{ES}^{4}-43.3 \mathrm{ES}^{3}+46.3 \mathrm{ES}^{2}\right.  \tag{8}\\
& +19.5 \mathrm{ES}+3.6) \mathrm{EM}
\end{align*}
$$

By adapting the same rationale to an extended range of accelerations (and, consequently, ES values), Eqns 2, 3 and 7 were combined to obtain, after algebraic simplification:

$$
\begin{equation*}
C_{\mathrm{AR}}=0.102\left(a_{\mathrm{f}}^{2}+96.2\right)^{0.5}\left(4.03 a_{\mathrm{f}}+3.6 e^{-0.408 a_{\mathrm{f}}}\right) \tag{9}
\end{equation*}
$$

Eqn 9 can be safely used to predict $C_{\mathrm{AR}}$ for $0<a_{\mathrm{f}}<8.24 \mathrm{~m} \mathrm{~s}^{-2}$.
The metabolic cost of decelerated running ( $C_{\mathrm{DR}}, \mathrm{J} \mathrm{kg}^{-1} \mathrm{~m}^{-1}$ ) is obtained by considering:

$$
\begin{equation*}
\mathrm{ES}=\frac{d_{\mathrm{f}}}{\boldsymbol{g}} \tag{10}
\end{equation*}
$$

where $d_{\mathrm{f}}\left(\mathrm{m} \mathrm{s}^{-2}\right)$ is forward deceleration (a negative value), and by combining Eqns 10, 4 and 7, as:

$$
\begin{equation*}
C_{\mathrm{DR}}=0.102\left(d_{\mathrm{f}}^{2}+96.2\right)^{0.5}\left(-0.85 d_{\mathrm{f}}+3.6 e^{1.33 d_{\mathrm{f}}}\right) \tag{11}
\end{equation*}
$$

Eqn 11 can be safely used for $-4.41<$ d.f. $<0 \mathrm{~m} \mathrm{~s}^{-2}$. As the fitting equation (Eqn 4) is based on data already showing an asymptotic trend within the experimental gradient range, we are encouraged to use it with confidence even for $-8.24<$ d.f. $<0 \mathrm{~m} \mathrm{~s}^{-2}$.

Eqns 9 and 11, alone or in combination, allow us to infer the metabolic cost of just accelerated running (as in sprints), in structured sequences of acceleration and deceleration bouts (shuttle running), and in sporting activities where complex combinations of accelerated and decelerated running irregularly occur (as in soccer, rugby, basketball, baseball, etc.).

A relevant comment is on the mechanical resemblance of the ES when applied to different motion activities. When referring to just the overall centre of mass, the mechanics of speed changing on a level can be converted into a constant speed at a given, equivalent (uphill or downhill) slope. This is the case of the ES of bicycles (Ardigò et al., 2003), invoked to easily estimate tyre rolling resistance, where the subject even refrains from pedalling on the downhill gradient, which makes the bike stationary on the treadmill (this is also a pure rolling resistance measurement as no air drag is acting on the subject).

When applying the ES concept to running, which incorporates the use of metabolic data obtained when moving on gradients, a concern about other components of the total mechanical work could arise. The internal mechanical work ( $W_{\mathrm{int}}, \mathrm{J} \mathrm{kg}^{-1} \mathrm{~m}^{-1}$ ), which accounts for the accelerations of body segments with respect to the body centre of mass (Cavagna and Kaneko, 1977), has been shown to be affected by many variables (Minetti, 1998):

$$
\begin{equation*}
W_{\mathrm{int}}=f v\left(1+\left(\frac{d}{1-d}\right)^{2}\right) q \tag{12}
\end{equation*}
$$

where $f$ is the stride frequency $(\mathrm{Hz}), v$ is progression speed $\left(\mathrm{m} \mathrm{s}^{-1}\right), d$ is the duty factor (the fraction of the stride for which one foot is in contact with the ground) and $q$ is a compound term incorporating anthropometric data of the body segments.

It is possible that legged species such as humans would adopt different values of these variables, and thus would be expected to have a different $W_{\mathrm{int}}$, when moving in the two 'equivalent' conditions. In particular, inferring the metabolism of level locomotion from gradient experiments where effort included the metabolic equivalent of a different (total) mechanical work value could introduce some bias. Moving on slopes, particularly uphill
running, is related to a much slower progression speed and a higher stride frequency (Minetti et al., 1994). Even the maintenance of the speed independency of the metabolic cost of transport on slopes cannot help in this respect, and a check for $W_{\text {int }}$ should be done for the two compared conditions. This is the case for extreme accelerations (or decelerations) such as during a 100 m sprint, where ES is so high that speed and stride frequency (but also stride length) of a manageable metabolic experiment on a gradient could potentially lead to an underestimation of $W_{\text {int }}$.

Another important precaution is to consider all other determinants of the total mechanical work in the activity under investigation. Air drag, for example, can be relevant at the highest speed of the acceleration phase of sprint running (but not in ES for rolling resistance or slope running in the lab). In contrast, for shuttle running, Eqns 9 and 11 can take care of the metabolic equivalent of the accelerative and decelerative phases, respectively, but the energy required to rotate the body at speed inversion is not included in the prediction.

This new mathematical model, based on the revamped concept of ES, can be implemented in a new activity logger aimed at detecting and monitoring daily and physical activity with an improved analysis of energy expenditure. Unlike the present computational scheme, where acceleration and deceleration phases in shuttle running have been modelled as exponential functions of time, activity monitors (with GPS) would start from the continuous daily recording of body geolocation, from which instantaneous speed and acceleration would be obtained and fed into the described model (Eqns 9 and 11).

