A slow $\dot{V}O_2$ on-response allows comfortable adoption of aerobically unaffordable walking and running speeds on short stair ascents

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ABSTRACT
The aim of this study was to investigate the mechanical and metabolic reasons for the spontaneous gait/speed choice when ascending a short flight of stairs, where walking on every step or running on every other step are frequently interchangeable options. The kinematics, oxygen uptake ($V_O_2$), ventilation and heart rate of 24 subjects were sampled during climbing one and two flights of stairs while using the two gaits. Although motor acts were very short in time (5–22 s), metabolic kinetics, extending into the 250 s after the end of climbing, consistently reflected the (metabolic equivalent of the) required mechanical energy and allowed comparison of the two ascent choices: despite a 250% higher mechanical power associated with running, measured $V_O_2$, ventilation and heart rate peaked at only +25% with respect to walking, and in both gaits at much lower values than $V_{O_2\text{max}}$ despite predictions based on previous gradient locomotion studies. Mechanical work and metabolic cost of transport, as expected, showed a similar increase (+25%) in running. For stairs up to a height of 4.8 m (30 steps at 53% gradient), running makes us consume slightly more calories than walking, and in both gaits with no discomfort at all. The cardio-respiratory–metabolic responses similarly delay and dampen the replenishment of phosphocreatine stores, which were depleted much faster during the impulsive, highly powered mechanical event, with almost overlapping time courses. This discrepancy between mechanical and metabolic dynamics allows us to afford climbs ranging from almost to very anaerobic, and to interchangeably decide whether to walk or run up a short flight of stairs.

KEY WORDS: Mechanics, Metabolism, $V_O_2$ kinetics, Incline locomotion, Pulse exercise

INTRODUCTION
Locomotion on flat ground is not very expensive: for example, walking costs about 2 ‘metabolic’ J to move 1 kg of body mass ($M$, kg) a (horizontal) distance of 1 m (at a speed of about 1.2 m s$^{-1}$; see Fig. 1). In contrast, uphill gaits require an increase in the potential energy of the body at each stride. For instance, an incline of +57% (about 30 deg), for which the ratio between the height gain ($\Delta h$) and the distance travelled on the gradient ($\Delta d$) is 0.5, is associated with an extra cost of about 20 metabolic J kg$^{-1}$ m$^{-1}$. In fact, the difference in gravitational potential energy (in ‘mechanical’ J) is $Mg\Delta h$ (or $Mg\Delta d$, where $g$ is acceleration due to gravity), and when expressed in (‘mechanical’) J kg$^{-1}$ m$^{-1}$ it reduces to 0.5g. The ‘metabolic’ cost is then calculated as ‘mechanical’ cost divided by muscle efficiency of positive work (0.5g/0.25=20). Such a gradient was chosen not just for illustrative purposes but because it represents the average steepness of most stairs in a residential building.

Gradient locomotion has been widely studied in the past (since Margaria, 1938) and the metabolic cost of walking and running has been measured for several inclines and speeds. Fig. 1 shows that level walking reports the lowest cost at a speed of 1.2 m s$^{-1}$, while at +53% gradient the cost is much higher (about 22 J kg$^{-1}$ m$^{-1}$, as expected from the previous paragraph) and displays a minimum at a speed of 0.45 m s$^{-1}$. In such a graph it is convenient to get additional information on the metabolic effort of each locomotor condition (gait, gradient, speed) by their spatial contiguity with iso-metabolic power hyperbolae (metabolic power (W kg$^{-1}$)=metabolic cost/speed). These curves are labelled as fractions of the maximum aerobic power (for a subject with 15 W kg$^{-1}$ or a $V_{O_2\text{max}}$ of about 44 ml O$_2$ kg$^{-1}$ min$^{-1}$): the grey area above 100% is where aerobic metabolism alone is no longer sufficient to sustain the exercise. The first remark here is that to ascend on a gradient corresponding to ‘average’ stairs requires a threefold amount of metabolic power versus level walking (both at the respective optimal speeds). The predicted ascent speed in order to maintain the same metabolic power (say, the same heart rate and ventilation) as level walking is obtained at the intersection between the relevant iso-power hyperbola (i.e. 25%) and the thick curve of metabolic cost of walking at a +53% gradient, resulting in a value of 0.13 m s$^{-1}$. Actually, such a low speed is never observed in (even sedentary) healthy subjects, who instead tend to choose the 3 times faster, metabolically optimal speed of 0.45 m s$^{-1}$ (see also Results). Now we are facing apparently conflicting results: although the spontaneous ascent speed is chosen according to minimization of the cost of transport, a criterion pervasively adopted across species (Alexander, 1989), why not to select a speed that would require a metabolic power much lower than 75%, the last being commonly associated with a higher perceived effort (prolonged tachycardia, tachypnoea, etc.)? The same question applies to running: Fig. 1 shows that level running (at a slow speed, namely 2.2 m s$^{-1}$) is associated with a metabolic power close to 70% of the aerobic limit, but on a +53% steep incline running at half that speed (the spontaneous ascent speed, see Results) implies a remarkable contribution of anaerobic metabolism (225%, more than twice the aerobic maximum power). So, why do we sometimes run up short flights of stairs (on every other step)?

