Contribution of the forelimbs and hindlimbs of the horse to mechanical energy changes in jumping

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Summary

The purpose of the present study was to gain more insight into the contribution of the forelimbs and hindlimbs of the horse to energy changes during the push-off for a jump. For this purpose, we collected kinematic data at 240 Hz from 23 5-year-old Warmbloods (average mass: 595 kg) performing free jumps over a 1.15 m high fence. From these data, we calculated the changes in mechanical energy and the changes in limb length and joint angles. The force carried by the forelimbs and the amount of energy stored was estimated from the distance between elbow and hoof, assuming that this part of the leg behaved as a linear spring. During the forelimb push, the total energy first decreased by 3.2 J kg^{-1} and then increased again by 4.2 J kg^{-1} to the end of the forelimb push. At the end of the forelimb push, the kinetic energy due to horizontal velocity of the centre of mass was 1.6 J kg^{-1} less than at the start, while the effective energy (energy contributing to jump height) was 2.3 J kg^{-1} greater. It was investigated to what extent these changes could involve passive spring-like behaviour of the forelimbs. The amount of energy stored and re-utilized in the distal tendons during the forelimb push was estimated to be on average 0.4 J kg^{-1} in the trailing forelimb and 0.23 J kg^{-1} in the leading forelimb. This means that a considerable amount of energy was first dissipated and subsequently regenerated by muscles, with triceps brachii probably being the most important contributor. During the hindlimb push, the muscles of the leg were primarily producing energy. The total increase in energy was 2.5 J kg^{-1} and the peak power output amounted to 71 W kg^{-1}.

Key words: *Equus caballus*, locomotion, biomechanics, elastic strain energy, energy storage, muscle work.

Introduction

The horse has outstanding locomotor abilities. Top racing horses can cover a distance of 1 mile at an average speed of some 15 m s^{-1}, while top show jumping horses can clear a fence of more than 2.30 m high with a rider on their back. Not surprisingly, locomotion of the horse has aroused a lot of scientific interest. In the late 19th century, Muybridge performed groundbreaking work; by taking sequential action photographs he was the first to prove that a running horse had all four feet in the air at some point during the gait cycle. Due to the development of sophisticated measuring equipment, more and more has become known about various aspects of horse locomotion (for an overview, see van Weeren, 2001). Detailed kinematics of the different gaits have been revealed by high speed motion capture (e.g. Clayton, 1994, 1995), forces carried by individual limbs have been quantified using force plates and instrumented horseshoes (Kai et al., 2000; Roepstorff and Drevemo, 1993), mechanical output about joints has been calculated using inverse dynamics for the forelimb (Meershoek and van den Bogert, 2001) and for the hindlimb (Dutto et al., 2004), tendon forces have been measured *in vivo* (Platt et al., 1994; Riemersma et al., 1996), and so on. Furthermore, various studies have been conducted on the anatomy of the musculoskeletal system, the physiological and mechanical properties of muscles and tendons (e.g. Biewener, 1998; Brown et al., 2003a,b; McGuigan and Wilson, 2003; Meershoek et al., 2001; Wilson et al., 2001), and the inertial properties of the different body segments (e.g. Buchner et al., 1997). This detailed knowledge of the musculoskeletal system has allowed researchers to develop forward dynamic models, and powerful computing facilities have made it possible to simulate walking in horses (van den Bogert et al., 1994; van den Bogert and Schamhardt, 1993).

Given the availability of sophisticated measurement equipment and the accumulation of knowledge over the years, one would expect that little remained to be discovered about horse locomotion. However, we were unable to find in the literature a comprehensive analysis of the contribution of the forelimbs and hindlimbs to the energy changes in galloping and jumping horses.

This is perhaps not so surprising if one realizes that in these locomotor tasks the forelimbs, and usually also the hindlimbs, are used asymmetrically. Hence, an in-depth analysis of the role of the limbs would require simultaneous measurement of the kinematics of the body segments and the ground reaction force vector under each of the four legs, which is almost impossible. However, several studies have contributed pieces of the puzzle. For example, for galloping, Minetti et al. (1999) have calculated mechanical energy changes from kinematics, while McGuigan et al. (2003) have estimated the amount of elastic energy stored and released by the forelimbs. For the hindlimb push in jumping, van den Bogert et al. (1994) have calculated mechanical energy changes from kinematics, while Dutto et al. (2004) have performed an inverse dynamics analysis using kinematics and ground reaction forces measured with a force plate. Unfortunately, however, the results of the latter two studies cannot be combined because the jump heights were very different: 1.50 m in the study of van den Bogert et al. (1994) and 63 cm in the study by Dutto et al. (2004).

The purpose of the present study was to gain more insight into the contribution of the forelimbs and hindlimbs of the horse to energy changes during the push-off for a jump. For this purpose, we collected kinematic data from 5-year-old Warmbloods performing free jumps over a 1.15 m high fence. From these data, we first calculated the ground reaction force vector and the mechanical energy changes of the body. To support the validity of the approach it was shown that the calculated ground reaction forces were similar to ground reaction forces measured in other studies using force plates. The mechanical energy changes were then combined with the changes in length and joint angles of the limbs. We were especially interested in the amount of energy stored and released by the forelimbs, which was estimated from the distance between elbow and hoof.

Materials and methods

In this study we used 23 5-year-old Dutch Warmblood horses *Equus caballus* L., whose average mass was 595 kg (standard deviation 45 kg) and average height, measured at the withers, was 1.67 m (standard deviation: 0.04 m). The horses were born in the spring of 1998 and based on the breeding values of their sire and dam had reasonably good expectations of their future jumping capacity. The complete history of the horses is described elsewhere (Santamaría et al., 2005). For the current paper it is relevant that the horses had been training intensively for jumping at the Dutch Equine Training Centre during the year preceding the experiments.

Kinematic data were collected while the horses performed free jumps over a vertical target fence in a jumping track. The height of this fence, 1.15 m, was chosen such that all horses could clear it without too much difficulty (at this stage in their career, the maximum height that some of the horses could clear with a rider on their back was about 1.40 m; others could jump over 1.50 m). The approach to the target fence was standardized: the target fence was preceded by two lower vertical fences placed at distances that restricted the horses to one canter stride in between each pair of fences. The second fence was 6.40 m from the first fence and the target fence 7.0 m from the second fence. More details of the experimental setting have been provided elsewhere (Santamaría et al., 2005).

The horses were familiarized with the experimental setting by having them practice in the jumping track a few days before the day of the actual measurements. For the measurements, skin markers were fixed at anatomical locations on the body (Fig. 1). The markers were monitored in stance and during jumping by six infrared cameras operating at 240 Hz (Pro Reflex, Qualisys Medical AB, Göteborg, Sweden). The cameras were placed laterally to the target fence on a semicircle, such that the field of view included the last canter stride before the target fence, the jump, and the first canter stride after the fence. After warming up, the horses performed free jumps until we had collected four successful jumps in which the fence was approached with a left lead of canter, as well as four successful jumps in which the fence was approached with a right lead of canter (i.e. with the left forelimb as trailing limb). From these, we selected for further analysis one jump in which the left forelimb was the leading limb, and one in which it was the trailing limb.