## Computational model of shuttle running

The model is based on the assumption that the accelerative and decelerative phases of a maximal shuttle run (SR) of different section (leg) distances are portions of the same patterns exhibited when performing a very long SR (say $20+20 \mathrm{~m}$ ). In a short-distance SR (for instance, a $10+10 \mathrm{~m} \mathrm{SR}$ ), speed will reach a lower maximum value than in a longer SR, but its rise from zero and descent to zero (in a single leg) will follow the same exponential pattern of the much longer-lasting acceleration and deceleration of the longest SR. This tendency also comes from a recent biomechanical analysis of SRs from $5+5$ to $20+20 \mathrm{~m}$ (P. Zamparo, G.P., A. Monte, F. Nardello, T. Otsu, N. Numazu, N. Fujii and A.E.M., unpublished), and, just for the acceleration phase, also from 20 m sprint experiments on the same subjects (to allow comparison, $20+20 \mathrm{~m}$ SR shows accelerative phases of about 13 m ).

The dynamics of speed change for acceleration and deceleration can be modelled according to a mono-exponential function (e.g. Furusawa et al., 1927; di Prampero et al., 2005):

$$
\begin{equation*}
v=v_{\max }\left(1-e^{-t / \tau}\right) \tag{13}
\end{equation*}
$$

where $v_{\max }$ is the asymptotic, maximum speed $\left(\mathrm{m} \mathrm{s}^{-1}\right)$, and $\tau$ is the time constant (s). Eqn 13 is valid for SR acceleration phases when $t \geq 0, \tau_{a_{\digamma}}>0$, and for SR deceleration phases when $t \leq 0, \tau_{d_{\mathrm{r}}}<0$.

In the computational model, it seemed useful to represent on the time axis a deceleration phase first $(t<0)$, followed by the acceleration $(t \geq 0)$, so that we could represent in the same graphic frame (one leg of) SRs of very different lengths (see Fig. 2 legend) and accommodate the iterative process to determine the maximum speed for each of them ( $\left.\hat{v}_{\text {max }, \text { SR }}\right)$.

The computational model has, as inputs, data from long-distance SRs (say $20+20 \mathrm{~m}$ ): $v_{\max }, \tau_{a_{\mathrm{f}}}$ and $\tau_{d_{\mathrm{f}}}$. These three parameters were obtained as follows: $v_{\max }$ and $\tau_{a_{\mathrm{f}}}$ came as unknowns of a non-linear


Fig. 2. Output of the computational version of the present model applied to the prediction of energy expenditure during shuttle runs at maximal speed and different distances. In the main graph, the exponential rise and decrease of speed [ $v\left(\mathrm{~m} \mathrm{~s}^{-1}\right)$, green curve], set by the maximum speed and the two tau ( $\tau$ ) coefficients, together with the total shuttle distance, are the actual inputs to the program. Deceleration has been drawn before the acceleration phase to represent just one leg of the shuttle run (SR) and as a strategy to accommodate, in the same graph, (half) SRs of different lengths. Curves for space travelled [ $s(m)$, white curve] and acceleration [a ( $\mathrm{m} \mathrm{s}^{-2}$ ), grey curve] were obtained by integration and differentiation, respectively. As a matter of graphical convenience, $s$ and $a$ have changed sign when time is negative (i.e. during the decelerative phase). Curves for equivalent slope (ES; orange), equivalent mass (EM; light green) and cost ( $C, \mathrm{~J} \mathrm{~kg}^{-1} \mathrm{~m}^{-1}$; purple) were computed according to Eqns $(2,10), 7,(9,11)$, respectively. ES for the deceleration phase has changed sign for graphical purposes. For each SR leg distance $(20+20 \mathrm{~m}, 15+15 \mathrm{~m}, 10+10 \mathrm{~m}$, $5+5 \mathrm{~m})$, the horizontal dashed line represents the maximum speed chosen from the iterative procedure devoted to making the sum of the deceleration and acceleration distances compatible with half of the SR overall distance. The dashed vertical lines delimit the zone of interest, here, for (half of) the SR of $20+20 \mathrm{~m}$, down to $5+5 \mathrm{~m}$ (see Materials and Methods, 'Computational model of shuttle running' for further details). The thick white curve refers to the apparent efficiency of positive muscle work according to the measured mechanics of gradient running (Minetti et al., 1994), with time confined to the zone of interest. The inset graph at the top left of the figure shows the reconstructed first leg of SRs of different distances, with the accelerative phase followed by the decelerative one. The output of the program includes the average values of metabolic cost due to speed changing and of the average apparent efficiency of positive work of the entire SR.
regression of Eqn 13, fitting speed data in the acceleration phase, while $\tau_{d_{\mathrm{f}}}$ was the only unknown parameter of a non-linear regression of Eqn 13 where $v_{\text {max }}$ was imposed (as one of the results from the other regression), fitting just deceleration data (see Appendix 1).

The time course of distance, speed, deceleration/acceleration, ES, EM and $C$ are based on the new equations developed in this paper, as explained in Fig. 2 legend. Then, depending on the SR distance of interest ( $s_{\mathrm{SR}}$, actually just one leg, 10 m for, say, $10+10 \mathrm{~m} \mathrm{SR}$ ), an iterative process finds the relevant average $C$, the average apparent efficiency of muscle positive work and other outcomes such as the maximum speed reached.

