

## RESEARCH ARTICLE

# Mechanical output in jumps of marmosets (*Callithrix jacchus*)

Maarten F. Bobbert<sup>1,\*</sup>, Rogier L. C. Plas<sup>1</sup>, Guido Weide<sup>1</sup>, H. E. (Bert) Clairbois<sup>1</sup>, Sam O. Hofman<sup>2</sup>, Richard T. Jaspers<sup>1</sup> and Ingrid H. C. H. M. Philippens<sup>2</sup>

**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  $51.8 \pm 6.2 \text{ W kg}^{-1}$  body mass, and the peak value to  $116.4 \pm 17.6 \text{ W kg}^{-1}$  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  $970 \text{ W kg}^{-1}$  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  $430 \text{ W kg}^{-1}$  muscle was close to the maximal power output of  $516 \text{ W kg}^{-1}$  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; Pandey 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; 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 ( $\dot{z}_{\text{COM}}$ ) was on average  $2.99 \text{ m s}^{-1}$ , 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,

<sup>1</sup>MOVE Research Institute Amsterdam, Faculty of Human Movement Sciences, VU University Amsterdam, Van der Boechorstraat 9, NL-1081 BT Amsterdam, The Netherlands. <sup>2</sup>Department of Immunobiology, Division Neuropathology, Biomedical Primate Research Centre, 2280 GH Rijswijk, The Netherlands.

\*Author for correspondence (M\_F\_Bobbert@fbw.vu.nl)

Received 3 April 2013; Accepted 30 September 2013

**List of symbols and abbreviations**

COM	centre of mass
$E$	effective energy, i.e. sum of potential and vertical kinetic energy of the COM
$\dot{E}$	rate of change of $E$ ( $=dE/dt$ )
$E_{\text{kin},z}$	kinetic energy due to the vertical velocity of the COM
$\dot{E}_{\text{kin},z}$	rate of change of $E_{\text{kin},z}$
$F_z$	measured vertical ground reaction force
$g$	acceleration due to gravity ( $9.81 \text{ m s}^{-2}$ )
$m$	body mass
$P$	power output of muscle tissue
$P_{\text{max}}$	maximum power output of muscle tissue in isokinetic or isotonic contractions
$t$	time
$\dot{z}_{\text{COM}}$	vertical velocity of the COM
$\ddot{z}_{\text{COM}}$	vertical acceleration of the COM
$\Delta E$	effective energy of the COM relative to effective energy at the start of the jump
$\Delta E_{\text{pot}}$	potential energy relative to potential energy at the start of the jump
$\Delta z_{\text{COM}}$	height of the COM relative to height of the COM at the start of the jump

**List of subscripts**

BMS	body mass specific
MMS	muscle mass specific
mean	mean of variable during push-off phase
peak	peak value of variable achieved during the push-off phase

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 on the basis of the force records. The increase in effective energy of the COM ( $\Delta E$ ) that occurred from the start of the push-off to take-off, expressed per kilogram body mass ( $\Delta E_{\text{BMS}}$ ), amounted to  $6.23 \text{ J kg}^{-1}$ ; divided by  $g$ , this yields the total increase in the height of the COM ( $\Delta z_{\text{COM}}$ ). The crucial information concerns the duration of the push-off and the values achieved for  $\dot{E}$ , the rate of change of  $\Delta E$ : the animals were able to achieve  $\Delta E_{\text{BMS}}$  in only 121 ms on average, so that mean body-mass-specific  $\dot{E}$  ( $\dot{E}_{\text{BMS,mean}}$ ) was almost  $52 \text{ W kg}^{-1}$ . Peak body-mass-specific  $\dot{E}$  ( $\dot{E}_{\text{BMS,peak}}$ ) was found to be  $116 \text{ W kg}^{-1}$ . In six animals we found  $\dot{E}_{\text{BMS,mean}}$  to be over  $55 \text{ W kg}^{-1}$  and  $\dot{E}_{\text{BMS,peak}}$  to be over  $130 \text{ W kg}^{-1}$ .

