

Joint work and power for both the forelimb and hindlimb during trotting in the horse

Darren J. Dutto^{1,*}, Donald F. Hoyt², Hilary M. Clayton³, Edward A. Cogger⁴ and Steven J. Wickler⁴

¹*School of Physical Education and Health, Eastern Oregon University, La Grande, OR 97850, USA,* ²*Department of Biological Sciences, California State Polytechnic University, Pomona, CA, USA,* ³*College of Veterinary Medicine, Michigan State University, East Lansing, MI, USA* and ⁴*Department of Animal and Veterinary Science, California State Polytechnic University, Pomona, CA, USA*

*Author for correspondence (e-mail: ddutto@eou.edu)

Accepted 7 August 2006

Summary

The net work of the limbs during constant speed over level ground should be zero. However, the partitioning of negative and positive work between the fore- and hindlimbs of a quadruped is not likely to be equal because the forelimb produces a net braking force while the hindlimb produces a net propulsive force. It was hypothesized that the forelimb would do net negative work while the hindlimb did net positive work during trotting in the horse. Because vertical and horizontal impulses remain unchanged across speeds it was hypothesized that net work of both limbs would be independent of speed. Additionally because the major mass of limb musculature is located proximally, it was hypothesized that proximal joints would do more work than distal joints. Kinetic and kinematic analysis were combined using inverse dynamics to calculate work and power for each joint of horses trotting at between 2.5 and 5.0 m s⁻¹.

Work done by the hindlimb was indeed positive (consistently 0.34 J kg⁻¹ across all speeds), but, contrary to our hypothesis, net work by the forelimb was essentially

zero (but also independent of trotting speed). The zero net work of the forelimb may be the consequence of our not being able to account, experimentally, for the negative work done by the extrinsic muscles connecting the scapula and the thorax. The distal three joints of both limbs behaved elastically with a period of energy absorption followed by energy return. Proximal forelimb joints (elbow and shoulder) did no net work, because there was very little movement of the elbow and shoulder during the portion of stance when an extensor moment was greatest. Of the two proximal hindlimb joints, the hip did positive work during the stride, generating energy almost throughout stance. The knee did some work, but like the forelimb proximal joints, had little movement during the middle of stance when the flexion moment was the greatest, probably serving to allow the efficient transmission of energy from the hip musculature to the ground.

Key words: equine, locomotion, joint kinetics, angular kinematics, work, power.

Introduction

In horses trotting at a constant speed over level ground, the forelimb produces net braking and the hindlimb net propulsion (Dutto et al., 2004b; Merckens et al., 1993). As braking is the reduction of speed, kinetic energy is reduced and one would expect the forelimb to do a small amount of negative work [≈ -31 J (0.07 J kg⁻¹), based upon a net horizontal impulse of -8.8 Ns, a forward velocity of 3.5 m s⁻¹, and contact time of 0.276 s (Dutto et al., 2004b)]. Because at constant speed, energy must be added to compensate for the energy absorption by the forelimb, one would expect the hindlimb to do positive work [≈ 77 J (0.18 J kg⁻¹), based upon a net horizontal impulse of 22 Ns, a forward velocity of 3.5 m s⁻¹, and contact time of 0.249 s (Dutto et al., 2004b)]. As trotting is a bounding gait, it can be reasonably described using a spring-mass model,

reducing each limb to a simple spring system (Abourachid, 2001; Herr and McMahon, 2000; McGuigan and Wilson, 2003). In the ideal spring-mass system during steady state locomotion, no work will be done in the vertical direction because energy absorption and generation will be equal.

The distal joints of both the fore- and hindlimbs are suited to function elastically and not for energy generation because small muscles with short, highly pinnate muscle fibers and long tendons incapable of producing significant power act upon them (McGuigan and Wilson, 2003; Payne et al., 2005a; Wilson et al., 2001). Therefore, one would expect the distal limbs with the long tendons to behave in a spring-like manner with a period of energy absorption and energy release resulting in little or no net work done (Biewener and Roberts, 2000; Ker et al., 1988). Power profiles for trotting horses for the distal interphalangeal and