The computational process starts from the (obvious) fact that the maximum speed reached at the end of the acceleration phase is the same as that at the start of the deceleration phase. The tentative value for $\hat{v}_{\text {max }, \text { SR }}$ starts from $v_{\text {max }}$ and decreases it by small amounts; for each of them (which in Fig. 2 corresponds to lowering the horizontal dashed lines): (1) deceleration and acceleration durations are calculated (as intersections with the two exponential curves for speed, and marked by two vertical dashed lines in Fig. 2), (2) deceleration and acceleration distances are obtained (as values on the $s$ curves, Fig. 2, corresponding to the two identified time
intervals) and (3) summed to obtain the total inferred SR distance (single leg), which (4) is compared with the $s_{\mathrm{SR}}$ by using a small threshold; (5) if the estimated distance is higher than the goal, the tentative value for $v_{\text {max, SR }}$ is lowered and a new iteration starts.

At the end of the process, the average metabolic cost of that SR $\left(C_{\mathrm{SR}}, \mathrm{J} \mathrm{kg}^{-1} \mathrm{~m}^{-1}\right)$, due just to speed changes ( $\mathrm{d} v$ ) of the body centre of mass, can be obtained by the $\Delta s$-weighted mean of the $C$ curve within the iteratively 'established' time frame of that specific SR (i.e. within each pair of vertical dashed lines in Fig. 2). The entire computational process was designed using Labview Programming Language (v13, National Instruments, Austin, TX, USA); the software ran on a MacBook Pro (Apple, Cupertino, CA, USA) laptop computer. Also, early stages of the mathematical model were tested by using Grapher (Apple).

The software algorithm also provides an estimate of the average 'apparent' efficiency of the positive mechanical work during each SR, based on the ES values during SRs. Level running (at constant speed) is associated with an equal amount of positive and negative work of the body centre of mass (due to equal excursions of potential and kinetic increases and decreases). That 'external' work could be called 'apparent' as some of the positive (negative) work is
not generated by muscles: instead, it comes 'at no metabolic cost' from mechanical strain energy released by (the amount previously stored, again at no metabolic cost, in) tendons. When running on uphill (downhill) slopes, positive (negative) work becomes predominant, and beyond the slope range of $\pm 0.35$, gradient running shows a monotonic increase (decrease) of the body centre of mass [thus, just positive (negative) work is done], which impairs the chances of storing (releasing) elastic energy in (from) tendons (Minetti et al., 1994).

Therefore, with respect to the slope, the apparent efficiency of positive mechanical work is assumed to be: (a) 0 for downhill slopes steeper than -0.35 , (b) an increasing value up to 0.80 at $i=0$ (in that range and in the next, different mixes of positive and negative work are performed), which is the maximum apparent efficiency of positive muscle work in level running at the maximum speed of SRs (Cavagna and Kaneko, 1977), (c) a decreasing value down to 0.25 (maximum muscle efficiency) at a slope equal to +0.35 , (d) beyond which 0.25 would be constant as only positive work is done (see Fig. 3).

In Fig. 2, the time course of apparent efficiency (eff, which depends on ES) is shown, within the relevant time frame, as a thick white curve. From the calculated average value along one SR leg [ eff $_{\text {mean }}$, assumed to be the same for the other leg(s)], we could infer how much mechanical energy saving via the elastic mechanism has occurred (zero for eff ${ }_{\text {mean }} \approx 0.25$ and the maximum possible when approaching 0.75-0.80).

Predictions of average $C_{\mathrm{SR}}$ (on the level) rely, as mentioned, on gradient running (Minetti et al., 1994; Giovanelli et al., 2016) where $W_{\text {int }}$ was the result of different values of the crucial variables involved (see Eqn 12). Thus, estimates of $C_{\text {SR }}$ based on the ES concept have to be corrected by adding the metabolic equivalent of the 'extra' $W_{\text {int }}$ that would fill the gap toward the actual $W_{\text {int }}$ of SR events. To do this, we compared single-stride $W_{\text {int }}$ data obtained during a 20 m sprint (G.P., P. Zamparo, N. Fuji, T. Otsu, N. Numazu, A.E.M. and A. Monte, unpublished) to the average values measured in steady running experiments at different gradients (Minetti et al., 1994). To allow a functionally meaningful estimation of the $W_{\text {int }}$ gap between the two conditions, data measured on slopes


Fig. 3. The apparent efficiency of positive muscle work (eff $w_{\text {tott }}$ ) versus ES. This graph is the result of investigations into running mechanics on the level (Cavagna and Kaneko, 1977) and on positive and negative gradients (Minetti et al., 1994), and of the proposed rationale linking it to accelerations and decelerations found in SRs (see Materials and Methods, 'Computational model of shuttle running').
were time aligned according to when, during the sprint, the ES value was close to the investigated uphill gradient.

Also, the metabolic energy of body turning at the end of SR legs is not included in the model based on Eqns 9 and 11. Here, three approaches are available, as detailed below: (i) estimating the minimum mechanical and metabolic cost to twist the body 180 deg about the vertical axis in the same time interval of the SR experiments, (ii) searching the literature to find the metabolic cost of running in circles of small radius, and (iii) inspecting studies about the metabolic cost of changing direction in running.