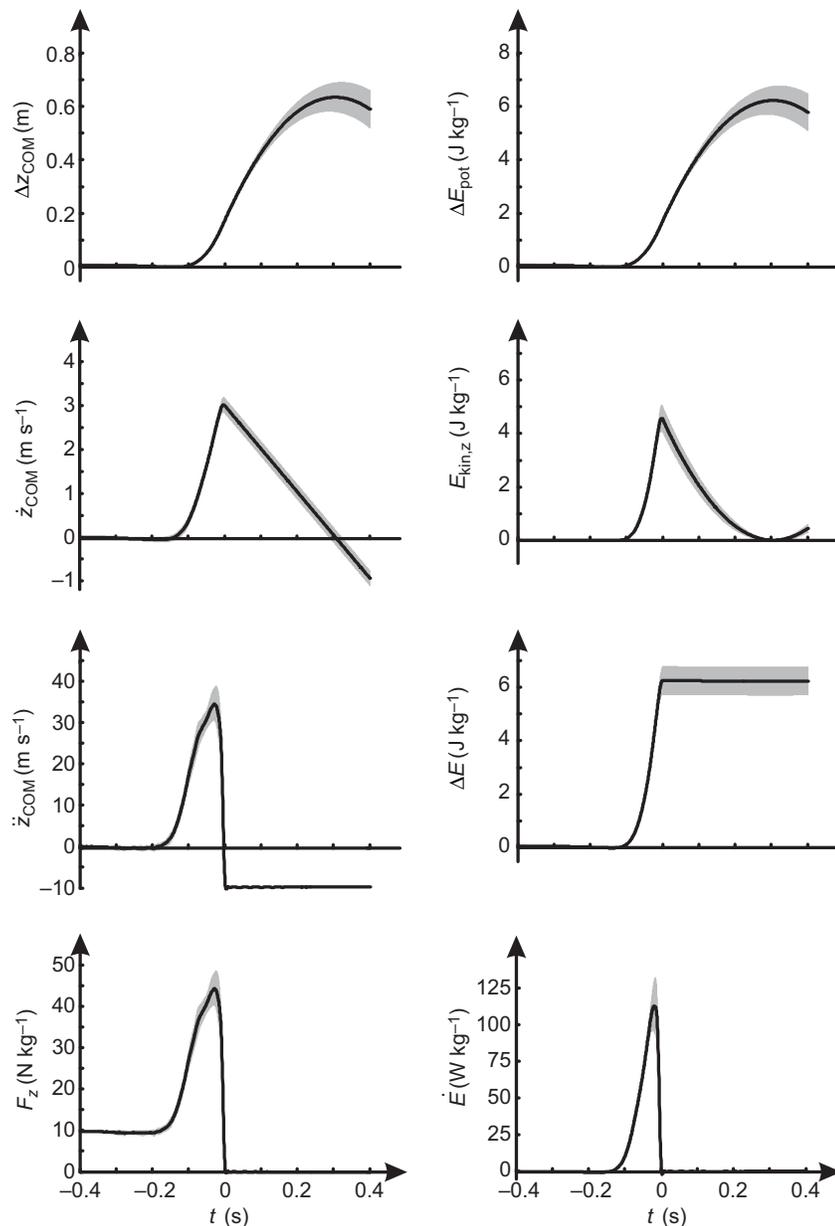
To allow us to relate the mechanical output to the muscles that effectively contribute to jumping, we determined the muscle masses in percentages of total body mass. In the two animals dissected, the hip extensors, knee extensors and plantar flexors had masses of 4.5%, 3.6% and 1.7% of body mass, respectively. Together, they made up 9.8% of body mass (9.6% in one animal, 10.1% in the other). The remaining muscles of the leg (notably hip adductors) made up another 2% of body mass. Consequently, we estimated mean muscle-mass-specific  $\dot{E}$  ( $\dot{E}_{\text{MMS,mean}}$ ) to be  $430 \text{ W kg}^{-1}$  and peak muscle-mass-specific  $\dot{E}$  ( $\dot{E}_{\text{MMS,peak}}$ ) to be  $970 \text{ W kg}^{-1}$ .