metacarpophalangeal joints seem to support this contention (Clayton et al., 1998; Khumsap et al., 2003). The two proximal joints of both limbs have muscles suited for generating or absorbing energy (Payne et al., 2005a; Payne et al., 2005b). This is also true for the muscular sling linking the torso to the pectoral girdle. For example, proximal extensor muscles in dogs and rats shorten and generate force (Carrier et al., 1998; Gillis and Biewener, 2001; Gregersen et al., 1998). Also both the lateral triceps and vastus lateralis of horses shorten during the stance phase of trotting (Hoyt et al., 2005). The power profile for the proximal limb should reflect the ability of the musculature to absorb energy (with a predominance of negative power) or generate energy (a predominance of positive power). The proximal forelimb has been modeled as a spring (McGuigan and Wilson, 2003), although published power profiles for the elbow and shoulder do not appear to support this conclusion (Clayton et al., 1998). It is unclear whether energy will be absorbed by the proximal joints of the forelimb, especially since the triceps actively shortens while the elbow extends during stance (Hoyt et al., 2005), which is not the situation that would appear to be associated with energy dissipation by the muscle.

The hindlimb proximal musculature is suited to generate energy. Inverse dynamic analyses have shown that work done at proximal joints increased during periods of acceleration (McGowan et al., 2005; Roberts and Scales, 2004), when locomoting on an incline (Roberts and Belliveau, 2005), and when jumping (Aerts, 1998; Dutto et al., 2004a; Jacobs et al., 1996). Muscle work from proximal hindlimb muscles also increases in response to greater energy demands trotting up hill in horses (Wickler et al., 2005), turkeys (Gabaldón et al., 2004), guinea fowl (Daley and Biewener, 2003) and tammar wallabies (Biewener et al., 2004). As described above, it is unlikely that work is done by the distal joints (even by muscles that are often thought of as doing work, such as the gastrocnemius and soleus) because of the invasive tendinous structure around the muscle fibers (Payne et al., 2005a). During jumping in the horse, work, as calculated using inverse dynamics, was done primarily by the knee during take-off (Dutto et al., 2004a). Thus, any work done by the hindlimb will come from either the knee or hip or both.

In this study, we tested the hypothesis that the forelimb should absorb energy (negative work) and the hindlimb increase energy (positive work) during the trotting stride. Further, it would be expected that the amount of work done by or on each limb to be independent of speed, since there is no change in vertical work required and total horizontal impulse is independent of speed (Dutto et al., 2004b). Finally, it would be expected that the distal joints of both the fore- and hindlimbs would behave elastically, whereas any work (positive or negative) would be done by muscles of the more proximal joints.

Materials and methods

Subjects and procedures

Four healthy horses (*Equus caballus* L.; two Arabian, one Thoroughbred, and a Quarter Horse-cross) with a mean body mass of 491 ± 38 kg (mean \pm s.d.) performed the experimental

protocol, approved by the university's Animal Care and Use Committee. Animals were conditioned to the testing protocol for several weeks prior to data collection. A surcingle with a reflective strip (Scotchlite Reflective Tape, 3M, St Paul, MN, USA) was placed around the thorax of the animal. This strip was part of the system used to monitor the animal's trotting velocity through the measurement area. A series of three infrared sensors were placed at known intervals. The sensors were triggered by the reflective tape and a timing program (Labview[®], v5.1, National Instruments Inc., Austin, TX, USA) permitted instantaneous determination of velocity through each of two consecutive timing zones, one of which included the force plate. If the speed in the two timing zones differed by more than 10%, the trial was not included in the analysis. Less than 2% of trials were excluded because of changing speed. After a brief warm-up, the animal was lead through the test area by a trained handler running along side. After each trial the horse was led back to the starting position. Approximately 1–5 min elapsed between trials. The test speeds were randomly varied from trial to trial. Trotting velocities between 2.5 and 5.0 m s⁻¹ were included in this analysis. A total of 126 trials were collected, from which 105 forelimb and 104 hindlimb contacts evenly distributed between animals were obtained for further analysis.

