Mechanical output in jumps of marmosets (Callithrix jacchus)

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ABSTRACT
In this study we determined the mechanical output of common marmosets (Callithrix jacchus) during jumping. Vertical ground reaction forces were measured in 18 animals while they jumped from an instrumented crossbar to a crossbar located 70 cm higher. From the vertical force time histories, we calculated the rate of change of mechanical energy of the centre of mass (dE/dt). The mean value of dE/dt during the push-off amounted to 51.8±6.2 W kg⁻¹ body mass, and the peak value to 116.4±17.6 W kg⁻¹ body mass. We used these values in combination with masses of leg muscles, determined in two specimens, to estimate mean and peak values of dE/dt of 430 and 970 W kg⁻¹ muscle, respectively. These values are higher than values reported in the literature for jumps of humans and bonobos, but smaller than those of jumps of bushbabies. Surprisingly, the mean value of dE/dt of 430 W kg⁻¹ muscle was close to the maximal power output of 516 W kg⁻¹ muscle reported in the literature for isokinetic contractions of rat medial gastrocnemius, one of the fastest mammalian muscles. Further study of the force–velocity relationship of muscle tissue of small primates is indicated.

KEY WORDS: Biomechanics, Muscle power, Muscle work, Mass-specific, Primates

INTRODUCTION
One of the challenging goals in movement science is to relate the total mechanical output of an animal during locomotor tasks to the output of the elements of the musculoskeletal system. The limits of mechanical output are approached in jumping, a locomotor task that is important for survival in many animals because it plays a role in catching prey or escaping from predators. Many studies have been conducted on the mechanics of jumping of various species (Aerts, 1998; Bobbert, 2001; Harris and Steudel, 2002; Henry et al., 2005; Peplowski and Marsh, 1997; Roberts et al., 2011; Scholz et al., 2006). In humans, the mechanical output in jumping has been successfully reproduced and analyzed with the help of musculoskeletal models (Bobbert, 2001; Bobbert and van Soest, 2001; Nagano et al., 2005; Pandy et al., 1990). However, humans are relatively poor jumpers compared with nonhuman primates such as bonobos (Scholz et al., 2006), gibbons (Channon et al., 2012) and bushbabies (Aerts, 1998). The jumping performance of small primates is especially puzzling. If a human musculoskeletal model is downscaled to the size of a 0.3 kg bushbaby, jump height drops from ~40 cm to ~10 cm (Bobbert, 2013). It is easy to understand why jump height does not remain constant with geometric downscaling: for jump height to remain constant, the vertical take-off velocity of the centre of mass (COM) must remain constant, but with shorter segments this would require higher angular velocities and hence higher muscle shortening velocities, and at higher shortening velocities muscle mechanical output would be hampered more by the force–velocity relationship (Bobbert, 2013). If small primates are able to jump higher than humans, their bodies must be anatomically and physiologically different from those of humans, and this raises interesting questions about the functional morphology and evolution of jumping animals. Alexander (Alexander, 1995) studied the relationship between leg design and jumping performance in humans and bushbabies with a musculoskeletal model that included series elastic structures and muscle forces depending on length and velocity. However, he derived the muscle parameters from mechanical output measured during jumping, and not from measured physiological muscle properties. To the best of our knowledge, there is currently no musculoskeletal model of a small primate that explains the mechanical output during jumping from the properties of muscle fibres and the way they are embedded in the musculoskeletal system.

In the present study, we determined the mechanical output during jumps of common marmosets (Callithrix jacchus (Linnaeus 1758)), and considered whether it would warrant a future in-depth analysis with the help of a detailed musculoskeletal model. Marmosets are becoming a standard nonhuman primate model for the study of health and disease because they are phylogenetically closely related to humans and mirror the physiological processes that take place in humans (Okano et al., 2012; ’t Hart et al., 2012; Tardif et al., 2011). In various studies, the animals are euthanized, and this allows for harvesting of muscle biopsies and post mortem study of musculoskeletal design. From casual observation, it appears that they jump more than half a metre high, which is higher than humans. For the present study, we had the opportunity to measure vertical ground reaction forces and calculate mechanical output during vertical jumps of common marmosets, which were subjects in an unrelated project. Additionally, we had the opportunity to dissect two marmosets and determine the mass of their leg muscles. Here we will present values for the mechanical output of marmosets during jumping, and compare them with values extracted from the literature for the mechanical output of other primate species.