Approach i : twist of the body can be modelled as a turning from angle $(\theta, \mathrm{rad}) 0$ to $\pi$ about the vertical axis, lasting a time $\Delta t(\mathrm{~s})$, with an initial and final angular speed ( $\omega, \mathrm{rad} \mathrm{s}^{-1}$ ) equal to zero and a time course following a sine function of time:

$$
\begin{equation*}
\omega=A \sin (B t) \tag{14}
\end{equation*}
$$

where $A$ is the peak speed, occurring at $\theta=\pi / 2$, equal to $\pi^{2} / 2$, and $B=\pi / \Delta t$. From this equation, the angle ( $\theta, \mathrm{rad}$ ) time course is:

$$
\begin{equation*}
\theta=\frac{A}{B}[1-\cos (B t)] \tag{15}
\end{equation*}
$$

and the angular acceleration $\left(\alpha, \operatorname{rad~s}^{-2}\right)$ :

$$
\begin{equation*}
\alpha=A B \cos (B t) \tag{16}
\end{equation*}
$$

can be calculated (by integration and differentiation, respectively, of Eqn 14). As rotational power ( $\dot{W}_{\text {rot }}, \mathrm{W}$ ) is defined as:

$$
\begin{equation*}
\dot{W}_{\mathrm{rot}}=I_{z} \alpha \omega, \tag{17}
\end{equation*}
$$

where $I_{z}$ is the moment of inertia $\left(\mathrm{kg} \mathrm{m}^{2}\right)$ of the body, the positive mechanical work of (half) a turn ( $W_{\text {turn }}, \mathrm{J}$ ) can be obtained as:

$$
\begin{equation*}
W_{\text {turn }}=\int_{0}^{\frac{\Delta t}{2}} \dot{W}_{\text {rot }} \mathrm{d} t \tag{18}
\end{equation*}
$$

which results in:

$$
\begin{equation*}
W_{\mathrm{turn}}=\frac{\pi^{4}}{8} I_{z} \tag{19}
\end{equation*}
$$

Finally, to incorporate the cost of turning ( $C_{\text {turn }}$ ) into the overall metabolic cost of SRs, namely as $\mathrm{J} \mathrm{kg}^{-1} \mathrm{~m}^{-1}$, Eqn 19 becomes:

$$
\begin{equation*}
C_{\mathrm{turn}}=\frac{\pi^{4}}{8 m \mathrm{eff}_{\text {muscle }} D_{\mathrm{SRleg}}} I_{z} \tag{20}
\end{equation*}
$$

where $m$ is body mass $(\mathrm{kg})$, eff muscle is muscle efficiency for positive work ( $0.25-0.30$ ) and $D_{\text {SRleg }}$ is the distance of a single SR leg (m). When considering $I_{z}=3.83 \mathrm{~kg} \mathrm{~m}^{2}$ and $m=75 \mathrm{~kg}$, Eqn 20 becomes:

$$
\begin{equation*}
C_{\text {turn }}=\frac{2.49}{D_{\text {SRleg }}} \tag{21}
\end{equation*}
$$

This estimate of $C_{\text {turn }}$ has to be considered the minimum cost of a 180 deg turn of the (slightly crouched) body about its vertical axis.

Approach ii: studies on the energy cost of running in small circles are rather scarce in the literature. To the authors' knowledge, the smallest investigated turn radius is 1 m (Minetti et al., 2011). The metabolic cost of running along that circle was found to be almost speed independent, and equal to $283.1 \pm 64.1 \mathrm{ml} \mathrm{O}_{2} \mathrm{~kg}^{-1} \mathrm{~km}^{-1}$, or $5.78 \pm 1.31 \mathrm{~J} \mathrm{~kg}^{-1} \mathrm{~m}^{-1}$. It has to be remembered that 1 m radius refers to the distance of the pivot from where the feet were placed; actually, the 'effective' turn of the body centre of mass occurred at a radius of $0.72-0.84 \mathrm{~m}$. From those data, the distance for half a circle
was 3.14 m , thus:

$$
\begin{equation*}
C_{\text {turn }}=\frac{18.1}{D_{\text {SRleg }}} . \tag{22}
\end{equation*}
$$

Approach iii: a paper on the metabolic cost of changing direction in running helps to add an estimate of the extra metabolic cost with respect to the predictions from Eqns 9 and 11. Zamparo and colleagues (2014) showed that shuttles with full inversion (180 deg), when compared with other runs with just the straight ( 0 deg ) stop-and-go, resulted (non-significantly, though) in about $+0.9 \mathrm{~J} \mathrm{~kg}^{-1} \mathrm{~m}^{-1}$ metabolic cost, in shuttle runs of 10 m (corresponding to about $9.0 \mathrm{~J} \mathrm{~kg}^{-1}$ turn $^{-1}$ ). Thus, the extra cost here is:

$$
\begin{equation*}
C_{\text {turn }}=\frac{9.0}{D_{\text {SRleg }}} \tag{23}
\end{equation*}
$$

expressed in $\mathrm{J} \mathrm{kg}^{-1} \mathrm{~m}^{-1}$.

## RESULTS

Fig. 4 shows the difference in mechanical internal work ( $W_{\text {int }}$ ) when considering data from from sprint (which can be considered as SRs at maximal performance) and from uphill running (at submaximal constant speed) at the same ES/slope. The comparison reveals about $1 \mathrm{~J} \mathrm{~kg}^{-1} \mathrm{~m}^{-1}$ of additional internal work ( $0.925 \pm 0.069 \mathrm{~J} \mathrm{~kg}^{-1} \mathrm{~m}^{-1}$ ) that has to be added, in the form of its metabolic equivalent:

$$
\begin{equation*}
C_{\text {extra } W_{\text {int }}}=3.083 \tag{24}
\end{equation*}
$$

in $\mathrm{J} \mathrm{kg}^{-1} \mathrm{~m}^{-1}$, for a muscle efficiency of 0.30 , to the $C_{\mathrm{SR}}$ estimate obtained from Eqns 9 and 11.