The time histories of the marker coordinates were first smoothed at 8 Hz using a 4th order zero-lag Butterworth filter. Next, we had to deal with the problem that markers placed on the skin may move considerably relative to the underlying skeletal landmarks (van Weeren et al., 1990a,b). For walking and trotting, the errors have been analysed and correction algorithms developed (van den Bogert et al., 1990), but for jumping no further information was available. To remedy the problem for the limbs we assumed, as others have done previously (Dutto et al., 2004; van den Bogert et al., 1994), that the limbs were chains of rigid segments interconnected in hinge joints, with joint axes and lengths of the rigid segments defined by the markers applied in square standing (Fig. 1). Assuming furthermore that the limbs moved only in the sagittal plane and that no error occurred in the markers on the hoofs, we optimised on each frame the configurations of the chains of the left forelimb and the left hindlimb by minimizing the sum of squared distances between the locations of the chain joints and the actual marker locations. The optimised coordinates of the chains were used to calculate distances between selected skeletal landmarks, segment angles and their derivatives, and joint angles. The distance between elbow and hoof of the left forelimb was used to estimate the force carried by the limb, assuming that it behaved like a linear spring with a stiffness of 166 N m^{-1} kg^{-1} (McGuigan and Wilson, 2003).

The segmental model of Buchner et al. (1997) was used to determine the locations of mass centres of the limb segments and the head and neck. To determine the location of the centre of mass of the trunk, which accounts for more than 65% of the total mass of the horse, a rigid template was defined using selected markers in square standing (see Fig. 1). Subsequently, for each frame during the jumps, the position and orientation of this template was found by minimizing the sum of squared
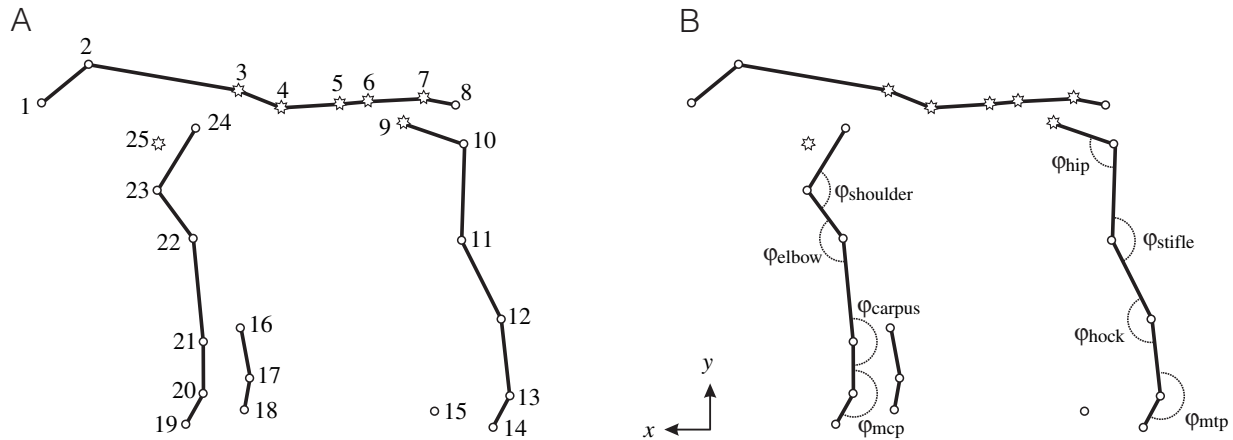
Fig. 1. Locations of anatomical markers (A) and definitions of joint angles (B). (A) Markers indicated with a star were used to construct a template of the trunk. Markers were in the following locations: 1, left crista facialis (cranial); 2, left wing of atlas; 3, spinous process of T6 (withers); 4, spinous process of T13; 5, spinous process of L2; 6, spinous process of L5; 7, spinous process of S2; 8, spinous process of S5; 9, left tuber coxae; 10, greater trochanter of the left femur; 11, lateral epicondyle of the left femur; 12, lateral side of distal end of the left talus; 13, lateral side of the head (distal end) of the 3rd metatarsal bone; 14, lateral side of the coronet of the left hind hoof; 15, medial side of the coronet of the right hind hoof; 16, right radial carpal bone; 17, medial side of the head (distal end) of the 3rd metacarpal bone; 18, medial side of the coronet of the right front hoof; 19, lateral side of the coronet of the left front hoof; 20, lateral side of the head (distal end) of the 3rd metacarpal bone; 21, left ulnar carpal bone; 22, lateral epicondyle of the left humerus; 23, greater tubercle (caudal part) of the humerus; 24, tuber of the left spina scapulae; 25, transverse process of C6. (B) Joint angles (φ) were calculated for the left hip, left stifle, left hock, left metatarsophalangeal joint (mtp), left metacarpophalangeal joint (mcp), left carpal joint, left elbow joint, and left shoulder joint.

differences between template marker locations and actual marker locations. The movement of the centre of mass of the trunk, and the trunk orientation, were extracted from the movement of the template during the jump. The motion of all segmental mass centres, combined with segment inertial parameters (Buchner et al., 1997), was used to calculate the position, velocity and acceleration of the centre of mass (COM) of the horse. For this calculation we had to assume that the right limbs moved symmetrically with the left limbs, because we did not have markers on the right shoulder, elbow, hip and stifle of the animals. The error incurred by this assumption is small, however, because the right forelimb and right hindlimb each contribute only about 6% of the total mass of the horse, and they do in fact move more or less in phase with their counterparts during the canter and jump.

From the motion of the segments and the COM of the horse, we calculated the following mechanical energy components: potential energy (E_{pot}), rotational energy (E_{rot}), kinetic energy due to the horizontal velocity of COM ($E_{kin,COM,x}$), kinetic energy due to the vertical velocity of COM ($E_{kin,COM,y}$), kinetic energy due to the velocity of segmental mass centres relative to the mass centre of the body (E_{rest}), and total energy (E_{tot}, sum of the previous terms). We also calculated the effective energy, i.e. the sum of E_{pot} and $E_{kin,COM,y}$, which is the energy ultimately contributing to jump height (Bobbert, 2001). Taking the derivative of E_{tot} with respect to time yielded total power output ($\dot{E}_{tot}$). The magnitude of the total ground reaction force ($\mathbf{F}_{GR}$) was calculated from body weight and acceleration of the centre of mass $\ddot{y}_{COM}$. Its line of action was calculated using the fact that the moment of the ground reaction force about the
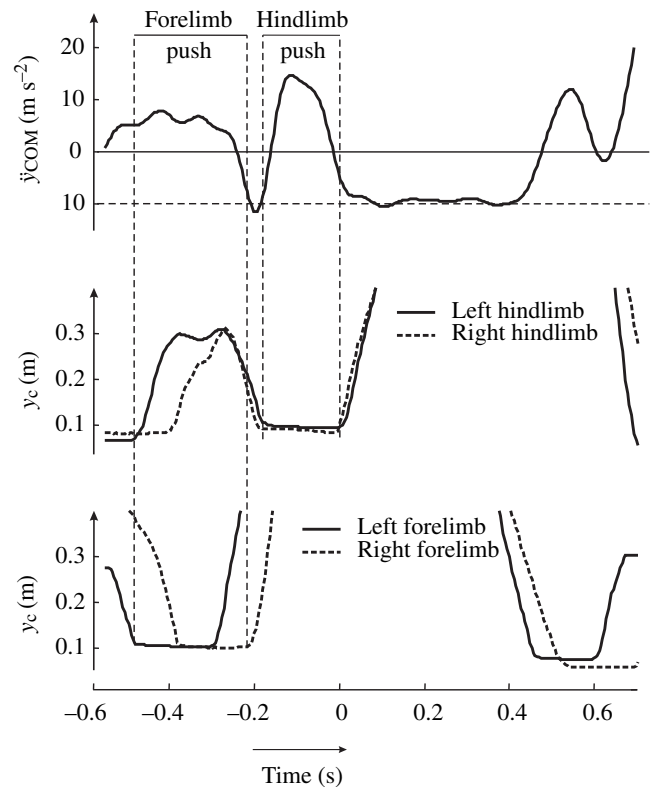