RESULTS
Mean time histories of the variables calculated for the jumps are shown in Fig. 1, with the grey area indicating standard deviation, and mean values of selected variables extracted from individual time histories are presented in Table 1. The animals lowered their COM by approximately 0.5–1.0 cm to come to a full crouch at the start of the push-off. During the push-off, the COM gained on average 18 cm in height. At take-off, vertical velocity of the COM (vCOM) was on average 2.99 m s⁻¹, allowing the animals to cover a vertical distance of 45.6 cm during the airborne phase according to ballistic equations. Note, however, that the time history of COM height and its derivatives do not accurately reflect what happened at the apex of the jump.
where the animals approached the 70 cm higher crossbar. As a matter of fact, there was quite some variation in jump height among the animals, with a few jumps ending suspiciously low. We therefore studied the collected images to determine how the animals worked their way onto the higher crossbar. In most of the jumps, the animals could easily grab the crossbar while they still had an upward velocity and had to put in little effort to get on top of it (e.g. see supplementary material Movie 1). In a few jumps, however, the animals had a low jump apex, could barely grab the crossbar, and had to work themselves onto it like acrobats. To our reassurance, the latter jumps corresponded to the jumps that had been labelled as suspiciously low themselves onto it like acrobats. To our reassurance, the latter jumps could barely grab the crossbar, and had to work their way onto the higher crossbar. In most of the jumps, the animals could easily grab the crossbar while they still had an upward velocity and had to put in little effort to get on top of it (e.g. see supplementary material Movie 1). In a few jumps, however, the animals had a low jump apex, could barely grab the crossbar, and had to work themselves onto it like acrobats. To our reassurance, the latter jumps corresponded to the jumps that had been labelled as suspiciously low.

**DISCUSSION**

We determined the mechanical output of marmosets during jumping, with the long-term purpose of understanding how it relates to the output of the elements of the musculoskeletal system. From the vertical ground reaction force history, we calculated $E_{\text{BMS,mean}}$ and $E_{\text{BMS,peak}}$ to be 52 and 116 W kg$^{-1}$, respectively. We used these values in combination with leg muscle mass to estimate $E_{\text{MMS,mean}}$ and $E_{\text{MMS,peak}}$, arriving at values of 430 and 970 W kg$^{-1}$, respectively. Given the precautions that we took in measuring and processing the vertical ground reaction forces, the numbers for $E_{\text{BMS,mean}}$ and $E_{\text{BMS,peak}}$ will be valid, but to estimate $E_{\text{MMS,mean}}$ and $E_{\text{MMS,peak}}$, we had to make several assumptions. Below, we shall first discuss possible limitations of our estimates of $E_{\text{MMS,mean}}$ and $E_{\text{MMS,peak}}$. Subsequently, we will compare them with muscle-mass-specific mechanical output measured in experiments on isolated muscles. Finally, we will compare the values for $E_{\text{MMS,mean}}$ and $E_{\text{MMS,peak}}$ that we obtained for marmosets with values reported in the literature for other primates.