**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  $\dot{E}_{\text{BMS,mean}}$  and  $\dot{E}_{\text{BMS,peak}}$  to be  $52$  and  $116 \text{ W kg}^{-1}$ , respectively. We used these values in combination with leg muscle mass to estimate  $\dot{E}_{\text{MMS,mean}}$  and  $\dot{E}_{\text{MMS,peak}}$ , arriving at values of  $430$  and  $970 \text{ W kg}^{-1}$ , respectively. Given the precautions that we took in measuring and processing the vertical ground reaction forces, the numbers for  $\dot{E}_{\text{BMS,mean}}$  and  $\dot{E}_{\text{BMS,peak}}$  will be valid, but to estimate  $\dot{E}_{\text{MMS,mean}}$  and  $\dot{E}_{\text{MMS,peak}}$  we had to make several assumptions. Below, we shall first discuss possible limitations of our estimates of  $\dot{E}_{\text{MMS,mean}}$  and  $\dot{E}_{\text{MMS,peak}}$ . Subsequently, we will compare them with muscle-mass-specific mechanical output measured in experiments on isolated muscles. Finally, we will compare the values for  $\dot{E}_{\text{MMS,mean}}$  and  $\dot{E}_{\text{MMS,peak}}$  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  $\dot{E}$ , which represents the rate of change of effective energy, i.e. the energy contributing to jump height. In the literature,  $\dot{E}$  is typically referred to as power (e.g. Henry et al., 2005; Roberts et al., 2011), but there are two reasons why  $\dot{E}$  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,  $\dot{E}$  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  $\dot{E}_{\text{mean}}$  and  $\dot{E}_{\text{peak}}$ , but we feel that  $\dot{E}_{\text{mean}}$  is the most interesting variable of the two. The reason is that  $\dot{E}_{\text{peak}}$  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  $\dot{E}_{\text{mean}}$ , 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  $\dot{E}_{\text{mean}}$ . In our calculation of  $\dot{E}_{\text{MMS,mean}}$ , 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  $\dot{E}_{\text{MMS,mean}}$  of  $430 \text{ W kg}^{-1}$  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



**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 ( $\Delta z_{\text{COM}}$ ,  $\dot{z}_{\text{COM}}$  and  $\ddot{z}_{\text{COM}}$ , 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  $\dot{E}$  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.

to a bar at a height of 80 cm). We can think of only one factor that may cause  $\dot{E}_{\text{MMS,mean}}$  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  $\dot{E}_{\text{MMS,mean}}$  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  $324 \text{ W kg}^{-1}$  (Spector et al., 1980), and that of the medial gastrocnemius of the rat during isokinetic contractions to  $516 \text{ W kg}^{-1}$  (Furrer et al., 2013). The latter value, which was obtained from muscles of which the temperature was kept at  $35^\circ\text{C}$  using a nebulizer system, is the highest that we have come across in the literature. How can our mean  $\dot{E}_{\text{MMS}}$  of  $430 \text{ W kg}^{-1}$  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  $\dot{E}_{\text{MMS,mean}}$  of some muscles must be even higher than the  $\dot{E}_{\text{MMS,mean}}$  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  $\dot{E}_{\text{mean}}$  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  $\dot{E}_{\text{MMS,mean}}$ , 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  $\dot{E}_{\text{MMS,mean}}$  during the push-off in jumping.

**Table 1. Selected variables calculated for the jumps of marmosets (N=18)**

Variable	Unit	Mean	s.d.
$\Delta z_{po}$	m	0.180	0.008
$\dot{z}_{to}$	$m\ s^{-1}$	2.99	0.17
$\Delta z_{air}$	m	0.456	0.052
$\Delta t_{po}$	s	0.121	0.008
$\Delta E_{BMS}$	$J\ kg^{-1}$	6.23	0.54
$\dot{E}_{BMS,mean}$	$W\ kg^{-1}$	51.8	6.2
$\dot{E}_{BMS,peak}$	$W\ kg^{-1}$	116.4	17.6

$\Delta z_{po}$ , vertical displacement of the centre of mass (COM) from start of push-off to take-off;  $\dot{z}_{to}$ , 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,  $\dot{E}_{MMS,mean}$  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 downscaling 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  $\dot{E}_{MMS,mean}$  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  $\dot{E}_{MMS,peak}$  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  $\dot{E}_{MMS,mean}$  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  $\dot{E}_{MMS,mean}$  value of  $480\ W\ kg^{-1}$  is an underestimate of the actual  $P_{MMS,mean}$  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  $\dot{E}_{MMS,mean}$  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.