Fig. 2. Typical time histories of the vertical acceleration of the centre of mass ($\ddot{y}_{COM}$) and of the height of the coronet y_c of each four hoofs during a jump in which the left forelimb was trailing. Time is expressed relative to the instant of take-off ($t=0$). Note that the experiments occurred in a sandy arena, which explains why the distance of the coronet to the ground may vary.
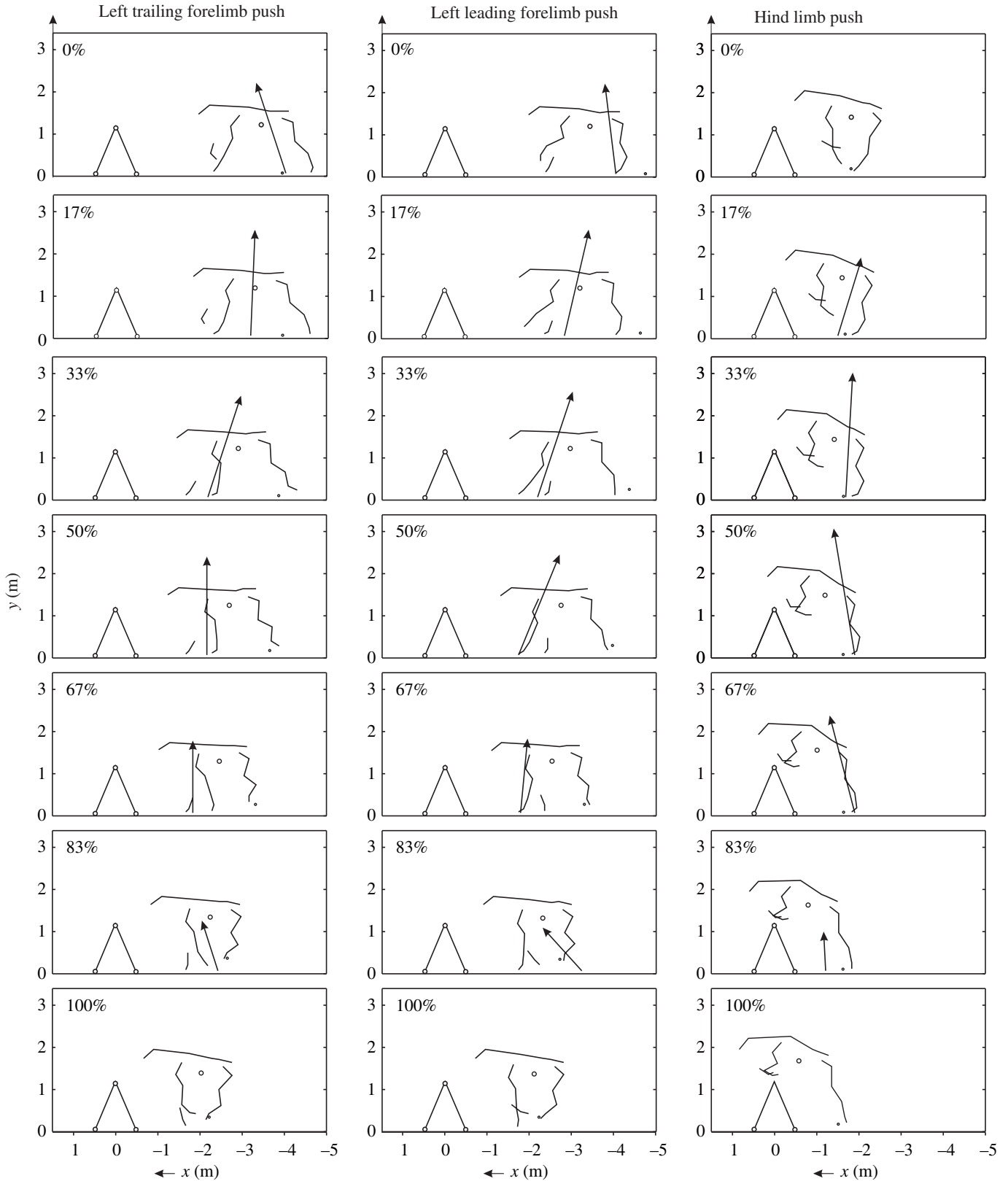
Fig. 3. Average stick diagrams for several instants (see inset) during the forelimb and hindlimb push. Diagrams were constructed from the average marker positions of the horses and the calculated ground reaction force vector (arrows). From each of 23 horses one jump was used in which the left forelimb limb was leading and one in which it was trailing. For each jump, time was normalized separately for the forelimb push and for the hindlimb push, and subsequently results were averaged over horses. Results for the hindlimb push are for the jumps in which the left forelimb was leading. Note the direction of the x axis. Circles indicate the COM.

centre of mass equals the rate of change of angular momentum, which also was calculated from the segmental motions.

The push off for the jump occurs during the last canter stride before the target fence. In a canter stride the sequence of limb placement is the following: trailing hindlimb – leading hindlimb – trailing forelimb – leading forelimb. Each limb is placed anterior relative to the previously placed limb. In the present study, the total push-off was divided into a forelimb push and a hindlimb push (Fig. 2). The forelimb push started with touchdown of the trailing forelimb and ended with take-off of the leading forelimb, as determined from hoof kinematics. The hindlimb push started with touchdown of the trailing hindlimb and ended with take-off of the leading hindlimb. Most horses placed the hindlimbs very close together for the final push, which sometimes caused the marker on the hoof of the right hindlimb to be temporarily lost from view. In those cases we used only the kinematics of the left hind hoof to define the hind limb push. During both the forelimb push and the hindlimb push, we also detected the instant that the total energy was minimal.

Results

Both the forelimb and the hindlimb push were subdivided in six equal time intervals. Fig. 3 presents stick diagrams for the resulting time nodes, constructed from the average marker positions of the horse and the calculated ground reaction force vector. The average results displayed in the figure represent the pattern of the individual results very well. The results for the forelimb push were quite similar regardless of the lead of canter, as can be confirmed by comparing the left panels in Fig. 3, in which the left forelimb was the trailing limb, with the middle panels, in which the left forelimb was the leading limb. Only at 50% of the forelimb push was the ground reaction force vector clearly located and oriented differently. The hindlimb push was perfectly symmetrical, regardless of the lead during the preceding forelimb push, so for conciseness we have only presented the average stick diagrams for the jumps with left lead of canter. In all phases where the ground reaction force magnitude was greater than body weight, the centre of pressure was in a realistic location (i.e. within the area of support). Non-realistic values were found for the centre of pressure during the last 25% of the forelimb push, and during the first 20% and last 20% of the hindlimb push.