The above considerations are based on data collected during locomotion on inclined paths/treadmills, about which biomechanical and metabolic research has been quite prolific in the past 90 years...
The reasons behind our spontaneous choice in terms of gait/speed combination for climbing a short flight of stairs probably reside in such a comprehensive approach to the puzzle: do humans decide to ascend faster just because they are often in a hurry?

In this study, using flights of stairs at two different heights, we aimed: (1) to assess the spontaneous ascent speed with the two gaits, (2) to quantify all the determinants of the total mechanical work, and (3) to measure metabolism kinetics during these tasks and also during the recovery period, from which the maximum metabolic power ($V_{O_2,peak}$) and the total metabolic energy spent in these (often interchangeable) conditions could be obtained.

**MATERIALS AND METHODS**

**Subjects**

Twenty-four non-athlete subjects (15 men and 9 women; age men: 30.0±10.2 years, women: 30.0±6.5 years; body mass men: 75.6±6.7 kg, women: 59.2±7.3 kg; height men: 1.77±0.04 m, women: 1.63±0.06 m, mean±s.d.) gave their written informed consent for the experimental procedure. The study was approved by the Ethics Committee of the University of Milan. Participants were free of any musculoskeletal, bone and joint, or cardiac and pulmonary diseases and were not taking any medication. Several restrictions were imposed on the volunteers: no food intake 3–4 h before and no stimulants (coffee, tea) or intense physical activity 12 h before the experimental protocol (Cooke, 1996).

**Experimental protocol**

Subjects participated in four experiments in a randomized sequence: walking up one flight of stairs (1FOS) at spontaneous speed (on all the steps), running up 1FOS at spontaneous speed (on every other step), walking up two flight of stairs (2FOS) at spontaneous speed (on all the steps), running up 2FOS at spontaneous speed (on every other step). Each experiment started with 10 min rest while sitting on a chair, with the goal of minimizing the effects of any previous physical activity and/or emotional conditioning. Subjects, who were unaware of the time passing, were instructed to relax as much as possible and to promptly start climbing at the experimenter’s command. Biological variables were continuously sampled during the pre-exercise rest for 5 min, during the climbing effort and at rest post-exercise (excess post-exercise oxygen consumption, EPOC) for another 5 min while sitting on another chair located at the end of the ascent. The height of the stairs was 2.57 m and 4.81 m, the overall distance covered (the diagonal displacement plus the distance to leave and reach the two chairs) was 5.93 m and 10.63 m, and the total number of steps was 16 and 30 for 1FOS and 2FOS, respectively. The measured stairs gradient was 53%.

**Data collection and analysis**

Oxygen uptake ($V_{O_2}$, ml O2 min$^{-1}$) and expiratory ventilation ($V_{E}$, 1 min$^{-1}$) at rest and during exercise were measured using a portable open-circuit metabograph. Expired air was analysed by breath using a COSMED K4b2 portable monitor (Rome, Italy), while single-beat heart rate ($f_{HR}$) was measured using a POLAR S810i portable monitor (Kajaani, Finland). Before each experimental session, the metabograph was calibrated with ambient air and with a known gas mixture. The turbine flowmeter was calibrated using a 3 l syringe at the beginning of the test protocol. Response delay calibration was performed according to the manufacturer’s instructions.