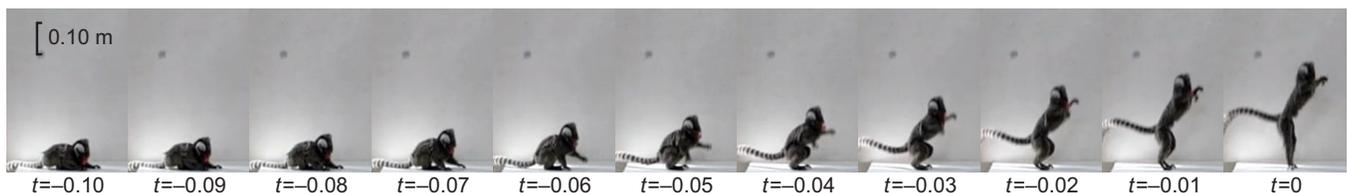
## MATERIALS AND METHODS

### 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  $0.365 \pm 0.041\ kg$ ). 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 Duit 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



**Fig. 2. Images of a marmoset jumping from the ground to a crossbar at a height of 80 cm.** The images were shot outside the tower to ensure proper lighting conditions and hence high image quality, and to achieve a good sagittal-plane view of the push-off. Time ( $t$ ) is expressed in seconds relative to take-off ( $t=0$ ).

**Table 2. Mechanical output ( $W\text{ kg}^{-1}$ ) during jumping in different primate species, and mass of leg muscles (left and right combined) as a fraction of total body mass**

Species	$\dot{E}_{\text{BMS,mean}}$	$\dot{E}_{\text{BMS,peak}}$	$\dot{E}_{\text{MMS,mean}}$	$\dot{E}_{\text{MMS,peak}}$	Leg muscle mass
Bushbaby ( <i>Galago senegalensis</i> ) <sup>a</sup>	171	797	683	3187	0.25
Marmoset ( <i>Callithrix jacchus</i> ) <sup>b</sup>	52	118	430	970	0.12
Bonobo ( <i>Pan paniscus</i> ) <sup>c</sup>	39	83	241	520	0.14
Human ( <i>Homo sapiens</i> ) <sup>d</sup>	27	49	181	332	0.17

$\dot{E}_{\text{BMS,mean}}$  and  $\dot{E}_{\text{MMS,mean}}$ , mean rate of increase of effective energy during push-off, expressed per kilogram body mass (BMS) or leg muscle mass (MMS);  $\dot{E}_{\text{BMS,peak}}$  and  $\dot{E}_{\text{MMS,peak}}$ , peak rate of increase of effective energy during push-off, expressed per kilogram body mass (BMS) or leg muscle mass (MMS).

<sup>a</sup> $\dot{E}_{\text{BMS,mean}}$  was calculated using jump J33 of specimen 1, in which jump height was 1.74 m and push-off duration of 100 ms (from Aerts, 1998).  $\dot{E}_{\text{BMS,peak}}$  was calculated using an  $\dot{E}_{\text{peak}}$  of 200 W. Relative leg extensor muscle mass was taken from Aerts (Aerts, 1998).

<sup>b</sup>Present study.

<sup>c</sup> $\dot{E}_{\text{BMS,mean}}$  was calculated using 0.78 m jump height, 0.6 m vertical displacement of the centre of mass during the push-off, and 350 ms push-off duration (from Scholz et al., 2006).  $\dot{E}_{\text{BMS,peak}}$  was calculated using an  $\dot{E}_{\text{peak}}$  of 3000 W. Relative leg extensor muscle mass was taken from table 3 in Payne et al. (Payne et al., 2006).