In this study, we used the vertical ground reaction force history to calculate $E$, which represents the rate of change of effective energy, i.e. the energy contributing to jump height. In the literature, $E$ is typically referred to as power (e.g. Henry et al., 2005; Roberts et al., 2011), but there are two reasons why $E$ will present a lower bound, a conservative estimate, of the power output of the muscle–tendon complexes. First, in addition to effective energy, there will be ineffective energy terms, such as rotational energy and kinetic energy due to horizontal velocity. In human vertical jumping, the ratio of effective energy to the total net work produced is some 0.87 at take-off (van Soest et al., 1993). It is not clear what this ratio will be in marmosets; on the one hand, marmosets have relatively low inertia of their segments because of their small scale (Bobbert, 2013), but on the other hand, they will have to rotate their shorter segments much faster to achieve the greater vertical velocities needed to jump higher than humans. In any case, also in marmosets, the ratio must remain below 1.0 (Bobbert and van Soest, 2001). Thus, $E$ provides a lower bound on the net mechanical output of the muscle–tendon complexes. Second, the net mechanical output is a lower bound on the actual mechanical output of agonistic muscle–tendon complexes, because there will be a certain amount of co-contraction and power dissipation by antagonistic muscle–tendon complexes. We presented values for both $E_{\text{mean}}$ and $E_{\text{peak}}$, but we feel that $E_{\text{mean}}$ is the most interesting variable of the two. The reason is that $E_{\text{peak}}$ may be composed of both the power output of muscle fibres and the power output of series elastic elements (Alexander and Bennet-Clark, 1977; Bobbert, 2001), with the latter depending on the rate of decrease of force of the muscle–tendon complexes. Because the series elastic elements are undamped, their power output is unbounded: the higher the rate of decrease of force, the greater the power output. Let us therefore focus on $E_{\text{mean}}$, which will be more closely related to the mean power output of muscle tissue ($P_{\text{mean}}$). The challenge now is to decide how much muscle mass is involved in producing $E_{\text{mean}}$. In our calculation of $E_{\text{MMS,mean}}$, we simply assumed that the effective muscle mass was composed of all the leg extensors and the adductor muscles. For the animals that we dissected, this effective muscle mass amounted to a total of 12% of body mass. While we admittedly dissected only two animals, these animals seemed representative of the group, and we had no reason to think that we were underestimating the effective leg muscle mass. More likely, we were overestimating the effective leg muscle mass by including the adductors. The arguments presented above are all reason to think that our $E_{\text{MMS,mean}}$ of 430 W kg$^{-1}$ is an underestimate rather than an overestimate of the actual mean power output of muscle tissue ($P_{\text{MMS,mean}}$) of marmosets. It should also be noted that some animals could presumably have jumped to a crossbar higher than the one to which they jumped in the tower (the animal depicted in Fig. 2 jumped
to a bar at a height of 80 cm). We can think of only one factor that may cause $E_{\text{MMS,mean}}$ to be an overestimate rather than an underestimate of $P_{\text{MMS,mean}}$, and that is the unknown contribution of muscles other than the leg muscles. We will return to this issue below.

How does our estimate of $E_{\text{MMS,mean}}$ compare with the maximal power output $P_{\text{MMS,max}}$ measured in experiments on isolated muscles? To the best of our knowledge, such experiments have not been performed on muscles of marmosets or other primates, surely for ethical reasons, but they have been performed on muscles of other animals such as cats and rats. $P_{\text{MMS,max}}$ of the medial gastrocnemius muscle of the cat in isotonic contractions amounts to 324 W kg$^{-1}$ (Spector et al., 1980), and that of the medial gastrocnemius of the rat during isokinetic contractions to 516 W kg$^{-1}$ (Furrer et al., 2013). The latter value, which was obtained from muscles of which the temperature was kept at 35°C using a nebulizer system, is the highest that we have come across in the literature. How can our mean $E_{\text{MMS,mean}}$ of 430 W kg$^{-1}$ be so close to the maximal $P_{\text{MMS}}$ of rat medial gastrocnemius muscle, with the latter obviously being higher than the mean $P_{\text{MMS}}$ in any workloop experiment on isolated fibres or fibre bundles? The dilemma becomes even bigger if marmosets also have slow muscles, which have much lower $P_{\text{MMS,max}}$ (Spector et al., 1980); after all, in that case $E_{\text{MMS,mean}}$ of some muscles must be even higher than the $E_{\text{MMS,mean}}$ values reported in this study. As mentioned above, we ignored the possible contribution of muscles other than the leg muscles, and hence perhaps divided our values of $E_{\text{mean}}$ by an estimated effective muscle mass that was too small. The collected images (e.g. Fig. 2) suggest that arm extensors and trunk extensors contribute some work over the first half of the push-off phase. Estimating these contributions would require an inverse dynamics analysis, for which we would need to combine kinematics with the full ground reaction force vector, which we did not have. If we were to include the arm and trunk extensor muscle mass in calculating $E_{\text{MMS,mean}}$, we would end up with a more acceptable value. However, this would bring only temporary solace, as will become clear when we include the jumping performance of other mammals into the evaluation of $E_{\text{MMS,mean}}$ during the push-off in jumping.