In addition, subjects’ initial acceleration and duty factor ($D$), i.e. the fraction of the stride period at which one foot is in contact with the ground, during walking and running were measured by means of a high-speed (210 Hz) camera (Casio EX-FH20, Tokyo, Japan).
Reflective markers were placed on the great trochanter and on the edge of each stair step. The video camera was positioned to face the subject’s left side, at a distance of 3 m and a halogen lamp was used to illuminate the reflective markers. The acceleration of the great trochanter, a surrogate of the body centre of mass, and its duration were calculated by performing a frame-by-frame analysis of motion (iMovie, Apple Inc.).

The total ‘net’ oxygen consumed ($V_{O_2,\text{total net}}$, ml O$_2$) was calculated from the $V_{O_2}$ integral over time (considering the $V_{O_2}$ during the whole exercise and EPOC, minus the basal $V_{O_2}$, $V_{O_2,\text{basal}}$, measured before the exercise started), according to the equation:

$$V_{O_2,\text{total net}} = \int_{t_i}^{t_f} \dot{V}_{O_2} \, dt - \dot{V}_{O_2,\text{basal}} \cdot (t_f - t_i), \quad (1)$$

where $t_i$ and $t_f$ are the beginning of the exercise and the end of the recovery periods, respectively.

The above procedures were applied to the total expiratory volume ($V_{E,\text{total net}}$) and total net number of heart beats (HBeat$_{\text{total net}}$). Oxygen-related variables were expressed per kg of body mass. Total $V_{O_2}$ values (Eqn 1) were converted to metabolic cost of transport ($C_{\text{met}}$, the energy needed to move 1 kg of body mass along 1 m, J kg$^{-1}$ m$^{-1}$) assuming an energy equivalent of 20.9 kJ l$^{-1}$ O$_2$ (corresponding to a non-proteic respiratory exchange ratio of 0.96) and divided by the relevant distance covered. Peak values for $V_{O_2}$, $V_E$ and $f_H$ were measured, and peak net values $\dot{V}_{O_2,\text{net}}$, $\dot{V}_{E,\text{net}}$ and $\dot{f}_H$ were calculated as the difference between peak and basal values.

Average vertical ($\dot{s}_{\text{vert}}$) and diagonal ($\dot{s}_{\text{diag}}$) speed were obtained as the ratio between the height or diagonal displacement, respectively, and ascent time (for both 1FOS and 2FOS).

The total mechanical work ($W_{\text{mech}}$, J), was calculated according to the equation:

$$W_{\text{mech}} = W_{\text{vert}} + W_{\text{int}} + W_{\text{accel}} + W_{\text{turn}}, \quad (2)$$

where $W_{\text{vert}}$ is the vertical work, $W_{\text{int}}$ is the internal work, $W_{\text{accel}}$ is the work done to horizontally accelerate the body centre of mass at the beginning of the manoeuvre, and $W_{\text{turn}}$ is the work done to turn between flights of stairs (only during 2FOS).

$W_{\text{vert}}$ (J) was obtained by considering the increase in potential energy as:

$$W_{\text{vert}} = Mg\Delta h,$$  \hspace{1cm} (3)

where $M$, $g$ and $\Delta h$ are, respectively, the individual body mass (kg), the acceleration due to gravity (9.81 m s$^{-2}$) and the height of the flight of stairs (m), also including the vertical distance of standing up from the chair.

The internal mechanical work ($W_{\text{int}}$, J), necessary to accelerate the limbs with respect to the body centre of mass was estimated as modelled by Minetti (1998):

$$W_{\text{int}} = Mf\dot{s}_{\text{diag}}(1 + (D/(1 - D))^2)qL_{\text{diag}}, \quad (4)$$

where $f$ is the stride frequency (Hz), $\dot{s}_{\text{diag}}$ is the average diagonal speed (m s$^{-1}$), $D$ is the measured duty factor (i.e. the fraction of the stride during which one foot is in touch with the ground: 0.45 for running and 0.65 for walking), $q$ is a constant reflecting the inertia properties of the four body limbs (estimated to be equal to 0.15 during stair ascent; Minetti et al., 2011) and $L_{\text{diag}}$ is the total distance travelled along the stairs (m).