Experimental set-up

A 30 m long runway was built for data collection. The cement runway (10 cm thick, 1.25 m wide) was covered by a 10 mm thick, high density, black rubberized mat (All Weather Rollout Runway, Dodge Regupol, Lancaster, PA, USA). A 0.6×0.9 m force plate (model 9287BA, Kistler Instruments, Winterthur, Switzerland) was located approximately in the middle of the runway supported by a 0.9 m thick pedestal of cement, isolated from the rest of the runway by vibration dampening material. The top of the force plate was covered with a rubberized mat of material identical to that covering the rest of the runway, to provide a continuous visual field for the animal. With the mat glued to the surface of the force plate, the natural frequency of the force plate was 384 Hz in the z axis (which was oriented vertically in this case) and 500 Hz in the two horizontal directions. These frequencies are somewhat lower than the natural frequency of the original plate (520 Hz and 750 Hz, respectively) but the observed decrements are within the tolerances recommended by the manufacturer. Three-dimensional force data were sampled at 1000 Hz for all tests, but only the horizontal (representing the fore–aft direction) and vertical forces were required for further analysis. Center of pressure was determined from the force records and validated in procedures similar to those previously reported in a study of jumping (Dutto et al., 2004a).

Video records of the right side of the subject during all trotting trials were obtained using a high-speed (250 Hz) digital camera (PCI 250, Redlake Imaging Corp., San Diego, CA, USA). The camera was situated orthogonal to the plane of movement, at a distance of 8 m from the runway, so that approximately 3.5 m of the runway was recorded (including the

force platform). Prior to experimental testing, a 36-point, two-dimensional calibration frame, located in the plane of movement over the force platform, was recorded. Video records of two-dimensional (sagittal plane) motion for kinematic analysis were recorded and stored directly to a computer. Retroreflective markers were placed over specific anatomical landmarks on the forelimb in locations similar to those previously reported (Clayton et al., 1998). Forelimb sites were the tuberosity on the scapular spine, the greater tubercle on the humerus, lateral epicondyle of the humerus, ulnar carpal bone, metacarpal attachment of the lateral collateral ligament (LCL), proximal hoof over the distal interphalangeal (FDIP) joint, and the anterior and posterior lateral hoof (Fig. 1). On the hindlimb, reflective markers were placed on the tubercoxae, greater trochanter, lateral femoral condyle, lateral malleolus, distal metatarsal condyle, center of rotation of the distal interphalangeal joint, and on the anterior, distal hoof (Fig. 1). These limb markers allowed the shoulder, elbow, wrist, metacarpophalangeal (MCP), and distal interphalangeal (FDIP) joints of the forelimb and the hip, knee, ankle, metatarsophalangeal (MTP) and distal interphalangeal (HDIP) joint angles to be calculated (Fig. 1). Limb segment markers were digitized using the automatic point tracking module of the Peak Motus[®] software (Peak Performance Technologies, Inc., Denver, CO, USA). Digitized coordinates were scaled to represent real-world Cartesian values using a two-dimensional direct linear transformation constructed with the recorded calibration parameters. To account for discrepancies of marker movement relative to the underlying skeletal landmarks, skin corrections were applied to all proximal markers using algorithms developed from horses trotting at 3 m s^{-1} (van

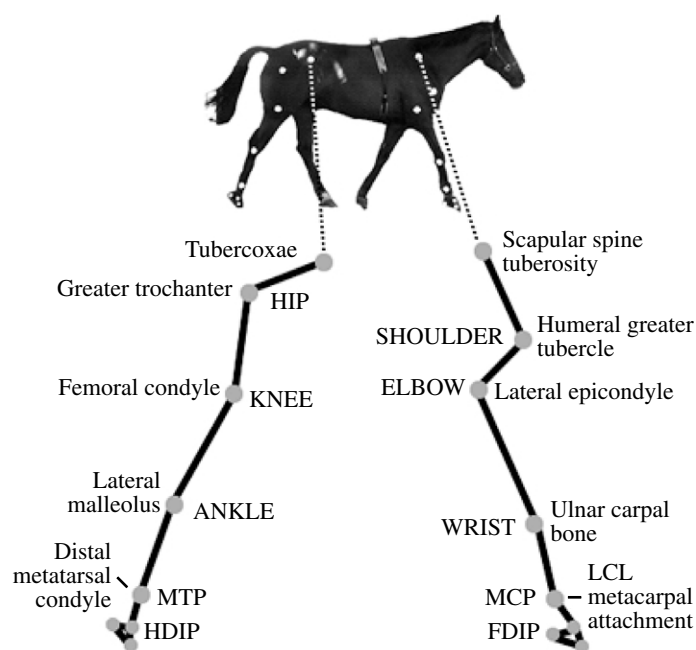


Fig. 1. Joint marker placement (labeling in lower case) and identification of joint angles (labeling in capitals; see text for details).