Input parameters for the computational model were: $v_{\max }=7.175 \mathrm{~m} \mathrm{~s}^{-1}, \tau_{a_{\mathrm{f}}}=0.803 \mathrm{~s}^{-1}$ and $\tau_{d_{\mathrm{f}}}=0.472 \mathrm{~s}^{-1}$ (data source for the quoted regressions is P. Zamparo, G.P., A. Monte, F. Nardello, T. Otsu, N. Numazu, N. Fujii and A.E.M., unpublished, maximal $20+20 \mathrm{~m}$ SR only); their coefficient of variation (CV) ranges from $7.7 \%$ to $10.9 \%$.


Fig. 4. $W_{\text {int }}$ for sprint and ES of uphill running. Step by step mechanical internal work ( $W_{\text {int }}$, means $\pm$ s.d., black squares) during the acceleration phase of a maximal 20 m sprint (G.P., P. Zamparo, N. Fuji, T. Otsu, N. Numazu, A.E.M. and A. Monte, unpublished), and during treadmill running on different uphill slopes at constant submaximal speed (means $\pm$ s.d., grey diamonds; Minetti et al., 1994) are compared. Each point of the second data series has been time aligned in the graph so as to appear where a step of the sprint sequence, because of its instantaneous forward acceleration ( $a_{f}$ ), reports an ES very close to the uphill treadmill slope.


Fig. 5. Experimental and estimated metabolic cost (C) of SR as a function of (half) distance. Predictions are shown as just ES [speed changes (dv) only], ES+extra internal mechanical work ( $W_{\text {int }}$ ) and ES + extra $W_{\text {int }}+$ turning cost.

Model-estimated maximum speed of SRs ( $\hat{v}_{\text {max }, \text { SR }}$ ) was compared with the (average value of) measured maximum speed, at the different SR distances, and resulted in an overestimation of $4.96 \pm 1.64 \%$.

Fig. 5 shows experimental results of $C_{\mathrm{SR}}$ using data from Buglione and di Prampero (2013) and Zamparo et al. (2015), and the predictions from the present model for each SR distance. Input parameters for the algorithm were $D_{\text {SRleg }}$ and the measured $v_{\max }, \tau_{a_{f}}$ and $\tau_{d_{\mathrm{f}}}$ from kinematic motion capture of $20+20 \mathrm{~m}$ SR experiments (P. Zamparo, G.P., A. Monte, F. Nardello, T. Otsu, N. Numazu, N. Fujii and A.E.M., unpublished), as mentioned. Here, inferred $C_{\text {SR }}$ from the comprehensive model is:

$$
\begin{equation*}
C_{\mathrm{SR}}=C_{\mathrm{AR}}+C_{\mathrm{DR}}+C_{\mathrm{turn}}+C_{\mathrm{extra} W_{\mathrm{int}}}, \tag{25}
\end{equation*}
$$

with $C_{\text {turn }}$ taken as an average of Eqns 22 and 23.
The values of $C_{\mathrm{AR}}$ and $C_{\mathrm{DR}}$, i.e. the main determinants of $C_{\mathrm{SR}}$, depend on the prevalence of high values of (positive or negative, respectively) ES during the SR leg. As short-distance SRs are travelled at higher acceleration and deceleration than long-distance SRs, average ES is high. It has to be mentioned, though, that within the time course of each SR leg, very short distances are travelled at the end of the braking phase and at the beginning of the accelerative phase. Thus, despite the high ES values of those phases, the influence of their related high cost on average $C_{\mathrm{AR}}$ and $C_{\mathrm{DR}}$ (units are $\mathrm{J} \mathrm{kg}^{-1} \mathrm{~m}^{-1}$ travelled) is mitigated by the distance-based weighted mean performed along each phase time axis.

When simulated acceleration/deceleration patterns from the measured average $v_{\text {max }}, \tau_{a_{\mathrm{f}}}$ and $\tau_{d_{\mathrm{f}}}$ and their associated ES values were fed into the relationship between slope and efficiency shown in Fig. 3, the average apparent efficiency of positive work (by assuming a fixed eff-/eff+ ratio of 5) was found to be $35.3 \%$, $29.9 \%, 23.2 \%$ and $17.5 \%$ for $20+20,15+15,10+10$ and $5+5 \mathrm{~m}$ shuttles, respectively. Those values are shown together with the ones experimentally obtained in Fig. 6.

## DISCUSSION

The proposed model, which includes a revision of previous equations and an extension to decelerations of the ES for speedchanging running (di Prampero et al., 2005) together with the cost of the additional internal work and of body turning, closely predicts (dashed curve in Fig. 5) the metabolic cost of SRs at different distances (Buglione and di Prampero, 2013; Zamparo et al., 2015),


Fig. 6. Experimental and estimated apparent eff $w_{\text {tot+ }}$ as a function of SR (half) distance.
a motor activity with bouts of maximal increases/decreases of running speed. Although the general trend of experimental $C$ of SRs is paralleled by the new ES predictions, the overall underestimation resulting from just considering the cost of speed changes (dv) suggests, for each specific motor act, that all the potential sources of metabolic extra cost should be considered. As already argued above, there is a subtle bias potentially embedded in the ES metaphor: the (steady) running $C$ at each slope (which is almost speed independent) incorporates the metabolic cost of mechanical internal work that depends on a submaximal stride frequency. When trying to infer $C$ for sprint running or, as here, in maximal SRs, the $W_{\text {int }}$ increase due to a much higher stride frequency has to be considered. In the proposed case, the cost of turning has been estimated but there are other metabolic components, such as isometric contractions and stabilizing co-contractions, that were not. These could be the reasons for the underestimation of $C_{\mathrm{SR}}$ at the shortest leg distance.