Fig. 1. Time histories of the variables calculated for the jumps of marmosets ($N=18$). Variables are height, velocity and vertical acceleration of the centre of mass ($\Delta z_{\text{COM}}, z_{\text{COM}}$ and $\dot{z}_{\text{COM}}$, respectively); total vertical force exerted on the instrumented crossbar ($F_z$); total effective energy ($\Delta E$) and its constituents, i.e. potential energy ($\Delta E_{\text{pot}}$) and kinetic energy due to $\dot{z}$ ($E_{\text{kin},z}$); and rate of change of total effective energy ($\dot{E}$). $F_z$, $\Delta E$, $E_{\text{pot}}$, $E_{\text{kin},z}$ and $E$ have been expressed per kilogram of body mass. Time ($t$) is expressed in seconds relative to take-off. Data shown are means, with grey areas indicating s.d.
Table 1. Selected variables calculated for the jumps of marmosets (N=18)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Unit</th>
<th>Mean</th>
<th>s.d.</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\Delta z_{po})</td>
<td>m</td>
<td>0.180</td>
<td>0.008</td>
</tr>
<tr>
<td>(z_v)</td>
<td>m s(^{-1})</td>
<td>2.99</td>
<td>0.17</td>
</tr>
<tr>
<td>(\Delta z_{air})</td>
<td>m</td>
<td>0.456</td>
<td>0.052</td>
</tr>
<tr>
<td>(\Delta t_{po})</td>
<td>s</td>
<td>0.121</td>
<td>0.008</td>
</tr>
<tr>
<td>(\Delta E_{BMS})</td>
<td>J kg(^{-1})</td>
<td>6.23</td>
<td>0.54</td>
</tr>
<tr>
<td>(\dot{E}_{BMS,mean})</td>
<td>W kg(^{-1})</td>
<td>51.8</td>
<td>6.2</td>
</tr>
<tr>
<td>(\dot{E}_{BMS,peak})</td>
<td>W kg(^{-1})</td>
<td>116.4</td>
<td>17.6</td>
</tr>
</tbody>
</table>

\(\Delta z_{po}\): vertical displacement of the centre of mass (COM) from start of push-off to take-off; \(z_v\): vertical velocity of the COM at take-off; \(\Delta z_{air}\): predicted vertical displacement of the COM during the airborne phase, based on ballistic equations; \(\Delta t_{po}\): duration of push-off; \(\Delta E_{BMS}\): increase in effective energy of the COM during push-off, expressed per kilogram body mass; \(\dot{E}_{BMS,mean}\): mean rate of increase of effective energy during push-off, expressed per kilogram body mass; \(\dot{E}_{BMS,peak}\): peak rate of increase of effective energy during push-off, expressed per kilogram body mass.

In Table 2, the mechanical output of marmosets during jumping is compared with that of other primate species. The value for \(\dot{E}_{BMS,mean}\) of marmosets is approximately twice that of humans, who are the weakest jumpers on the list by all standards. Furthermore, \(\dot{E}_{BMS,mean}\) for jumps in marmosets is approximately 2.4 times the value for jumps of humans and 1.8 times the value for jumps of bonobos. Considering these numbers, one should keep in mind that isometric downsampling of a human musculoskeletal model to the size of a marmoset causes a 30% reduction in \(\dot{E}_{BMS,mean}\) mainly because the muscle shortening velocities reached by the downscaled model are unfavourable for power production (Bobbert, 2013). So actual marmosets, despite being much smaller, are by far outperforming humans and bonobos. Impressive as this may be, it does not bring marmosets to the top position, which is taken by bushbabies (Galago senegalensis), with values of \(\dot{E}_{BMS,mean}\) of approximately 680 W kg\(^{-1}\). The mechanical output in jumps of bushbabies has been studied in detail by Aerts (Aerts, 1998). Aerts focused on the high \(\dot{E}_{BMS,peak}\) of more than 3000 W kg\(^{-1}\), which dwarfs the values observed in other animals. In his study, Aerts (Aerts, 1998) combined inverse dynamics and a geometric musculoskeletal model to elucidate the precise nature of the mechanism powering the jumps, and came to the conclusion that the high peak power was due to ‘power amplification’ by series elastic elements of the knee extensors. However, the force of the mm. vasti [fig. 7a in Aerts (Aerts, 1998)] was not decreasing when peak power of the mm. vasti [fig. 9a in Aerts (Aerts, 1998)] occurred, which rules out recoil of series elastic elements. If we take the peak power output of the mm. vasti of approximately 145 W [fig. 9a in Aerts (Aerts, 1998)] and divide it by a mass of approximately 0.032 kg (Aerts mentions a value of 12.5% body mass for the left and right mm. vasti together), we end up with 4500 W kg\(^{-1}\) as the lower bound for \(P_{MMS,max}\), which is unrealistic. Most likely, the musculoskeletal model used by Aerts (Aerts, 1998) was too simple to accurately attribute joint moments and powers to individual muscle–tendon complexes. However, the value of \(\dot{E}_{BMS,mean}\) that we calculated from his data (Table 1) seems indisputable, and even if we distribute it over all the muscles in the animal, which together make up some 35% of body mass (Grand, 1990), we still end up with an \(\dot{E}_{BMS,mean}\) value of approximately 480 W kg\(^{-1}\). Unless the animals exploit some hitherto undescribed mechanism to store energy in series elastic components before the start of the jump, the \(\dot{E}_{BMS,mean}\) value of 480 W kg\(^{-1}\) is an underestimate of the actual \(\dot{P}_{MMS,mean}\) of the extensor muscles of bushbabies, and we remain faced with the puzzle of how the mean \(P_{MMS}\) of small primates can be close to the maximum \(P_{MMS}\) of rat gastrocnemius muscle. As a first next step towards solving this puzzle, investigation of the force–velocity relationship of muscle tissue of small primates seems indicated.