Considering the similarity of the left lead jumps and the right lead jumps, we decided to average the mechanical variables over all jumps for the sake of conciseness in presenting the results. Average time histories for force and power are shown in Fig. 4, and average time histories for energy are presented in Fig. 5. The amount of kinetic energy due to velocity of segmental mass centres relative to COM was negligible and is not presented. Because average time histories tend to smooth out peaks that occur asynchronously in different horses, we also extracted relevant values from the individual curves; their means and standard deviations are presented in Table 1 for the forelimb push and in Table 2 for
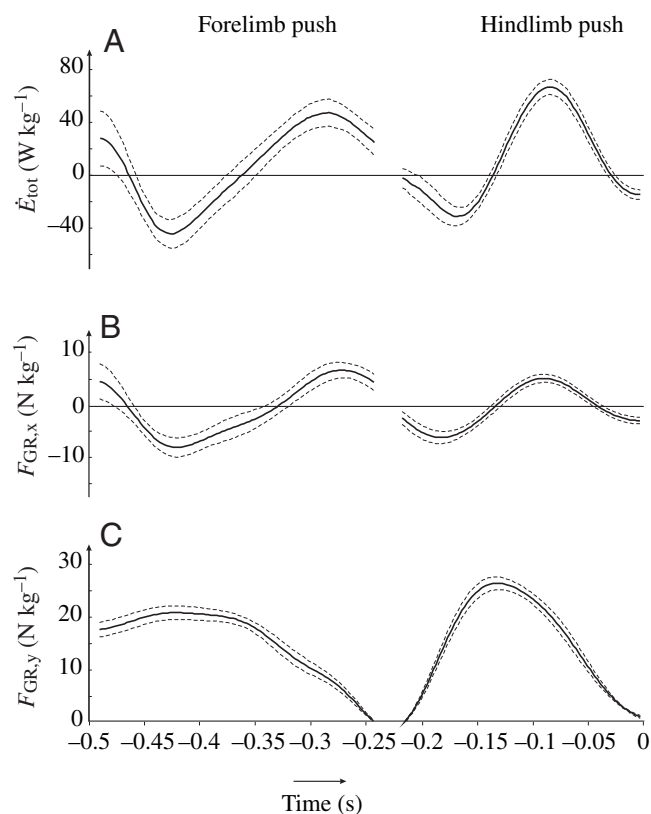

Fig. 4. Average time histories of (A) total power output ($\dot{E}_{tot}$), (B) the horizontal component of the calculated ground reaction force ($F_{GR,x}$) and (C) the vertical component of the calculated ground reaction force ($F_{GR,y}$). From each of 23 horses one jump was used in which the left forelimb limb was leading and one in which it was trailing. For each jump, time was normalized separately for the forelimb push and for the hindlimb push, and subsequently results were averaged over horses and jumps, regardless of lead. Solid lines indicate averages; broken lines indicate 95% confidence intervals.

the hindlimb push. During the forelimb push, the total energy first dropped by 3.2 J kg^{-1} and then increased again by 4.2 J kg^{-1}. During the hindlimb push, the total energy first dropped only slightly by 1.6 J kg^{-1} and then increased again by 4.1 J kg^{-1}. The changes in total energy during the forelimb push were primarily due to changes in $E_{kin,COM,x}$. At the end of the forelimb push, this energy term was 1.6 J kg^{-1} less than at the start of the forelimb push, corresponding to a reduction of the horizontal velocity of COM from 6.3 to 6.0 m s^{-1}. The effective energy increased by 2.3 J kg^{-1} during the forelimb push. During the hindlimb push, the increase in total energy was due almost entirely to a change in effective energy by 4 J kg^{-1}. The large inter-individual variation in total energy was primarily due to inter-individual differences in the overall speed during the push-off. This can be confirmed from Fig. 5, which presents not only the 95% confidence limits for the absolute energy changes but also the 95% confidence limits for the energy changes relative to the mean value during the push-off; the latter are much smaller than the former. The same was true for $E_{kin,COM,x}$ and E_{pot}, with

differences in offset of E_{pot} being primarily due to differences in size of the horses.

To gain insight into the role of the limbs, it is important to look at the changes in their length and joint angles. Average
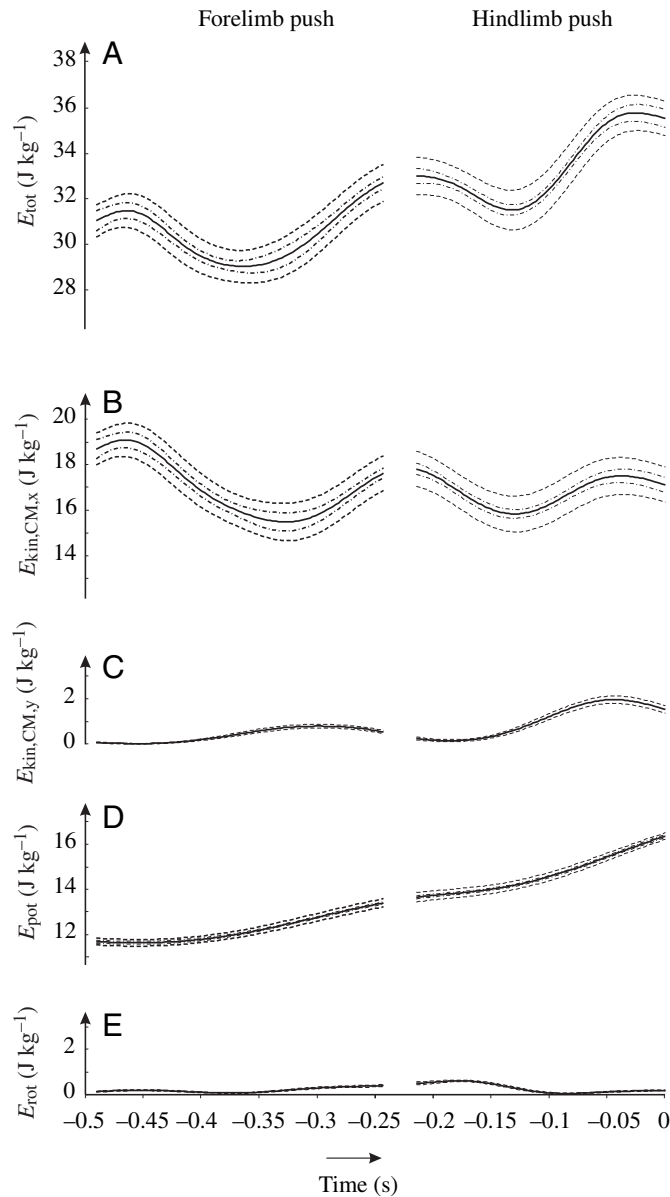

Fig. 5. (A–E) Average time histories of energy components. From each of 23 horses one jump was used in which the left forelimb limb was leading and one in which it was trailing. For each jump, time was normalized separately for the forelimb push and for the hindlimb push, and subsequently results were averaged over horses and jumps, regardless of lead. Solid lines indicate averages; broken lines indicate 95% confidence intervals. Dash-dotted lines indicate 95% confidence intervals obtained when the individual curves were first corrected for the mean value. (A) E_{tot}, total mechanical energy; (B) $E_{kin,COM,x}$, kinetic energy due to the horizontal velocity of the centre of mass; (C) $E_{kin,COM,y}$, kinetic energy due to the vertical velocity of the centre of mass; (D) E_{pot}, potential energy; (E) E_{rot}, rotational energy. The kinetic energy due to the velocity of segmental mass centres relative to the mass centre of the body was negligible and is not shown.