$W_{\text{accel}}$ (J) was obtained using the equation:

$$W_{\text{accel}} = M L_{\text{accel}} \int_0^{a} a \, dl_{\text{horiz}}, \quad (5)$$

where $L_{\text{accel}}$, $a$ and $l_{\text{horiz}}$ are the distance travelled at the end of acceleration (m), the instantaneous acceleration (m s$^{-2}$) and horizontal displacement just before ascending (m) the stairs, respectively.

For the 2FOS, $W_{\text{turn}}$ was also calculated. The metabolic work needed to execute the turn has been estimated according to Minetti...
et al. (2011) as 283.1 ml O$_2$ kg$^{-1}$ km$^{-1}$, where subjects moved in circles of about 1 m radius. $W_{turn}$ was obtained by assuming a muscular efficiency of 0.25 and half a circumference distance per turn, and expressed as J kg$^{-1}$ turn$^{-1}$.

Average mechanical power ($\dot{W}_{mech}$, W) was calculated as the ratio between $\dot{W}_{mech}$ and exercise time. Mechanical cost of transport ($C_{mech}$) was calculated by dividing $\dot{W}_{mech}$ by body mass and the relevant displacement, either vertical ($\Delta h$, $C_{mech, vert}$) or diagonal ($L_{diag}$, $C_{mech, diag}$). Metabolic cost of transport ($C_{met}$) is also presented relative to those two displacements ($C_{net, vert}$ and $C_{net, diag}$, respectively). Ascent efficiency (Eff) was obtained as the ratio between $C_{mech}$ and $C_{net}$.

The ratio between running and walking for 1FOS and 2FOS was calculated for $\dot{W}_{mech}$, $\dot{V}_{O_2, net}$, $\dot{V}_{E, net}$, $\dot{V}_{E, net}$, $C_{mech}$, and $C_{met}$-total.

**Statistical analysis**

Descriptive statistics were used, with the data presented as means±s.d. A Shapiro–Wilk's test was used to verify the normality of the data distribution. A paired two-tailed Student's $t$-test was used in order to compare, for each variable, the different conditions (2FOS versus 1FOS, running versus walking). One-sample $t$-test was used to compare the ratio of pooled running/walking data with the reference value 1. An alpha level of 0.05 was adopted for all statistical tests, which were performed using SPSS software (version 15.0).

**RESULTS**

Mean values of diagonal and vertical speed, cardio-respiratory variables and heart rate are shown in Table 1. There were no significant differences between 1FOS and 2FOS, indicating that these variables are independent of the number of flights of stairs.

Components of total mechanical work are presented in Fig. 2. $\dot{W}_{mech}$, $C_{mech}$ and $C_{net}$ for 1FOS and 2FOS (Table 2) were significantly higher during running compared with walking. No significant difference in Eff between walking and running was found in 1FOS, though significantly higher values for walking were found in 2FOS (Table 2).

The ratio between running and walking values of $\dot{W}_{mech}$, $\dot{V}_{O_2, net}$, $\dot{V}_{E, net}$, $\dot{V}_{E, net}$, $C_{mech}$, and $C_{met}$-total, separately during 1FOS and 2FOS is reported in Fig. 3A. Pooled (1FOS and 2FOS) running/walking ratios for each variable are shown in Fig. 3B. According to the statistical analyses, all variables were significantly higher than 1.