In conclusion, the values for \(\dot{E}_{BMS,mean}\) and \(\dot{E}_{BMS,mean}\) of jumping marmosets determined in the present study by far surpass those of jumping humans, albeit not those of jumping bushbabies. In our opinion, this warrants the development of a detailed musculoskeletal model for in-depth analysis of the mechanical output in jumping marmosets. Building such a model requires the determination of the contractile properties of marmoset muscles, as well as post mortem determination of musculoskeletal design, preferably of animals whose mechanical output during jumping has been previously studied. We are currently studying muscle fibre type distribution in the m. vastus lateralis of marmosets, as well as the power generating capacity of skinned fibre segments isolated from this muscle. We hope to succeed in the near future in building a realistic musculoskeletal model of marmosets that explains the high mechanical output of these animals during jumping.

**MATERIALS AND METHODS**

**Animals**

We studied jumps of 18 healthy common marmosets (Callithrix jacchus) from the purpose-bred colony of the Biomedical Primate Research Centre (BPRC) in The Netherlands (nine males and nine females, 3–4 years of age, mass 0.36±0.04 kg). The measurements took place in the pre-intervention phase of a different project of BPRC, in which the animals were enrolled. According to the Dutch law on animal experimentation, the study was approved by the Ethical Review Committee of the BPRC. The animals were pair-housed under conventional conditions in spacious cages with a varying enriched cage environment and were under intensive veterinary care throughout the study. The facility was under controlled conditions of humidity (>60%), temperature (22–26°C) and lighting (12 h:12 h light:dark cycles). The marmosets were fed daily with pellet chow for New World monkeys (Special Diet Services, Witham, Essex, UK), enriched with peanuts, biscuits, fruit, vegetables and an occasional mealworm. Water was available *ad libitum*.

**Recording of jumps**

During two subsequent weeks, each animal spent 10 min in a tower (35×35×220 cm; see Fig. 3A) to which it had been habituated (see Verhave et al., 2009). The tower had a transparent front so that the animal could be...
Table 2. Mechanical output (W kg⁻¹) during jumping in different primate species, and mass of leg muscles (left and right combined) as a fraction of total body mass

<table>
<thead>
<tr>
<th>Species</th>
<th>E_BMS,mean</th>
<th>E_BMS,peak</th>
<th>E_BMS,mean</th>
<th>E_BMS,peak</th>
<th>Leg muscle mass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bushbaby (Galago senegalensis)</td>
<td>171</td>
<td>797</td>
<td>683</td>
<td>3187</td>
<td>0.25</td>
</tr>
<tr>
<td>Marmoset (Callithrix jacchus)</td>
<td>52</td>
<td>118</td>
<td>430</td>
<td>970</td>
<td>0.12</td>
</tr>
<tr>
<td>Bonobo (Pan paniscus)</td>
<td>39</td>
<td>83</td>
<td>241</td>
<td>520</td>
<td>0.14</td>
</tr>
<tr>
<td>Human (Homo sapiens)</td>
<td>27</td>
<td>49</td>
<td>181</td>
<td>332</td>
<td>0.17</td>
</tr>
</tbody>
</table>

*E_BMS,mean* and *E_BMS,peak*, mean rate of increase of effective energy during push-off, expressed per kilogram body mass (BMS) or leg muscle mass (MMS); *E_BMS,peak* and *E_BMS,mean*—peak rate of increase of effective energy during push-off, expressed per kilogram body mass (BMS) or leg muscle mass (MMS).