time histories for relevant length measures of the left forelimb and hindlimb are shown in Fig. 6, and joint angle histories are shown in Fig. 7. At this point it is relevant to note that during the stance phase of the limbs, it made little difference for most of the variables whether we calculated them from the original marker coordinates or from the corrected coordinates, obtained by fitting chains of rigid segments to the limbs. However, there were a few important variables for which it did make a difference: the distance between elbow and coronet, the shoulder angle and the elbow angle. The mean time-histories of these variables without correction have been shown with dotted curves for the trailing forelimb in Figs 6 and 7. With correction, the distance from elbow to coronet in the trailing left forelimb went from 0.889±0.026 m to 0.836±0.042 m and back again to 0.888±0.029 m during the forelimb push. When the left forelimb was leading, these values were 0.897±0.025 m, 0.853±0.033 m, and 0.899±0.029 m, respectively. As explained in Materials and methods, the distance between elbow and coronet was used to estimate the

Table 1. *Mean values of selected variables during forelimb push*

Variable	Forelimb push		
	Start	Min E_{tot}	End
E_{tot} (J kg^{-1})	31.7±1.8	28.5±2.0	32.7±2.2
$E_{kin,COM,x}$ (J kg^{-1})	19.3±1.8	15.4±2.2	17.7±2.1
$E_{kin,COM,y}$ (J kg^{-1})	0±0.1	0.4±0.2	0.5±0.2
E_{pot} (J kg^{-1})	11.7±0.4	12.1±0.5	13.5±0.5
E_{rot} (J kg^{-1})	0.2±0.1	0.1±0.0	0.4±0.1
E_{rest} (J kg^{-1})	0.5±0.1	0.5±0.1	0.7±0.2
$\dot{x}_{COM}$ (m s^{-1})	6.3±0.3	5.6±0.4	6.0±0.4

Values are means ± S.D. (*N*=23).

Start, at touch-down of the trailing limb; min E_{tot}, instant that a local minimum was reached in total energy; End, completion of forelimb push.

$\dot{x}_{COM}$, horizontal velocity of centre of mass (COM); $E_{kin,COM,x}$, kinetic energy due to $\dot{x}_{COM}$; $E_{kin,COM,y}$, kinetic energy due to vertical velocity of COM; E_{pot}, potential energy; E_{rot}, rotational energy; E_{rest}, kinetic energy due to velocity of segmental mass centres relative to COM; E_{tot}, sum of all energy terms.

Table 2. *Mean values of selected variables during hindlimb push*

Variable	Hindlimb push		
	Start	Min E_{tot}	End
E_{tot} (J kg^{-1})	33.0±2.3	31.4±2.4	35.5±2.1
$E_{kin,COM,x}$ (J kg^{-1})	17.8±2.1	15.8±2.2	17.1±2.1
$E_{kin,COM,y}$ (J kg^{-1})	0.2±0.2	0.5±0.2	1.5±0.4
E_{pot} (J kg^{-1})	13.7±0.6	14.1±0.5	16.4±0.4
E_{rot} (J kg^{-1})	0.5±0.2	0.3±0.1	0.2±0.1
E_{rest} (J kg^{-1})	0.8±0.2	0.6±0.2	0.4±0.1
$\dot{x}_{COM}$ (m s^{-1})	6.0±0.4	5.7±0.4	5.9±0.4

Values are means ± S.D. (*N*=23).

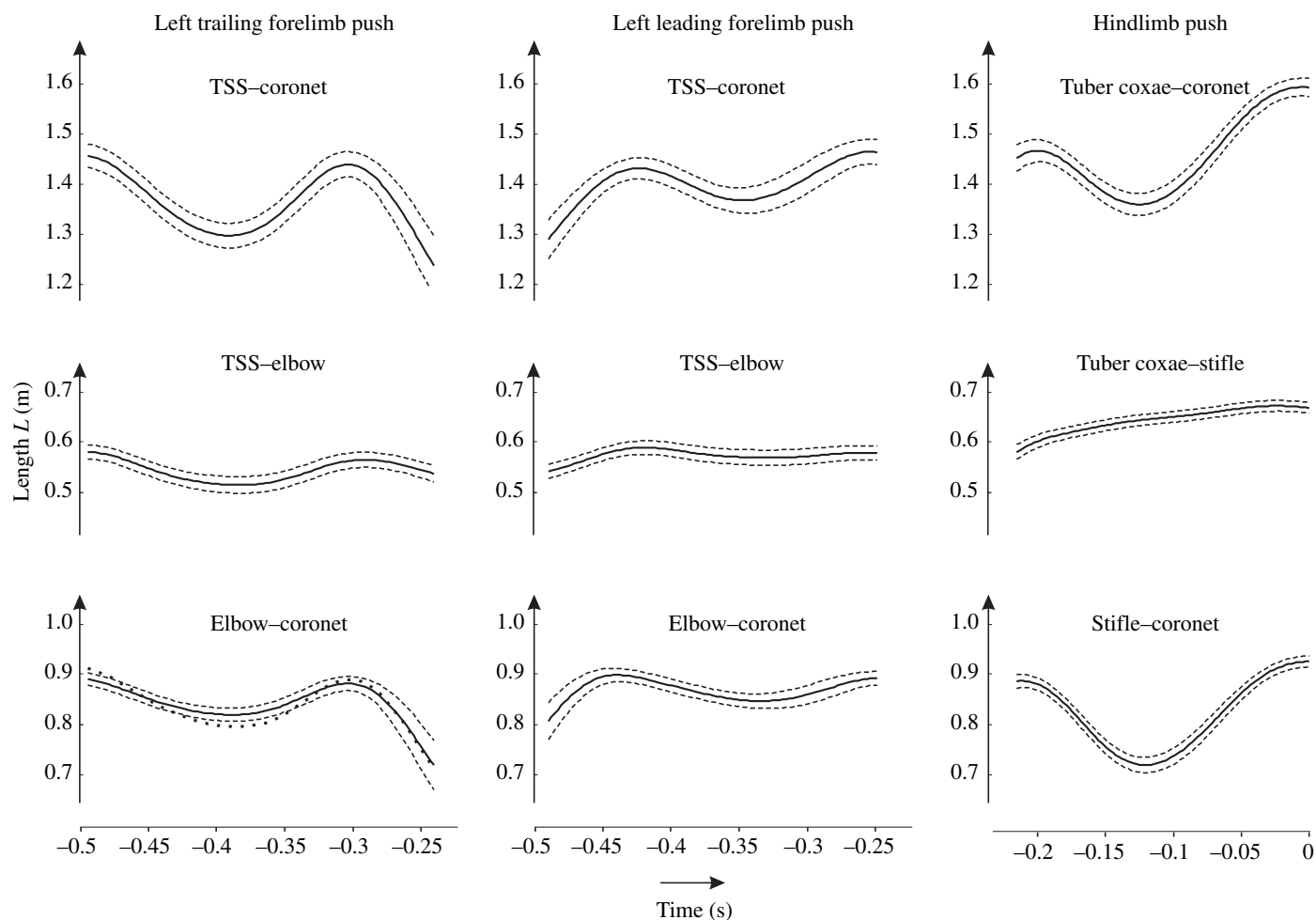Abbreviations of variables as in Table 1.