<sup>d</sup>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 frames  $s^{-1}$  of a marmoset jumping from the ground to a crossbar at a height of 80 cm; the

footage was shot outside the tower to ensure proper lighting conditions and hence high image quality, and to achieve a good sagittal-plane view of the push-off. A movie of a marmoset jumping in the tower is available (supplementary material Movie 1). Most animals made several jumps from the instrumented crossbar during the 10 min they spent in the tower. The analogue signals from the force transducers were sampled at 2000 Hz using a 24-bit simultaneous sampling bridge module (National Instruments type 9237, Austin, TX, USA), and stored. Fig. 5 shows a typical force record of an animal that moved along the instrumented crossbar, sat still for some time, and then jumped to the next crossbar. Off-line, the sections of the force signals that corresponded to jumps were selected and processed further as detailed below. In addition to the forces we also collected images at 240 frames  $s^{-1}$  during each trial, which allowed us to study off-line where the animals were in the tower and what they were doing; supplementary material Movie 1 of a marmoset jump presents a subset of these images.



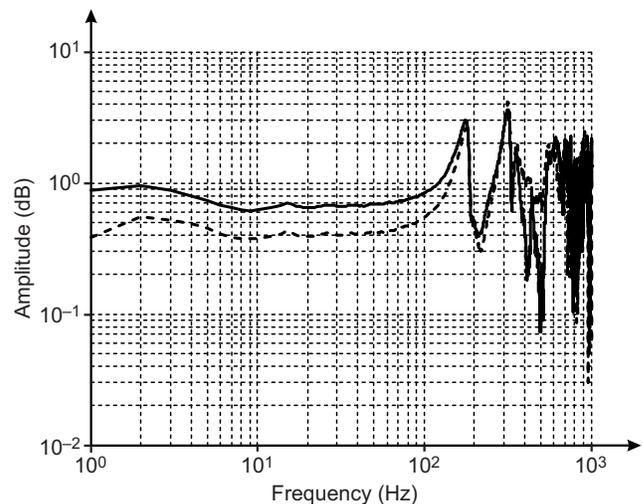
**Fig. 3. Experimental setup.** (A) Tower in which the marmosets could move freely between the ground and crossbars. (B) One crossbar (darker than others) was mounted on two force transducers (cubes), one on each side. After being released into the tower at ground level, an animal would typically climb 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.

#### Calculation of mechanical output

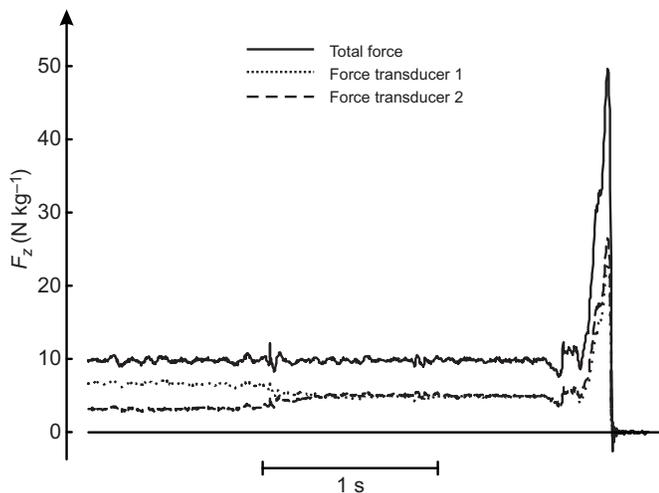
If we take as reference the situation in which the animal is sitting still, i.e. has zero velocity of the COM, the effective energy gained during the push-off ( $\Delta E$ ) equals the sum of the change in potential energy ( $\Delta E_{\text{pot}}$ ) and kinetic energy due to the vertical velocity of the COM ( $E_{\text{kin,z}}$ ):

$$\Delta E(t) = \Delta E_{\text{pot}}(t) + E_{\text{kin,z}}(t) = m \cdot g \cdot \Delta z_{\text{COM}}(t) + 0.5 \cdot m \cdot [\dot{z}_{\text{COM}}(t)]^2, \quad (1)$$

where  $t$  is time,  $m$  is body mass,  $g$  is the acceleration due to gravity ( $9.81\text{ m s}^{-2}$ ),  $\Delta z_{\text{COM}}$  is the height of the COM relative to that at the start