In addition to the metabolic cost prediction, the model combines the ES concept with biomechanical findings about the mix of positive/negative work in running on different gradients (Minetti et al., 1994) and predicts values of apparent efficiency of muscle positive work, at the different SR lengths, which closely resembles (see Fig. 6) the measured values (P. Zamparo, G.P., A. Monte, F. Nardello, T. Otsu, N. Numazu, N. Fujii and A.E.M., unpublished). Experimental data and predictions suggest that SRs shorter than $15+15 \mathrm{~m}$ do not exploit the elastic energy storage/ release typical of the 'landing-take-off sequence' operated by tendons, as witnessed by efficiency values compatible with muscle activity only (as already found in $5+5 \mathrm{~m}$ SR by Zamparo et al., 2016). Recently, it has been proposed, based on a combination of experiments and modelling, that elastic energy stored in tendons at the beginning of a maximal sprint is remarkable (Lai et al., 2016). This stored energy, different from that coming from an otherwise wasted potential and kinetic energy of the body centre of mass in the typical running bounce, derives from part of the positive work done by muscle contraction to explosively accelerate the body in the first few steps in sprinting. It is likely that, in this case, muscle power enhancement, rather than the muscle work saving, is the main goal and it is achieved through 'muscle power amplification' (Galantis and Woledge, 2003). Because of the central role and the (net) amount of muscle positive work in the early stages of sprinting, we expect that the decreased apparent efficiency at short SRs (caused
by the prevalence of high ES of the initial strides), which is part of our results, remains compatible with those recent findings.

Limitations due to extrapolation of Eqn 8 at very high slopes (or ES) have been improved by Eqns 9 and 11, which now completes the prediction range by including negative gradients (or ES); this allows us to safely infer the metabolic cost of running acceleration and deceleration for a speed change from -8.24 to $8.24 \mathrm{~m} \mathrm{~s}^{-2}$, corresponding to ES from $-84 \%$ to $+84 \%$. Although the upper limit is very close to the maximum acceleration ability of humans, this is not true for the lower limit: previous papers dealing with the maximum negative power during drop landing (Minetti et al., 1998) and with kinetic analysis of speed changes during maximal SRs of different lengths (P. Zamparo, G.P., A. Monte, F. Nardello, T. Otsu, N. Numazu, N. Fujii and A.E.M., unpublished) show that, as expected from the force-velocity relationship of muscle contraction, eccentric performance is also much higher than concentric performance in in vivo, complex motor acts. Thus, as Giovanelli and co-authors (2016) extended the metabolic cost measurements of running to much higher uphill gradients than previously (from $+45 \%$ to $+84 \%$ ), the same should be done for downhill running at (equivalent) slopes up to almost double ( $\times 1.7$, in absolute terms) the actual uphill limit (namely, from $-45 \%$ to $-143 \%$ ).

Approximations in the mathematical and computational model can affect overall predictions. Although the new equations for $C$ (Eqns 3 and 4) very closely fit experimental data for gradient running (Minetti et al., 2002; Giovanelli et al., 2016), their asymptotic trend, particularly for steep downhill slopes, can be improved by investigating a wider gradient range (as mentioned) and the theoretically non-linear relationship between 'unavoidable' metabolic cost and gradient (see Appendix 2).

The inset graph in Fig. 2 reveals that the assumption ruling the simulation, i.e. that short-distance SRs use 'truncated' portions of acceleration and deceleration phases displayed at the maximum investigated distance, generates speed time courses with a sharp peak in between. This slightly differs from the experimental patterns (P. Zamparo, G.P., A. Monte, F. Nardello, T. Otsu, N. Numazu, N. Fujii and A.E.M., unpublished). As the inaccuracy pertains to a zone where small accelerations and decelerations (and the related ES values) occur, we are confident that a potential correction (spline) would not alter the conclusion from the obtained predictions.

By inspecting the newly obtained $C$ curve for acceleration and the corresponding ES (thick purple and orange lines in Fig. 2, respectively), a much simpler rule of thumb for replacing Eqn 9 emerges as:

$$
\begin{equation*}
C_{\mathrm{AR}}=\frac{a_{\mathrm{f}}}{0.29}+3.6 \tag{26}
\end{equation*}
$$

Eqn 26 can be safely used when estimating the metabolic cost of accelerations in the range $0.80<a_{\mathrm{f}}<8.24 \mathrm{~m} \mathrm{~s}^{-2}$ (or $0.08<\mathrm{ES}<0.84$ ). This comes as no surprise because, as mentioned previously (Minetti et al., 2013), the units of mechanical (and metabolic) cost of transport, $\mathrm{J} \mathrm{kg}^{-1} \mathrm{~m}^{-1}$, correspond to $\mathrm{m}^{-2}$. Thus, at ES corresponding to accelerated running where only positive work is involved, the $C_{\mathrm{AR}}$ is simply obtained by dividing $a_{\mathrm{f}}$ by a customary efficiency value ( 0.29 , here optimized to get average $C_{\mathrm{AR}}$ very close to predictions of Eqn 9 for all SR distances) to obtain its metabolic equivalent, then summed to the cost of level running (i.e. $3.6 \mathrm{~J} \mathrm{~kg}^{-1} \mathrm{~m}^{-1}$ ).

Unfortunately, no easy rule of thumb for decelerated running allows us to replace Eqn 11, mostly because of the complex mix between positive and negative mechanical work, and their efficiencies, occurring at negative slopes/ES (Minetti et al., 1994).