Fig. 6. Average time histories of selected distances *L* in the forelimb and hindlimb. From each of 23 horses one jump was used in which the left forelimb limb was leading and one in which it was trailing. For each jump, time was normalized separately for the forelimb push and for the hindlimb push, and subsequently results were averaged over horses. Results for the hindlimb push were averaged over all jumps regardless of lead. Solid lines indicate averages; broken lines indicate 95% confidence intervals. Dotted curve for distance elbow–coronet in the trailing forelimb represents the result obtained with uncorrected skin marker positions. TSS, tuber of spina scapulae.

force carried by the forelimb. The results are presented in Fig. 8. As expected, the left forelimb reached its peak force during the first part of the forelimb push when it was trailing, and during the second part when it was leading. The peak force carried by this limb was 13.6 ± 2.5 N kg^{-1} when it was trailing and 10.4 ± 2.6 N kg^{-1} when it was leading (values are means $\pm$ S.D. of peak values extracted from individual curves). Fig. 8 also shows the total force obtained by adding the force in the left limb during the jumps in which it was trailing to the force in that limb for the jumps in which it was leading, just to give a rough estimate of the contribution of the forelimbs to the ground reaction force.

Discussion
Evaluation of energy changes and limb kinematics calculated from positional data of skin markers
All calculations made in this paper were based on kinematics of markers placed on the skin. Unfortunately, the skin

may move considerably relative to the underlying skeletal landmarks (van Weeren et al., 1990a,b), which may compromise the validity of the results. Although we took precautions to reduce the errors by fitting a template to the trunk and fitting chains of rigid segments to the limbs, a critical examination of the validity of the calculated energy changes and limb kinematics seems indicated. Energy changes were previously calculated from kinematics for trotting (Preedy and Colborne, 2001), for galloping (Minetti et al., 1999) and for jumping (van den Bogert et al., 1994). Unfortunately, none of these authors critically evaluated the approach or the results obtained. An obvious problem is, of course, that no independent estimate of energy changes is available. However, one can go one step further and calculate ground reaction forces from kinematics, as we have done in this study. If the ground reaction forces are similar to forces derived from force plate measurements, this is strong support for the validity of the calculations. If they are not, however, this does not necessarily mean that the energy calculations are invalid; after
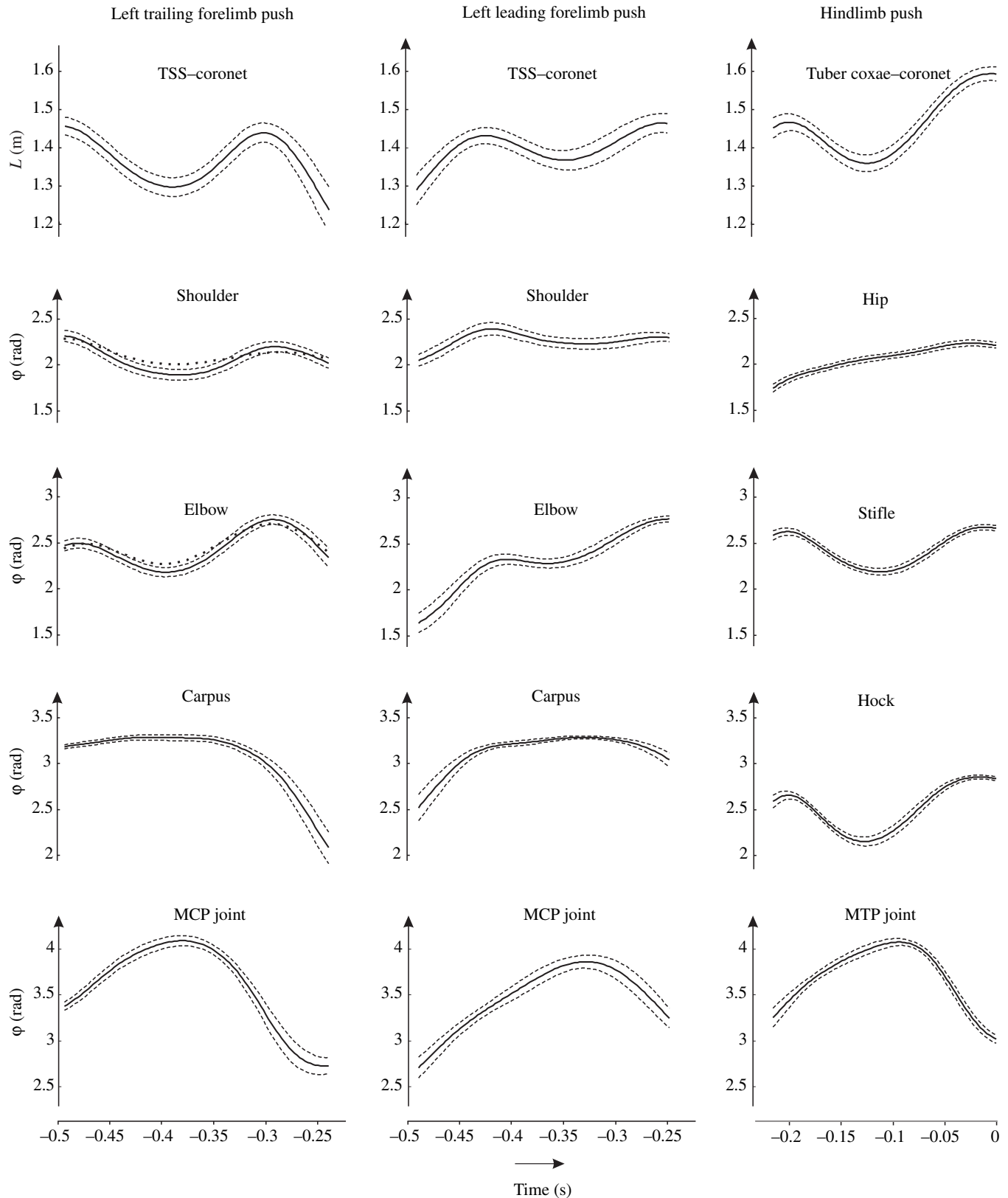
Left trailing forelimb push   Left leading forelimb push   Hindlimb push