*Present study.*

*Recalculated from original data of Bobbert et al.* (Bobbert et al., 2008). Relative leg extensor muscle mass was taken from Klein Horsman et al. (Klein Horsman et al., 2007).

observed, and contained five horizontal crossbars. The animals entered the tower at the bottom and could move around freely between the ground and the bars. One of the crossbars was lightweight (0.2 kg) and very stiff. This crossbar was bolted down on two force transducers (Futek, model LSB200-25 lb, Irvine, CA, USA), one at each end (Fig. 3B), so that the total vertical force exerted on the crossbar could be recorded. The system had a resonance frequency of approximately 180 Hz (Fig. 4). After being released into the tower at ground level, an animal would typically climb or jump up into the tower and reach the instrumented crossbar. There it would sit or move to and fro for a while, and then spontaneously jump to the next crossbar located 70 cm higher. Because of the dimensions of the tower and the placement of the crossbars, the jumps were practically vertical. Fig. 2 shows frames made with a camera (Casio Exilim EX-F1, Tokyo, Japan) at 300 fps for a while, and then spontaneously jump to the next crossbar located 70 cm higher.

Fig. 3. Experimental setup. (A) Tower in which the marmosets could move freely between the ground and crossbars. (B) One crossbar (darker than others) was mounted on two force transducers (cubes), one on each end. After being released into the tower at ground level, an animal would typically climb or jump up into the tower and reach the instrumented crossbar, from which it would spontaneously jump to the next crossbar located 70 cm higher.

Fig. 4. Frequency spectrum of the response of the two force transducers to an impulse force input to the crossbar. The resonance frequency of the system was approximately 180 Hz.

Calculation of mechanical output

If we take as reference the situation in which the animal is sitting still, i.e. has zero velocity of the COM, the effective energy gained during the push-off (∆E) equals the sum of the change in potential energy (∆E_pot) and kinetic energy due to the vertical velocity of the COM (E_kin):

$$
\Delta E(t) = \Delta E_{pot}(t) + E_{kin}(t) = m \cdot g \cdot \Delta z_{COM}(t) + 0.5 \cdot m \cdot \left[ \dot{z}_{COM}(t) \right]^2,
$$

where \( t \) is time, \( m \) is body mass, \( g \) is the acceleration due to gravity (9.81 m s⁻²), \( \Delta z_{COM} \) is the height of the COM relative to that at the start of the push-off.
of the jump, and $\dot{z}_{\text{COM}}$ is the vertical velocity of the COM. It follows that:

$$\frac{dE(t)}{dt} = F_z(t) \cdot g \cdot m \cdot \dot{z}_{\text{COM}}(t) + m \cdot \ddot{z}_{\text{COM}}(t) \cdot \dot{z}_{\text{COM}}(t) = \left[ m \cdot g + m \cdot \ddot{z}_{\text{COM}}(t) \right] \cdot \dot{z}_{\text{COM}}(t) = F_z(t) \cdot \dot{z}_{\text{COM}}(t),$$

(2)

where $F_z$ is the measured vertical force and $\dot{z}_{\text{COM}}$ is the vertical acceleration of the COM, which can be obtained from $F_z$ according to:

$$\dot{z}_{\text{COM}}(t) = \left[ F_z(t) - m \cdot g \right] / m.$$

Time integration of $\dot{z}_{\text{COM}}(t)$ yields $z_{\text{COM}}(t)$:

$$z_{\text{COM}}(t) = z_{\text{COM}}(0) + \int_0^t \dot{z}_{\text{COM}}(\tau) \, d\tau.$$

(4)

Subsequently, $\dot{z}_{\text{COM}}(t)$ may be multiplied by $m \cdot \ddot{z}_{\text{COM}}(t)$ to obtain $E_{\text{kin},\text{tot}}(t)$, and used to calculate $E_{\text{pot},\text{tot}}(t)$. Time integration of $E_{\text{COM}}(t)$ yields $\Delta G_{\text{COM}}(t)$, which may be multiplied by $m \cdot g$ to calculate $\Delta E_{\text{pot}}(t)$. Finally, $\Delta E(t)$ may be obtained by taking the sum of $E_{\text{kin},\text{tot}}(t)$ and $E_{\text{pot},\text{tot}}(t)$, or, alternatively, by time integration of $E_{\text{tot}}(t)$.