Weeren et al., 1992). The subjects in the present study were required to trot at a range of speeds, not simply at 3 m s^{-1} . Maximum residual error for the determination of joint moments using the maximum residual skin displacement error from the use of the skin correction algorithms has been found to be 2% when calculating joint moments from horses trotting at $\approx 3.4 \text{ m s}^{-1}$ (Clayton et al., 1998), making it possible that error will increase at greater departure from 3 m s^{-1} . However, joint range of motion (ROM) does not increase significantly for the proximal joints with increased speed (see Results below). Thus, any error from the application of skin correction is less than if no skin correction were applied, and will allow a reasonable interpretation of the results. Both kinematic coordinate and ground reaction force data were smoothed with a dual pass fourth order Butterworth digital filter using cut-off frequencies of 10 Hz (kinematic) and 56 Hz (force), both cut-off frequencies were determined to preserve a majority of the signal while removing unwanted noise, and are similar to those used in a previous study on trotting (Clayton et al., 1998).

Data analysis

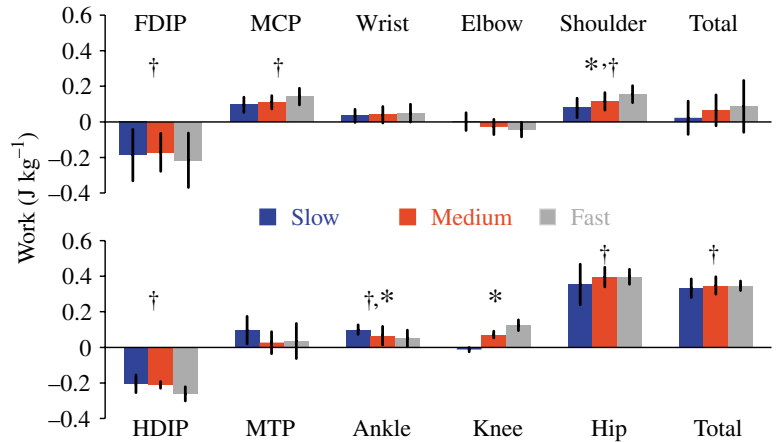
Kinematic and ground reaction force data were synchronized during data collection (Labview[®], v5.1, National Instruments Inc., Austin, TX). Recorded data were combined with inertial parameters of the limb segments (Buchner et al., 1997). Only the stance phase of the gait cycle was included for further analysis. Joint ROM was determined for each joint. Sagittal plane net joint moments were calculated using an inverse dynamics solution (Winter, 1990) adapted for use on horse data (Colborne et al., 1998). Moments on the anatomical flexor side were assigned a negative value and those on the extensor side were assigned a positive value. Joint power was calculated as the product of the joint moment and angular velocity. Net joint moment and net joint power were normalized to stance duration and to horse mass. The average moment during stance was calculated for each trial. Net work was determined by integration of the joint power during stance. In order to examine changes with speed, relevant variables from all trials were divided into three bins indicative of slow ($2.50\text{--}3.25 \text{ m s}^{-1}$), medium ($3.25\text{--}4.00 \text{ m s}^{-1}$) and fast ($4.00\text{--}5.00 \text{ m s}^{-1}$) speeds. The value of a variable for a horse in a given speed bin was the average of 7–9 trials. This resulted in there being four values (one for each horse) in each speed bin. An ANOVA with repeated measures was used to determine differences in speed with $P=0.05$. Variables that were assessed statistically included joint ROM, average moment, negative work, positive work, and total work for each joint and the total limb. A *t*-test ($P=0.05$) was used to determine whether total work done by the limb and each of the joints was different from zero.