The proposed rule of thumb for the cost of accelerated running is a handy tool when literature data on the metabolic cost of constantspeed running at different gradients is not available, as in animal locomotion. For each specific species, values 0.29 and 3.6 in Eqn 26 should be replaced by the relevant 'efficiency of positive muscle work' ( 0.25 if unknown) and by the average cost of transport for bouncing gaits (trot or gallop) on the level at constant speed, respectively. For instance, Eqn 26 for accelerated locomotion in horses (data from Minetti et al., 1999), could become:

$$
\begin{equation*}
C_{\mathrm{AR}}=\frac{a_{\mathrm{f}}}{0.25}+2.2 \tag{27}
\end{equation*}
$$

Different from SRs, where Eqn 26 successfully predicted the cost of accelerations, Eqn 27 is a suggestion to be tested in future metabolic experiments on horses.

As shown in this paper and in the previous literature (di Prampero et al., 2005; Osgnach et al., 2010; Gaudino et al., 2013, 2014; Minetti et al., 2013; Coutts et al., 2015; Kempton et al., 2015; di Prampero et al., 2015), the ES concept can be profitably used in estimating the metabolic cost of speed-changing running. Other than shedding light on the metabolic effects of remarkable speed oscillation in a gait, where inherent velocity changes occur even at constant speed, the present revised methodology has potentially wide application in the monitoring of activity in daily life (submaximal speed changes) and exercise physiology, particularly in sport activities where unsteady locomotion is prevalent (submaximal and maximal speed changes). Also, the time course of metabolic power (=instantaneous cost $\times$ instantaneous speed) can be calculated starting from one of the proposed computation frameworks (the 'rule of thumb' equations) to work out the maximum metabolic performance required in prey/predator settings. The next step would be the development of a model for speed-changing walking, with predictions compared with the experimental measurements published so far in the literature.

## APPENDIX 1

## Note about the statistical analysis of SR kinematics

The 3D coordinates of each body segment, sampled at 100 Hz by a 35-camera system (Vicon Oxford Metrics, Oxford, UK) in a recent study on SR kinematics (P. Zamparo, G.P., A. Monte, F. Nardello, T. Otsu, N. Numazu, N. Fujii and A.E.M., unpublished), allowed us to obtain the displacement speed of the body centre of mass. Speed data from acceleration and deceleration phases of just the first leg in maximal $20+20 \mathrm{~m}$ SRs were analysed. The acceleration phase was fitted according to Eqn 13 by means of a non-linear regression model where both $v_{\max }$ and $\tau$ were estimated. The deceleration phase was fitted according to the same equation, by means of a non-linear regression model where $v_{\max }$ was imposed (as a result from the previous regression) and $\tau$ was estimated. This statistical strategy was adopted, first, to better capture the experimental trend of running speed to reach the maximum value 'in acceleration' and, second, to avoid speed discontinuity of SR leg pattern as reconstructed from Eqns 3 and 4. Such a granted continuity later allowed the computational algorithm to iteratively find, for each SR distance, the correct acceleration and deceleration timing compatible with that distance (see 'Computational model of shuttle running', above).

## APPENDIX 2

## Note about the statistical model equation

The proposed regression equations (Eqns 3 and 4) incorporate a linear function of gradient $i$ (see below) and an exponential component. The former, as mentioned, accounts for the inspection
trends in Fig. 1 at steep gradients and their role in representing the minimum gravitational work that has to be done. The latter has been conceived to represent the deviation of $C$ from the two linear components at gradients in the range $-0.35<i<+0.35$, where $C$ probably also reflects the metabolic equivalent of other mechanical determinants as the cost of mixed positive and negative work, which tends to disappear outside that gradient range (Minetti et al., 1994).

The approximation $i=\sin (\operatorname{atan} i)$ holds only in the range $-0.45<i<$ +0.45 , with a tendency of Eqn 5 to even deviate consistently $(-16 \%$ at $i=+0.80$ ) from Eqn 4. For the aims of this paper, devoted to improving the predictive efficacy of Eqn 1 at even steeper uphill slopes and to extend the ES model to the estimation of metabolic cost of running decelerations, the suggested linearized regression $C=a i+b e^{c i}$ can be regarded as an approximate model incorporating part of the effects of the minimum gravitational work that has to be done. We leave the deepening of understanding about the discrepancy between observed $C$ at very steep gradients and Eqn 5 to future investigations.

## Acknowledgements

The authors are indebted to Paola Zamparo and Andrea Monte for enriching discussions on the outcomes from the model/methodology.

## Competing interests

The authors declare no competing or financial interests.

## Author contributions

Conceptualization: A.M.; Methodology: A.M.; Software: A.M.; Formal analysis: A.M.; Investigation: G.P.; Data curation: A.M., G.P.; Writing - original draft: A.M.; Writing review \& editing: A.M., G.P.

## Funding

This research received no specific grant from any funding agency in the public, commercial or not-for-profit sectors.