**DISCUSSION**

This investigation reports that when people freely move on a short height of stairs, they walk at 0.47 m s$^{-1}$ and/or run (on every other step) at 1.1 m s$^{-1}$, irrespective of FOS number. Despite the two different gaits and ascent speeds, and thus mechanical
power needed (running/walking ≈ +250%), cardiorespiratory and metabolic parameters increased only slightly when running (running/walking ≈ +25%; see Fig. 3B). Ascending 1FOS or 2FOS made no difference to the results (Fig. 3A), allowing us to conclude that the combination of slow cardio-respiratory–metabolic kinetics and very short exercise duration makes the two gaits almost interchangeable for stairs up to about 5 m height (at a gradient close to 53%). This is well illustrated in Fig. 4, where $P_{O_2}$ kinetics are very similar in walking and running at each ascent level. A more comprehensive picture of the difference between mechanical and metabolic power of the gaits in the same ascent condition (1FOS) is shown in Fig. 5 for a representative subject. Although the metabolic equivalent of mechanical power of ascent by walking and running (vertical rectangles in Fig. 5) is very different between the two (running/walking ≈ +250%) and both of them exceed the maximum aerobic power (dash–dot horizontal line in Fig. 5), the measured time course of metabolic power is almost identical for the two gaits (black and grey dots in Fig. 5), showing peaks of the order of 1/4 to 1/5 of $V_{O_2,max}$. Thus, ascending a short flight of stairs by walking on every step or running on every other step, in both cases at spontaneous speed, makes no difference in terms of the metabolic power (and hence perceived effort) involved during and after the end of exercise.

**Mechanical considerations**

From Eqn 3, the minimum amount of mechanical work done to transport 1 kg of body mass 1 m vertically (i.e. the minimum mechanical cost of vertical transport) is:

$$W_{vert} = g,$$

and thus for 1FOS and 2FOS it amounts to 9.81 J kg$^{-1}$ m$^{-1}$, irrespective of the gait and speed. Our mechanical results (see Table 2) indicate a $C_{mech,vert}$ of 10.48 and 11.07 J kg$^{-1}$ m$^{-1}$ for walking up 1FOS and 2FOS. For running, average $C_{mech,vert}$ between 1FOS and 2FOS was 12.58 J kg$^{-1}$ m$^{-1}$, i.e. 20% higher than...
walking, confirming that the overall mechanics of both gait is dominated by the gravitational term (see Fig. 2). The determinants of the higher running (metabolic and mechanical) cost are $W_{\text{int}}$ and $W_{\text{accel}}$ (in 1FOS). $W_{\text{int}}$, by following Eqn 4, is increased by 23% in running because of: (1) a 155% higher average speed, (2) a 27% higher stride frequency [i.e. 27=(155+100)/2=100] because of landing on every other step, along the same overall vertical distance, and (3) a 31% lower duty factor, resulting in a 62% lower compound value of duty factor in Eqn 4. Another important component of the total mechanical work of running is $W_{\text{accel}}$, with a value that is about 14 times higher than for walking as running reaches a higher speed value. The same rationale could apply also to 2FOS experiments, where the mechanical cost of turning is also incorporated in the total mechanical computation.

In summary, the overall mechanical cost of transport associated with stair ascent in our experimental protocol is higher than expected from the mere gravitational component because of the internal work and acceleration, which are even higher in running. Acceleration in particularly would be an almost negligible component in a long-lasting stair ascent, but becomes substantial when the exercise duration is short (5–13 s).

**Metabolic considerations**

The rather unorthodox estimate of the effects on oxygen consumption of a very short-lasting exercise, as obtained by sampling it during the subsequent 5 min recovery period raises the question about the reliability of what we termed a ‘micro $V_{O2}$’ approach in capturing the entire metabolic event. With respect to traditional and consolidated metabolic assessment based on 1–2 min, steady-state high $O_2$ consumption, the sampling rate during both the very short exercise and EPOC, together with the challenged metabograph response during long-lasting recovery at near-basal rate (low signal to noise ratio) could affect the reliability of the present data. The assumption here was that most of the required metabolic energy for such a short exercise comes from phosphocreatine (PCr) and that 5 min of recovery would suffice to replenish its stores. To check for consistency, the average of absolute 2FOS/1FOS ratios (while pooling gaits) and running/walking ratios (while pooling FOS data) were calculated both for $C_{\text{mech}}$ and $C_{\text{met}}$. The mean absolute difference of FOS ratios was only 5% and 9% for $C_{\text{mech}}$ and $C_{\text{met}}$, respectively, while that for the gait ratios was 17% and 32%, respectively. This indicates that the costs are slightly affected by the number of FOS, as should be expected, while they more strongly depend on the chosen gait, with running being both mechanically and metabolically more expensive. Consistency is also supported by efficiency results, which ranges in the four conditions from 14% to 17%. When pooling 1FOS and 2FOS data, efficiency ranges from 14% to 16%; by considering that at a gradient of 53% the monotonically ascending path of the body centre of mass implies (i) the presence only of positive work (Margaria, 1938; Minetti et al., 1993, 1994) and (ii) the precluded elastic energy-saving paradigm of running (Minetti et al., 1994), the almost invariant efficiency is not a surprise.