Fig. 7. Average time histories of joint angles φ as well as total length L of the limbs. TSS, tuber of spina scapulae. From each of 23 horses one jump was used in which the left forelimb limb was leading and one in which it was trailing. For each jump, time was normalized separately for the forelimb push and for the hindlimb push, and subsequently results were averaged over horses. Results for the hindlimb push were averaged over all jumps regardless of lead. Solid lines indicate averages; broken lines indicate 95% confidence intervals. Dotted curves for the elbow angle and shoulder angle in the trailing forelimb represent the average results obtained with uncorrected skin marker positions.
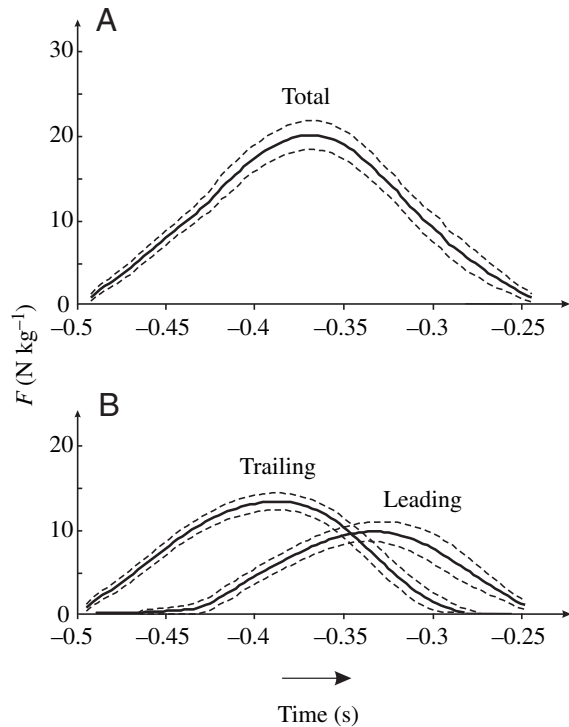
Fig. 8. Average time histories of forces carried by the left forelimb. From each of 23 horses one jump was used in which the left forelimb limb was leading and one in which it was trailing. Force magnitude *F* was estimated from the distance between elbow and coronet, assuming that this part of the leg operated like a linear spring with a stiffness of 166 N m^{-1} kg^{-1}. For each jump, time was normalized separately for the forelimb push and for the hindlimb push, and subsequently results were averaged over horses. The top diagram shows the sum of the two curves, to be compared with the calculated ground reaction force in Fig. 4. Solid lines indicate averages; broken lines indicate 95% confidence intervals.

all, energy calculations are based on positions and velocities, whereas force calculations are based on accelerations and thus require one extra differentiation with respect to time.

In the literature, we found one paper by Schamhardt et al. (1993) reporting ground reaction forces measured using a force plate while a horse was jumping a 1.10 m high fence. Time histories were presented in that paper for the ground reaction forces under each of the individual limbs, but for obvious reasons these time histories pertain to different jumps and, unfortunately, they were not synchronized. The forces of the hindlimbs may safely be added, because the hindlimbs operate almost symmetrically, but adding the forces of the forelimbs will tend to overestimate the total force because the forelimbs operate asymmetrically (Fig. 8). In any case, for each of the forelimbs Schamhardt et al. (1993) report a peak horizontal braking force of about 4 N kg^{-1} in the first part of the forelimb push, and a peak propulsive force of 1–2 N kg^{-1} in the second part of the forelimb push, with the braking impulse being greater than the forward impulse. Total forces calculated in the present study were of similar magnitude (Fig. 4), and also the braking impulse was greater than the forward impulse. Albeit

reassuring, this is not conclusive because considerable variation has been reported in the extent to which horses slow down before jumping over an obstacle (Merkens et al., 1991; Schamhardt et al., 1993). This was also true for the horses in the present study; the reduction in horizontal velocity during the forelimb push ranged from 0.05 to 0.71 m s^{-1} [the horse jumping 1.10 m high in the study of Schamhardt et al. (1993) produced a net braking impulse with both forelimbs of about 0.5 Ns kg^{-1}; if it were only for the forelimbs, this horse would have slowed down by 0.5 m s^{-1}]. The peak vertical force during the forelimb push reported by Schamhardt et al. (1993) was about 17 N kg^{-1} in the trailing forelimb and 13 N kg^{-1} in the leading forelimb. These numbers add up to a total force value greater than the one calculated in this study (Fig. 4), but this is not problematic because the force peaks of the trailing and leading forelimb do not occur simultaneously (Fig. 8). In contrast with the forelimbs, the hindlimbs operate almost symmetrically during the push off. The peak braking force and the subsequent peak propulsive force of both hindlimbs together were about 6-8 N kg^{-1} in the study of Schamhardt et al. (1993). These peak values are very similar to the values calculated from kinematics in this study (Fig. 4). The same was true for the peak vertical force, which was about 23 N kg^{-1} in the study by Schamhardt et al. (1993).

Support for the validity of the variables calculated from kinematics can also be obtained from the fact that the results were in line with biomechanical principles. For instance, as required, the vertical force calculated in the airborne phase was close to zero (Fig. 2; see also Santamaría et al., 2004b), the effective energy in this phase was almost constant (Santamaría et al., 2004b), and the vertical displacement of COM in the airborne phase calculated from the vertical velocity of COM at take-off was within 1 cm from the displacement derived directly from the height of COM (Santamaría et al., 2004a,b). In this study we could even go so far as to calculate the centre of pressure of the ground reaction force. Because this brings together both the calculated ground reaction force and the rate of change of angular momentum, it is most vulnerable to errors. Nevertheless, during the major part of the forelimb push and the hindlimb push, the centre of pressure was found to be at a plausible location (Fig. 3), supporting the validity of the force and energy calculations from kinematics. During the last 20% of the forelimb push, the centre of pressure was found outside the base of support (Fig. 3), which is obviously impossible. Moreover, in this phase the horizontal component of the ground reaction force was unrealistically high (it is a friction force, so it cannot be larger than the vertical component of the ground reaction force). In this phase of the push-off, the animals had started to flex their trunk and the template did not fit as well as it did in the earlier phases of the push-off, which probably caused the force calculations to run awry. In the first 20% of the hindlimb push the centre of pressure was also found outside the base of support (Fig. 3), but thereafter it behaved realistically again until the last 20% of the push-off. It should be stressed again that unrealistic centre of pressure and force values do not necessarily mean that the energy values were

erroneous, because calculation of the latter involves lower derivatives than calculation of the former.

Due to the relatively small mass of the limbs, errors in limb kinematics would hardly show up in the energy and force calculations, and therefore the validity of the calculated limb kinematics requires a separate treatise. The key question is whether fitting chains of rigid segments to the limbs, as we did, helps to correct for movement of skin markers relative to the bony landmarks. The data collected by van Weeren et al. (1990a,b) would be suitable to investigate this for walking and trotting, but to the best of our knowledge such an investigation has not been conducted so far, so independent support for the validity of the limb kinematics is lacking. However, some confidence can be gained from the following. One of the most important variables in the present study was the distance between elbow joint and coronet, because it was used to estimate the force and energy storage in the forelimbs. As is appropriate for a passive spring, we found that the maximum distance at touch-down of the left forelimb was the same as that at lift-off, albeit that its largest value was about 1 cm greater in the jumps in which it was leading than in those in which it was trailing. Also, the peak forces calculated for the trailing and leading left forelimb were 13.6 and 10.4 N kg^{-1}, respectively, not far from the peak vertical forces of 17 N kg^{-1} and 13 N kg^{-1} measured using a force platform by Schamhardt et al. (1993). Moreover, the sum of the force curves of the trailing and leading left forelimb (Fig. 8) approximates the magnitude of the calculated total ground reaction force (Fig. 4). These findings, we feel, lend indirect support for the validity of the calculated limb kinematics. Below, we shall assume that the calculations of energy changes and limb kinematics are correct.