Results

Forelimb versus hindlimb

Total work done by the forelimb was essentially zero and that for the hindlimb was consistently positive (Fig. 2). In the

Fig. 2. Net work done at each joint ranges (joint abbreviations as in Figs 3 and 4) and total work done by the limb (forelimb on the top and hindlimb on the bottom) for each of the three speed ranges (slow $<3.25 \text{ m s}^{-1}$, medium $3.25\text{--}4.00 \text{ m s}^{-1}$ and fast $>4.00 \text{ m s}^{-1}$). Colored bars indicate the means, and black lines the standard deviation. Joints: FDIP and HDIP, fore and hind distal interphalangeal, respectively; MCP, metacarpophalangeal, MTP, metatarsophalangeal. *Significant difference ($P < 0.05$ using repeated-measures ANOVA) in speed; †significant difference from 0.



forelimb, the small amounts of positive work done by the MCP, wrist and shoulder were offset by negative work done on the FDIP joint. The elbow did no net work during stance as the net joint moment was largest when there was little joint motion (Fig. 3). Work done by the shoulder tended to increase ($P=0.020$) with speed, causing the total work to appear to increase, but these increases in total work were not statistically significant. The shoulder could not do much work since, like the elbow, at the time that the joint moment was largest, the amount of joint motion was minimal. The work done by the hindlimb was 0.34 J kg^{-1} across all speeds (Fig. 2). Most of this work appears to be done by the hip, which generated energy as can be seen by the consistently positive power observed at the joint (Fig. 4). Like the FDIP, work is done on the HDIP. The ankle and knee did small amounts of positive work, with the work done by the ankle significantly decreasing and the work done by the knee increasing with speed. Thus, the decrease in work done in the ankle was offset by the increase in work done at the knee.

Changes in joint mechanics with speed

In the forelimb, the work done by the shoulder increased significantly with speed (Fig. 2; $P=0.020$). The increase in work was due to a slightly longer and greater extensor moment when the shoulder was extended during the last 30% of stance (Fig. 3). The small increases in work done by the shoulder with increased speed did not cause total work done by the forelimb to increase. The remaining joints of the forelimb experienced no changes in total work between the different speed ranges. For further analysis, the negative and positive work done by each joint and total limb were determined. At the shoulder, the amount of positive work done increased significantly with speed (Fig. 6; $P=0.009$), resulting in the increase in total work done at the joint. The MCP increased both the negative and positive amounts of work done through a combination of increased moment (Fig. 5) and increased range of motion (slow: $38 \pm 8^\circ$, medium: $42 \pm 8^\circ$, fast: $50 \pm 9^\circ$; $P=0.02$). However the proportion of negative to positive work remained the same, resulting in no change in total work done by the joint. For the whole limb, the magnitude of both negative and positive work

increased at higher speeds resulting in no net changes in total work done.

In the hindlimb, total work done by both the ankle and knee changed with speed. The work done by the ankle decreased slightly (Fig. 2; $P=0.042$). However, both the negative and positive work done at the ankle remained constant across speeds (Fig. 6). Work done by the knee increased with greater speeds. This occurred as the amount of negative work done decreased and positive work increased with increased speed (Fig. 6). Increased positive work by the knee occurred early in stance when the negative moment was large and the knee was flexing (Fig. 4). The amount of negative work done on the hip increased at higher speeds, however the amount of negative work done was extremely small (Fig. 6). The remaining joints and total limb had no changes with speed.

Distal versus proximal limb

Examining the plot of total power generated by the forelimb and hindlimb provided another way to examine total energy absorption/generation by the limbs (Fig. 7). Neither limb changed the amount of net work done during stance, indicating that the area under the power curves remained constant (even for the forelimb where negative and positive work did increase with speed, however the net work remained constant). Summing the power for the three distal joints of each limb (forelimb: FDIP, MCP, wrist; hindlimb: HDIP, MTP, ankle) illustrated that these three joints experienced relatively equivalent periods of energy absorption and generation, of relatively similar magnitudes between the limbs (although negative and positive power increased for the forelimb; Fig. 7A,C). Power of the proximal forelimb joints (elbow and shoulder) had oscillating periods of energy absorption and generation phases during stance (Fig. 7B). Hindlimb proximal joint power was consistently positive at all speeds, and higher in the fastest speed range (Fig. 7D), primarily due to the energy generated at the hip (Fig. 4).