Although these results, in relative terms, support the consistency of micro $V_{O2}$ experiments across different conditions, the low value of efficiency in absolute terms (with respect to muscle efficiency; Woledge et al., 1985) suggests potential bias, particularly in the metabolic assessment of exercise. To investigate the amount and the reasons for such a discrepancy, a comprehensive review of the literature reporting the metabolic cost of human ascent on a treadmill or laddermill at a similar gradient and speed to that used in this study was carried out (see Table 3). Average $C_{\text{met}}$ of these investigations (where only Halder et al., 2018, has been excluded because of a much steeper gradient) was 22.0±2.5 J kg$^{-1}$ m$^{-1}$ for walking and 26.1±2.9 J kg$^{-1}$ m$^{-1}$ for running upstairs. Differently from level locomotion, where running $C_{\text{met}}$ is almost double walking values (+100%; e.g. Saibene and Minetti, 2003), running cost on treadmills at a staircase gradient seems to be just +18% higher. $C_{\text{met}}$ obtained in the present study was +53% and +70% more expensive for walking and running, respectively, than values in the literature and running here was +32% costlier than walking. The reasons for these discrepancies are to be found in the mechanical and metabolic characteristics of the experimental protocol and analysis, which deviate from the customary constant speed ascent and long-lasting steady-state acquisition of metabolic data.

Apart from the additional cost of acceleration and of turning (in 2FOS only), we can speculate that, differently from walking...
economy that seems to benefit from moving at a +53% gradient on steps (rather than on the inclined treadmill surface; see Table 3), running on every other step could involve a greater vertical excursion of the body centre of mass trajectory to ensure the step rise is cleared before each landing. This could partially explain the +32% increase in $C_{\text{net}}$ in running with respect to walking (when compared with +18% of the literature), as obtained in this study. So far, no investigation has been published on the mechanics and energetics of staircase running at +53% gradient. However, even after removing from our results the metabolic equivalent of accelerative work (estimated by Eqn 5 or by a recent model for intermediate oxidative muscle fibres (Wüst et al., 2013) is the basis for a related higher metabolic cost from the $V_O_2$ on-phase, and thus for the overestimation found in the present experiments. The present set-up also suffers for the lack of a long-lasting steady-state condition (see Fig. 4) contributing, with its strong signal, to make a more weighted integral of the $V_O_2$ time course, and thus to converge towards a more realistic cost.

The decreasing portion of $V_O_2$, off-kinetics could incorporate determinants of the overall $O_2$ debt other than just the one devoted to replenishment of PCr stores: (1) lactate accumulation could occur in the case of local PCr stores decreasing below a given threshold, and (2) entropy could increase as a result of a change in temperature and the increasing portion of the metabolic on-kinetics continue to increase beyond the end of exercise, when the subject is recovering seated on the chair, for 40–50 s, after which off-kinetics begins (similar to fig. 4 in di Prampero et al., 1973, where the authors in an ancillary experiment adopted a protocol similar to the present study). This is a clear example of a ‘pulse work rate’ (Hughson et al., 1988; Rossiter, 2011) where oxygen consumption continues to increase presumably in order to rebuild the energy sources utilized during the exercise (PCr, myoglobin) (Hughson et al., 1988) and/or due to the limb-to-lung delay (Rossiter, 2011). Short stair climbing, even at preferred walking and running speed can be seen as an example of daily-life pulse exercise.