## References

Alexander, R. M. (2002). Stability and maneuverability of terrestrial vertebrates. Integr. Comp. Biol. 42, 158-164.
Ardigò, L. P., Saibene, F. and Minetti, A. E. (2003). The optimal locomotion on gradients: walking, running or cycling? Eur. J. Appl. Physiol. 90, 365-371.
Buglione, A. and di Prampero, P. E. (2013). The energy cost of shuttle running. Eur. J. Appl. Physiol. 113, 1535-1543.
Cavagna, G. A. and Kaneko, M. (1977). Mechanical work and efficiency in level walking and running. J. Physiol. 268, 467-481.
Coutts, A. J., Kempton, T., Sullivan, C., Bilsborough, J., Cordy, J. and Rampinini, E. (2015). Metabolic power and energetic costs of professional Australian Football match-play. J. Sci. Med Sport. 18, 219-224.
di Prampero, P. E., Fusi, S., Sepulcri, L., Morin, J. B., Belli, A. and Antonutto, G. (2005). Sprint running: a new energetic approach. J. Exp. Biol. 208, 2809-2816. di Prampero, P. E., Botter, A. and Osgnach, C. (2015). The energy cost of sprint running and the role of metabolic power in setting top performances. Eur. J. Appl. Physiol. 115, 451-469.
Furusawa, K., Hill, A. V. and Parkinson, J. L. (1927). The dynamics of "sprint" running. Proc. R. Soc. Lond. B. 102, 29-42.
Galantis, A. and Woledge, R. C. (2003). The theoretical limits to the power output of a muscle-tendon complex with inertial and gravitational loads. Proc. R. Soc. Biol. Sci. 270, 1493-1498.
Gaudino, P., laia, F. M., Alberti, G., Strudwick, A. J., Atkinson, G. and Gregson, W. (2013). Monitoring training in elite soccer players: systematic bias between running speed and metabolic power data. Int. J Sports. Med. 34, 963-968.
Gaudino, P., Alberti, G. and laia, F. M. (2014). Estimated metabolic and mechanical demands during different small-sided games in elite soccer players. Hum. Mov. Sci. 36, 123-133.
Giovanelli, N., Ortiz, A. L. R., Henninger, K. and Kram, R. (2016). Energetics of vertical kilometer foot races; is steeper cheaper? J. Appl. Physiol. 120, 370-375. Kempton, T., Sirotic, A. C., Rampinini, E. and Coutts, A. J. (2015). Metabolic power demands of rugby league match play. Int. J Sports Physiol. Perform. 10, 23-28.
Lai, A., Schache, A. G., Brown, N. A. T. and Pandy, M. G. (2016). Human Ankle plantar flexor muscle-tendon mechanics and energetics during maximum acceleration sprinting. J. R. Soc. Interface 13, 20160391.

Margaria, R. (1938). Sulla fisiologia e specialmente sul consumo energetico della marcia e della corsa a varia velocità ed inclinazione del terreno. Atti Acc. Naz. Lincei 6, 299-368.
Minetti, A. E. (1998). A model equation for the prediction of mechanical internal work of terrestrial locomotion. J. Biomech. 31, 463-468.
Minetti, A. E., Ardigò, L. P. and Saibene, F. (1994). Mechanical determinants of the minimum energy cost of gradient running in humans. J. Exp. Biol. 195, 211-225.
Minetti, A. E., Ardigò, L. P., Susta, D. and Cotelli, F. (1998). Using leg muscles as shock absorbers: theoretical predictions and experimental results of drop landing performance. Ergonomics 41, 1771-1791.
Minetti, A. E., Ardigò, L. P., Reinach, E. and Saibene, F. (1999). The relationship between mechanical work and energy expenditure of locomotion in horses. J. Exp. Biol. 202, 2329-2338.

Minetti, A. E., Ardigò, L. P., Capodaglio, E. M. and Saibene, F. (2001). Energetics and mechanics of human walking at oscillating speeds. Am. Zool. 41, 205-210.
Minetti, A. E., Moia, C., Roi, G. S., Susta, D. and Ferretti, G. (2002). Energy cost of walking and running at extreme uphill and downhill slopes. J. Appl. Physiol. 93, 1039-1046.
Minetti, A. E., Cazzola, D., Seminati, E., Giacometti, M. and Roi, G. S. (2011). Skyscraper running: physiological and biomechanical profile of a novel sport activity. Scand. J. Med. Sci. Sports. 21, 293-301.

Minetti, A. E. Gaudino, P., Seminati, E. and Cazzola, D. (2013). The cost of transport of human running is not affected, as in walking, by wide acceleration/ deceleration cycles. J. Appl. Physiol. 114, 498-503.
Osgnach, C., Poser, S., Bernardini, R., Rinaldo, R. and di Prampero, P. E. (2010). Energy cost and metabolic power in elite soccer: a new match analysis approach. Med. Sci. Sports Exerc. 42, 170-178.
Wilson, A. M., Hubel, T. Y., Wilshin, S. D., Lowe, J. C., Lorenc, M., Dewhirst, O. P., Bartlam-Brooks, H. L. A., Diack, R., Bennitt, E., Golabek, K. A. et al. (2018). Biomechanics of predator-prey arms race in lion, zebra, cheetah and impala. Nature 554, 183-188.
Woledge, R. C., Curtin, N. A. and Homsher, E. (1985). Energetic aspects of muscle contraction. Inc. Monogr. Physiol. Soc. 41, 1-357.
Zamparo, P., Zadro, I., Lazzer, S., Beato, M. and Sepulcri, L. (2014). Energetics of shuttle runs: the effects of distance and change of direction. Int. J. Sport Physiol. Perf. 9, 1033-1039.
Zamparo, P., Bolomini, F., Nardello, F. and Beato, M. (2015). Energetics (and kinematics) of short shuttle runs. Eur. J. Appl. Physiol. 115, 1985-1994.
Zamparo, P., Pavei, G., Nardello, F., Bartolini, D., Monte, A. and Minetti, A. E. (2016). Mechanical work and efficiency of $5+5 \mathrm{~m}$ shuttle running. Eur. J. Appl. Physiol. 116, 1911-1919.


[^0]:    ${ }^{1}$ Physiomechanics Lab, Department of Pathophysiology and Transplantation, University of Milan, 20133 Milan, Italy. ${ }^{2}$ 'Beniamino Segre’ Research Centre, Accademia Nazionale dei Lincei, 00165 Rome, Italy.
    *Author for correspondence (alberto.minett@unimi.it)
    (D) A.E.M., 0000-0002-0120-4406; G.P., 0000-0002-0109-4964