While the calculation is mechanically straightforward, its validity in practice is jeopardized by drift, caused by (double) integration over time of small errors in initial conditions. To ensure that we ended up with valid results, we used only jumps preceded by an interval in which the animal was indeed sitting almost still. To select these jumps, we first smoothed $F_z(t)$ using a 5 Hz fourth-order low-pass Butterworth filter, detected where jumps occurred, and subsequently searched in the last 2 s preceding each jump for an interval of at least 0.5 s in which $F_z$ did not depart more than 2% from body mass. In each of the animals, we found at least one jump that met this criterion. For each of these jumps, we took the original $F_z(t)$, smoothed it using an 80 Hz fourth-order low-pass Butterworth filter, and determined $\ddot{z}_{\text{COM}}(t)$. We then started the integration of $\ddot{z}_{\text{COM}}(t)$ at the end of the interval in which the animal was sitting almost still, with $\dot{z}_{\text{COM}}(0)$ set to zero.

In order to calculate $E_{\text{pot}}(t)$ and $\Delta E(t)$, it was necessary to define the start of the push-off phase. Formally, the push-off starts when the COM starts to move upward and $\dot{E}$ becomes positive, but we pragmatically defined the start of the push-off to be the instant that $\dot{E}$ surpassed 2 W kg$^{-1}$. For the end of the push-off, we took the instant that $F_z$ dropped to zero.

To enable comparisons among species, $\Delta E$ and $E$ are often expressed per kilogram of body mass to obtain body-mass-specific values, henceforth referred to as $\Delta E_{\text{MMS}}$ and $E_{\text{MMS}}$, respectively. Also, attempts are made to relate $\Delta E$ and $E$ to the amount of muscle mass that effectively contributes to the jump, in order to obtain muscle-mass-specific values, henceforth referred to as $\Delta E_{\text{MMS}}$ and $E_{\text{MMS}}$, respectively.

**Determination of muscle mass**

We had the opportunity to determine muscle masses post mortem in two marmosets. One animal, female M09053 (0.410 kg, 27 months old), had died unexpectedly before the start of the study during alphaxalone (14 mg kg$^{-1}$) sedation. The second animal, female M09024 (0.332 kg, 36 months old), was euthanized 5 weeks after the jumping measurements were completed. The bodies of the animals were frozen directly after death and kept at $-40^\circ$C until further analyses. Prior to the dissection, the hind-limbs were defrosted and the muscle groups of the left leg were removed one by one and weighed (Metler PC440 scale, Mettler-Toledo, Columbus, OH, USA). We report the total masses for functional muscle groups, defined as suggested elsewhere (Scholz et al., 2006): the hip extensors (m. gluteus maximus, m. gluteus medius, m. semitendinosus, m. semimembranosus, m. biceps femoris), hip adductors (m. adductor brevis, m. adductor magnus, m. adductor longus), knee extensors (m. vastus lateralis, m. vastus medialis, m. vastus intermedius, m. rectus femoris) and plantar flexors (m. soleus, m. gastrocnemius medialis, m. gastrocnemius lateralis, m. tibialis posterior, m. flexor digitorum longus tibialis, m. flexor digitorum longus fibularis).

**Statistics**

From one animal we did not obtain a force record that met our criteria; from each of the other animals we obtained between one and four good jumps. In total, 49 jumps met our criteria and were fully analyzed as described. If an animal had more than one jump, we averaged the results over these jumps. Finally, we determined means and standard deviations over animals.

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**Competing interests**

The authors declare no competing financial interests.

**Author contributions**

M.F.B. conceived and designed the experiments, analysed and interpreted the findings, and drafted and revised the article. R.L.C.P. executed part of the experiments, interpreted findings, and drafted part of the article. G.W. executed part of the experiments, interpreted findings, and drafted part of the article. H.E.C. designed and built the force measurement setup. S.O.H. executed part of the experiments and interpreted the findings. R.T.J. conceived and designed the experiments. I.H.C.H.M.P. conceived and designed the experiments and drafted part of the article.

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**Supplementary material**

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**References**


**Movie 1.** A marmoset performing a jump in the experimental setup. Movie shot at 240 frames s$^{-1}$ (Casio Exilim EX-FH25) of a marmoset jumping in the tower from the instrumented crossbar (black) to a crossbar located 70 cm higher.