It is known that metabographs are reliable for steady-state $V_O_2$ measurements, while some inaccuracy is expected for the $V_O_2$ transient, as processing algorithms only rarely take into account pulmonary oxygen stores (Aliverti et al., 2009); this could partially be responsible, within consistent results, of the higher costs.

Table 3. The different metabolic costs of walking and running during steady-state acquisition at a similar gradient and speed to the present study

<table>
<thead>
<tr>
<th>Reference</th>
<th>Instrumentation</th>
<th>Incline (%) ; speed (m s$^{-1}$)</th>
<th>Walking cost (J kg$^{-1}$ m$^{-1}$)</th>
<th>Running cost (J kg$^{-1}$ m$^{-1}$)</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lehmann and Engelmann, 1933</td>
<td>Laddermill</td>
<td>+53%; –</td>
<td>18.7</td>
<td></td>
<td>Experimental data</td>
</tr>
<tr>
<td>Kamon, 1970</td>
<td>Laddermill</td>
<td>+53%; walking at 0.47 m s$^{-1}$</td>
<td>20.7</td>
<td></td>
<td>Handrails allowed</td>
</tr>
<tr>
<td>Ardigo et al., 2003 on Margaria, 1938</td>
<td>Treadmill</td>
<td>+53%; walking at 0.47 m s$^{-1}$</td>
<td>22.0</td>
<td></td>
<td>Extrapolated from a 3D contour</td>
</tr>
<tr>
<td>Minetti et al., 2002</td>
<td>Treadmill</td>
<td>+53%; walking at 0.47 m s$^{-1}$</td>
<td>23.4</td>
<td></td>
<td>Extrapolated from 5th order polynomial</td>
</tr>
<tr>
<td>Giovannelli et al., 2016</td>
<td>Treadmill</td>
<td>+57%; running at 0.7 m s$^{-1}$</td>
<td>24.2</td>
<td></td>
<td>Experimental data</td>
</tr>
<tr>
<td>Ortiz et al., 2017</td>
<td>Treadmill</td>
<td>+57%; walking at 0.4 m s$^{-1}$, running at 0.8 m s$^{-1}$</td>
<td>25.3</td>
<td></td>
<td>Experimental data</td>
</tr>
<tr>
<td>Halder et al., 2018</td>
<td>Stair machine</td>
<td>+82%; walking at 0.36 m s$^{-1}$</td>
<td>27.7 gross</td>
<td></td>
<td>Handrails allowed</td>
</tr>
</tbody>
</table>

A biphasic $V_O_2$ on-response, classically observed at the pulmonary level (Linnarsson, 1974), has recently been found at the level of the single fibre (Wüst et al., 2013), where the first phase has been attributed to mitochondrial calcium-dependent activation that precedes ADP feedback in controlling the metabolic transient. Such an activation phase (not affecting the off-transient) is likely to be the determinant of the asymmetry/imbalance between the on-phase oxygen deficit and the EPOC described in that study (Wüst et al., 2013). The 30–40% lower oxygen deficit reported for low and intermediate oxidative muscle fibres (Wüst et al., 2013) is the basis for the overestimation found in the present experiments. The present set-up also suffers for the lack of a long-lasting steady-state condition (see Fig. 4) contributing, with its strong signal, to make a more weighted integral of the $V_O_2$ time course, and thus to converge towards a more realistic cost.
duration of such tasks limit the exercise $\dot{V}_{O_2,\text{peak}}$ to values well below $\dot{V}_{O_2,\text{max}}$. $\dot{V}_{O_2}$ measurements extended to a few minutes after the end of a few seconds of exercise (micro $V_{O_2}$ experiments) led to consistent (but probably inaccurate) efficiency and metabolic cost values for the two gaits that reliably parallel the expected (and assessed) mechanical constraints. Further development of this investigation includes the extension of the experimental protocol to higher climbing distances on stairs, where additional burdens in exercise $\dot{V}_{O_2,\text{peak}}$ level and more substantial differences in the metabolic response of walking or running could change the spontaneous speed and the interchangeability of the two gaits.

Competing interests
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Author contributions

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