**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.



**Fig. 5. Typical force record of an animal that moved along the instrumented crossbar, sat still for some time, and then jumped to the next crossbar.**

of the jump, and  $\dot{z}_{\text{COM}}$  is the vertical velocity of the COM. It follows that:

$$\begin{aligned} \frac{dE(t)}{dt} &= \dot{E}(t) = m \cdot g \cdot \dot{z}_{\text{COM}}(t) + m \cdot \dot{z}_{\text{COM}}(t) \cdot \ddot{z}_{\text{COM}}(t) \\ &= [m \cdot g + m \cdot \ddot{z}_{\text{COM}}(t)] \cdot \dot{z}_{\text{COM}}(t) = F_z(t) \cdot \dot{z}_{\text{COM}}(t), \quad (2) \end{aligned}$$

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

$$\ddot{z}_{\text{COM}}(t) = [F_z(t) - m \cdot g] / m. \quad (3)$$

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

$$\dot{z}_{\text{COM}}(t) = \dot{z}_{\text{COM}}(0) + \int_0^t \ddot{z}_{\text{COM}}(t) \cdot dt. \quad (4)$$

Subsequently,  $\dot{z}_{\text{COM}}(t)$  may be multiplied by  $m \cdot \dot{z}_{\text{COM}}(t)$  to obtain  $\dot{E}_{\text{kin},z}(t)$ , and used to calculate  $E_{\text{kin},z}(t)$ . Time integration of  $\dot{z}_{\text{COM}}(t)$  yields  $\Delta z_{\text{COM}}(t)$ , 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  $E_{\text{kin},z}(t)$  and  $\Delta E_{\text{pot}}(t)$ , or, alternatively, by time integration of  $\dot{E}(t)$ .

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  $\dot{E}_{\text{mean}}$  and  $\Delta E$ , 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  $2 \text{ W kg}^{-1}$ . 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  $\dot{E}$  are often expressed per kilogram of body mass to obtain body-mass-specific values, henceforth referred to as  $\Delta E_{\text{BMS}}$  and  $\dot{E}_{\text{BMS}}$ , respectively. Also, attempts are made to relate  $\Delta E$  and  $\dot{E}$  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  $\dot{E}_{\text{MMS}}$ , 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 ( $14 \text{ mg kg}^{-1}$ ) 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  $-40^\circ\text{C}$  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 (Mettler 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.

## Acknowledgements

The authors thank Mr F. Batenburg for his excellent technical support of the jumping experiments in the tower, and PhD student Ms S. K. Tolboom for carrying out the habituation and behavioural training of the animals.

## 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.

## Funding

This study was supported by an internal grant of the Biomedical Primate Research Centre.

## Supplementary material

Supplementary material available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.089177/-DC1>

## References

- Aerts, P. (1998). Vertical jumping in *Galago senegalensis*: the quest for an obligate mechanical power amplifier. *Philos. Trans. R. Soc. B* **353**, 1607-1620.
- Alexander, R. M. (1995). Leg design and jumping technique for humans, other vertebrates and insects. *Philos. Trans. R. Soc. B* **347**, 235-248.
- Alexander, R. M. and Bennet-Clark, H. C. (1977). Storage of elastic strain energy in muscle and other tissues. *Nature* **265**, 114-117.
- Bobbert, M. F. (2001). Dependence of human squat jump performance on the series elastic compliance of the triceps surae: a simulation study. *J. Exp. Biol.* **204**, 533-542.
- Bobbert, M. F. (2013). Effects of isometric scaling on vertical jumping performance. *PLoS ONE* **8**, e71209.
- Bobbert, M. F. and van Soest, A. J. (2001). Why do people jump the way they do? *Exerc. Sport Sci. Rev.* **29**, 95-102.
- Bobbert, M. F., Casius, L. J. R., Sijpkens, I. W. T. and Jaspers, R. T. (2008). Humans adjust control to initial squat depth in vertical squat jumping. *J. Appl. Physiol.* **105**, 1428-1440.
- Channon, A. J., Usherwood, J. R., Crompton, R. H., Günther, M. M. and Vereecke, E. E. (2012). The extraordinary athletic performance of leaping gibbons. *Biol. Lett.* **8**, 46-49.