Contribution of the forelimb push to energy changes

The total energy first decreased by 3.2 J kg^{-1} until about the middle of the forelimb push, and then increased by 4.2 J kg^{-1} (Fig. 5, Table 1). At the end of the forelimb push, however, $E_{kin,COM,x}$ was 1.6 J kg^{-1} less than at the start while the effective energy was 2.3 J kg^{-1} greater than at the start. It is tempting to speculate that the forelimbs operate as the pole in pole vaulting (Leach and Ormrod, 1984) or as a pogo-stick (Wilson et al., 2001), the idea being that kinetic energy is first stored in the forelimb tendons, and subsequently released to regenerate kinetic energy and potential energy. For this 'pogo-stick mechanism' to fully explain the mechanical energy changes during the forelimb push, the two forelimbs together should be able to store all the energy lost, about 3.2 J kg^{-1} or 1900 J. It has been claimed: "*In a 500 kg horse, about 1000 J of elastic energy are stored in the digital flexor tendons and suspensory ligament (interosseus muscle) of each leg in each stride*" (Wilson et al., 2001). In a later study, McGuigan and Wilson (2003) conceptually divided the forelimb into two springs: a proximal spring from the proximal end of the spina scapulae to the elbow, and a distal spring from the elbow to the foot. The latter was shown to behave as a linear spring with a stiffness of 166 N m^{-1} kg^{-1}, or 100 kN m^{-1} (these values

follow unmistakably from their Fig. 2, but McGuigan and Wilson themselves arrive at a stiffness of 60 kN m^{-1}). In the present study, at the instant that the minimum was reached in total energy, the length of the distal spring was reduced on average by 5.3 cm in the left forelimb when it was trailing and by 4.4 cm when it was leading (see also Fig. 6), and the amount of energy stored was estimated to be on average 246 J and 140 J, respectively (note that the stored energy increases with the square of the compression; because the latter varied among horses, the average stored energy cannot be derived from the average compression). This means that the total energy stored in both distal springs together was only about 400 J on average. The leg as a whole, of course, shortens more than the distal spring (Fig. 6), which was partly due to shortening of the proximal spring [only partly, because the concept developed by McGuigan and Wilson (2003) does not take into account the important changes in elbow angle (Fig. 7)]. However, the proximal spring is not really a spring: although biceps has a fibrous component, the leg above the elbow is primarily made up of muscle. Although some energy might surely be stored in series elastic elements of these muscles, most of the compression involves energy dissipation by muscle fibres acting eccentrically, transforming energy into heat. The left forelimb reached a peak compression of only 7.1 cm when it was leading, but a peak compression of no less than 15.6 cm when it was trailing. Obviously, in the trailing forelimb there is room for considerable dissipation of energy by the elbow extensors, such as the large triceps brachii, and muscles spanning the shoulder, such as supraspinatus. Perhaps lengthening of the muscle fibres of the digital flexors also dissipates some energy. Additionally, the muscles connecting the scapula to the trunk and neck may dissipate energy while actively resisting rotation of the shoulder blade relative to the trunk. Finally, some energy storage may occur in the vertebral column (Minetti et al., 1999).

The energy stored in elastic components will be released again and contribute to the gain of total energy during the second half of the forelimb push, but the energy dissipated needs to be regenerated in concentric contractions, primarily of the muscles just mentioned. Note that the length of the leading left forelimb was about 4 cm greater at take-off than at touch-down (Figs 6, 7) due to elbow extension (Fig. 7). This implies that the elbow extensors in the leading forelimb generate more energy than they dissipate.

Contribution of the hindlimb push to energy changes

The contribution of the hindlimb push to total energy changes during jumping was previously studied by van den Bogert et al. (1994) and Dutto et al. (2004). van den Bogert et al. (1994) studied the kinematics of the hindlimb push in elite show-jumping horses clearing a 1.5 m high fence. From their kinematic data they calculated that the horses produced no less than 13 000 J, most of which was attributed to a change in $E_{kin,COM,x}$ (the horizontal velocity was initially 4.5 m s^{-1}, dropped to 3.5 m s^{-1}, and then increased to 6.5 m s^{-1}). Assuming that the horses had a mass of 600 kg they produced

almost 22 J kg^{-1}, thereby outperforming the lesser galago, leopard and antelope, which are able to produce only 20 J kg^{-1} (for references, see Bennet-Clark, 1977). Dutto et al. (2004) conducted an inverse dynamics analysis of the hindlimb push in horses jumping a 0.63 m high fence, which was approached at a trotting speed of 3.25 m s^{-1}. The sum of the work performed about the hip, stifle, tarsus and MTP-joint was only 1.4 J kg^{-1} for both limbs together. These values are very different from the ones that we observed in the present study, in which the total energy increased by about 2.5 J kg^{-1} during the hindlimb push. It seems that the height of the fence and the speed at which it is approached (which was controlled by the riders in the study of van den Bogert et al., 1994) is of decisive importance for the energy changes during the jump.

In the present study, the positive work contribution by the hindlimb is reflected by an increase in the total length of the legs from touch-down to take-off. At touch-down, the length of the legs was not maximal, primarily because the hip was flexed. The length of the hindlimbs first decreased by 11.8 cm and then increased by 23.1 cm (Fig. 6). Interestingly, the initial decrease in length of the leg was smaller than the decrease in the distance between stifle and coronet (Fig. 6), which amounted to 17.9 cm on average. The reason was that the hip joint extended (Fig. 7), which implies that part of the energy produced by the hip extensor muscles was stored in the distal tendons. During the second half of the push off, in which all joints of the hindlimb were extending, the calculated ground reaction force vector passed in between the joints of the left hindlimb (Fig. 3), suggesting that all joints of the limb were contributing to work and power output. This conclusion is different from that reached by Dutto et al. (2004), who decided that the stifle joint only produced positive work during the first part of the hindlimb push. In the present study, peak power output during the hindlimb push was found to be 75 W kg^{-1}, much more than the 30 W kg^{-1} observed in the study of Dutto et al. (2004) and much less than the 59 000 W (or about 100 W kg^{-1}) found in the study by van den Bogert et al. (1994). Again, height of the jump and approach speed seems to be of decisive importance.

Concluding remarks

It was argued that during the forelimb push in jumping the amount of energy stored in the distal tendons was on the order of 400 J, and that a considerable amount of energy was first dissipated and subsequently regenerated. Clearly, during the push-off in jumping the forelimbs are not used as mere passive springs. Although suggestions were given as to which muscles were involved in the dissipation and regeneration of energy, disclosure of the precise role of the different muscles requires further studies in which kinematic data are combined with force plate measurements and electromyography. During the hindlimb push, the muscles of the leg were primarily producing energy. The total increase in energy, about 2.5 J kg^{-1}, was different from values reported in other studies, presumably because of differences in the height of the fence and the speed at which it was approached. A future study will be concerned with how the energy changes during the forelimb and hindlimb push depend on the height of the fence.

List of symbols

COM	centre of mass of the body
E_{pot}	potential energy
E_{rot}	rotational energy
$E_{kin,COM,x}$	kinetic energy due to the horizontal velocity of COM
$E_{kin,COM,y}$	kinetic energy due to the vertical velocity of COM
E_{rest}	kinetic energy due to the velocity of segmental mass centres relative to the mass centre of the body
E_{tot}	total energy
$\dot{E}_{tot}$	total power output
F	force
$\mathbf{F}_{GR}$	ground reaction force
L	length
t	time
$\dot{x}_{COM}$	horizontal velocity of COM
y_c	height of the coronet
$\ddot{y}_{COM}$	vertical acceleration of the centre of mass
φ	joint angle

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