- Furrer, R., Jaspers, R. T., Baggerman, H. L., Bravenboer, N., Lips, P. and de Haan, A. (2013). Attenuated increase in maximal force of rat medial gastrocnemius muscle after concurrent peak power and endurance training. *BioMed Res. Int.* **2013**, 935671.
- Grand, T. I. (1990). The functional anatomy of body mass. In *Body Size in Mammalian Paleobiology; Estimation and Biological Implications* (ed. J. Damuth and B. J. MacFadden), pp. 39-48. Cambridge: Cambridge University Press.
- Harris, M. A. and Steudel, K. (2002). The relationship between maximum jumping performance and hind limb morphology/physiology in domestic cats (*Felis silvestris catus*). *J. Exp. Biol.* **205**, 3877-3889.
- Henry, H. T., Ellerby, D. J. and Marsh, R. L. (2005). Performance of guinea fowl *Numida meleagris* during jumping requires storage and release of elastic energy. *J. Exp. Biol.* **208**, 3293-3302.
- Klein Horsman, M. D., Koopman, H. F. J. M., van der Helm, F. C. T., Prosé, L. P. and Veeger, H. E. J. (2007). Morphological muscle and joint parameters for musculoskeletal modelling of the lower extremity. *Clin. Biomech. (Bristol, Avon)* **22**, 239-247.
- Nagano, A., Komura, T., Yoshioka, S. and Fukashiro, S. (2005). Contribution of non-extensor muscles of the leg to maximal-effort countermovement jumping. *Biomed. Eng. Online* **4**, 52-52.
- Okano, H., Hikishima, K., Iriki, A. and Sasaki, E. (2012). The common marmoset as a novel animal model system for biomedical and neuroscience research applications. *Semin. Fetal Neonatal Med.* **17**, 336-340.
- Pandy, M. G., Zajac, F. E., Sim, E. and Levine, W. S. (1990). An optimal control model for maximum-height human jumping. *J. Biomech.* **23**, 1185-1198.
- Payne, R. C., Crompton, R. H., Isler, K., Savage, R., Vereecke, E. E., Günther, M. M., Thorpe, S. K. S. and D'Août, K. (2006). Morphological analysis of the hindlimb in apes and humans. I. Muscle architecture. *J. Anat.* **208**, 709-724.
- Peplowski, M. M. and Marsh, R. L. (1997). Work and power output in the hindlimb muscles of Cuban tree frogs *Osteopilus septentrionalis* during jumping. *J. Exp. Biol.* **200**, 2861-2870.
- Roberts, T. J., Abbott, E. M. and Azizi, E. (2011). The weak link: do muscle properties determine locomotor performance in frogs? *Philos. Trans. R. Soc. B* **366**, 1488-1495.
- Scholz, M. N., D'Août, K., Bobbert, M. F. and Aerts, P. (2006). Vertical jumping performance of bonobo (*Pan paniscus*) suggests superior muscle properties. *Proc. Biol. Sci.* **273**, 2177-2184.
- Spector, S. A., Gardiner, P. F., Zernicke, R. F., Roy, R. R. and Edgerton, V. R. (1980). Muscle architecture and force-velocity characteristics of cat soleus and medial gastrocnemius: implications for motor control. *J. Neurophysiol.* **44**, 951-960.
- 't Hart, B. A., Abbott, D. H., Nakamura, K. and Fuchs, E. (2012). The marmoset monkey: a multi-purpose preclinical and translational model of human biology and disease. *Drug Discov. Today* **17**, 1160-1165.
- Tardif, S. D., Mansfield, K. G., Ratnam, R., Ross, C. N. and Ziegler, T. E. (2011). The marmoset as a model of aging and age-related diseases. *ILAR J.* **52**, 54-65.
- van Soest, A. J., Schwab, A. L., Bobbert, M. F. and van Ingen Schenau, G. J. (1993). The influence of the biarticularity of the gastrocnemius muscle on vertical-jumping achievement. *J. Biomech.* **26**, 1-8.
- Verhave, P. S., Vanwersch, R. A. P., van Helden, H. P. M., Smit, A. B. and Philippens, I. H. C. H. M. (2009). Two new test methods to quantify motor deficits in a marmoset model for Parkinson's disease. *Behav. Brain Res.* **200**, 214-219.