Discussion

In this study, we examined three hypotheses. The first hypothesis was based upon previous observations of ground

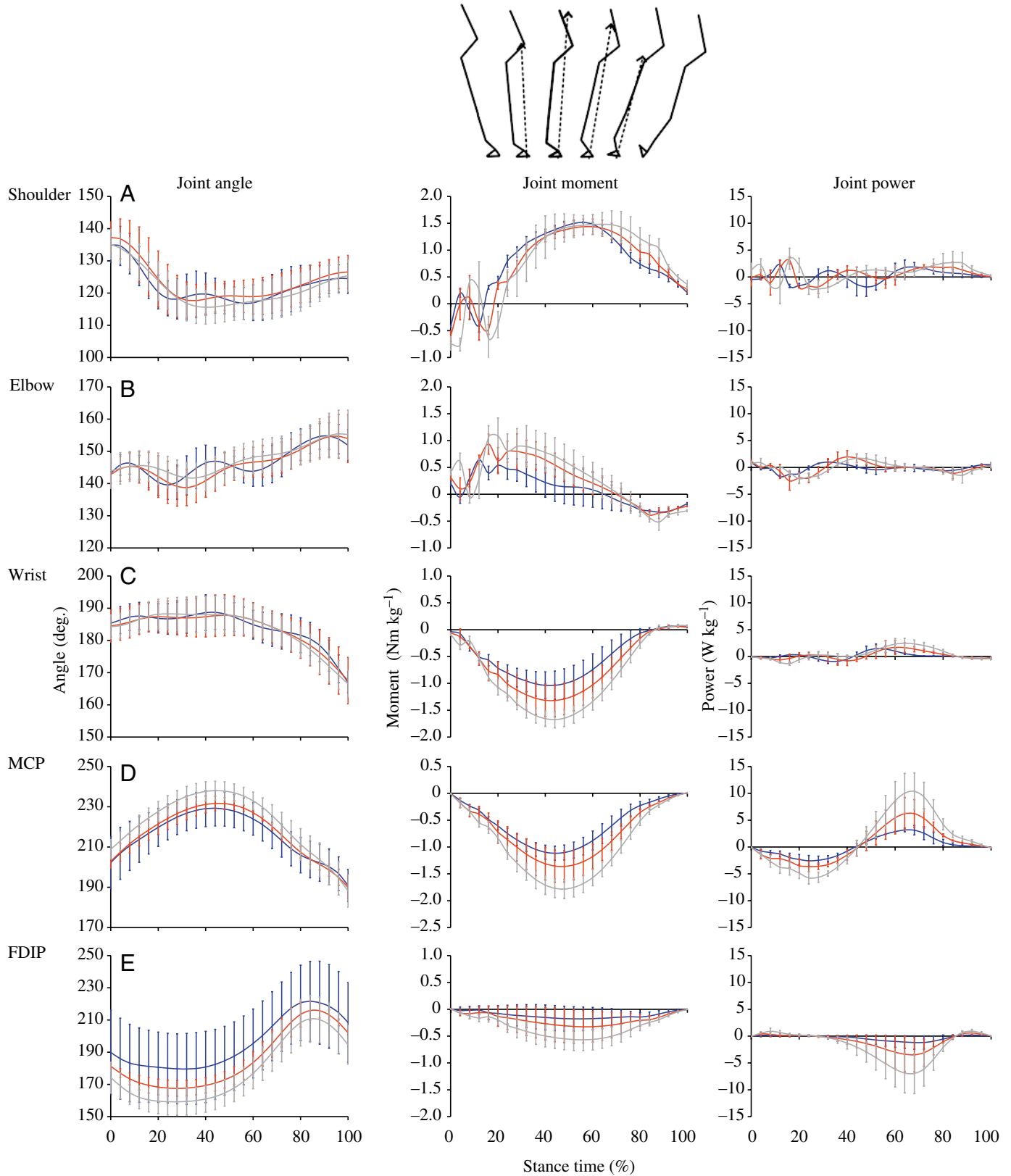


Fig. 3. Joint angles, moments and powers for the forelimb (shoulder, A; elbow, B; wrist, C; MCP, metacarpophalangeal, D; FDIP, forelimb distal interphalangeal, E). The blue line represents slow speeds ($<3.25\text{ m s}^{-1}$), the red line medium speeds ($3.25\text{--}4.00\text{ m s}^{-1}$) and the grey line fast speeds ($>4.0\text{ m s}^{-1}$). The error bars on each curve are the standard deviation. The stick figure representations at the top are from every 20% of stance of the forelimb from one medium speed trial (with the same orientation as the forelimb in Fig. 1) with the direction and magnitude of the resultant ground reaction force included as a broken line.

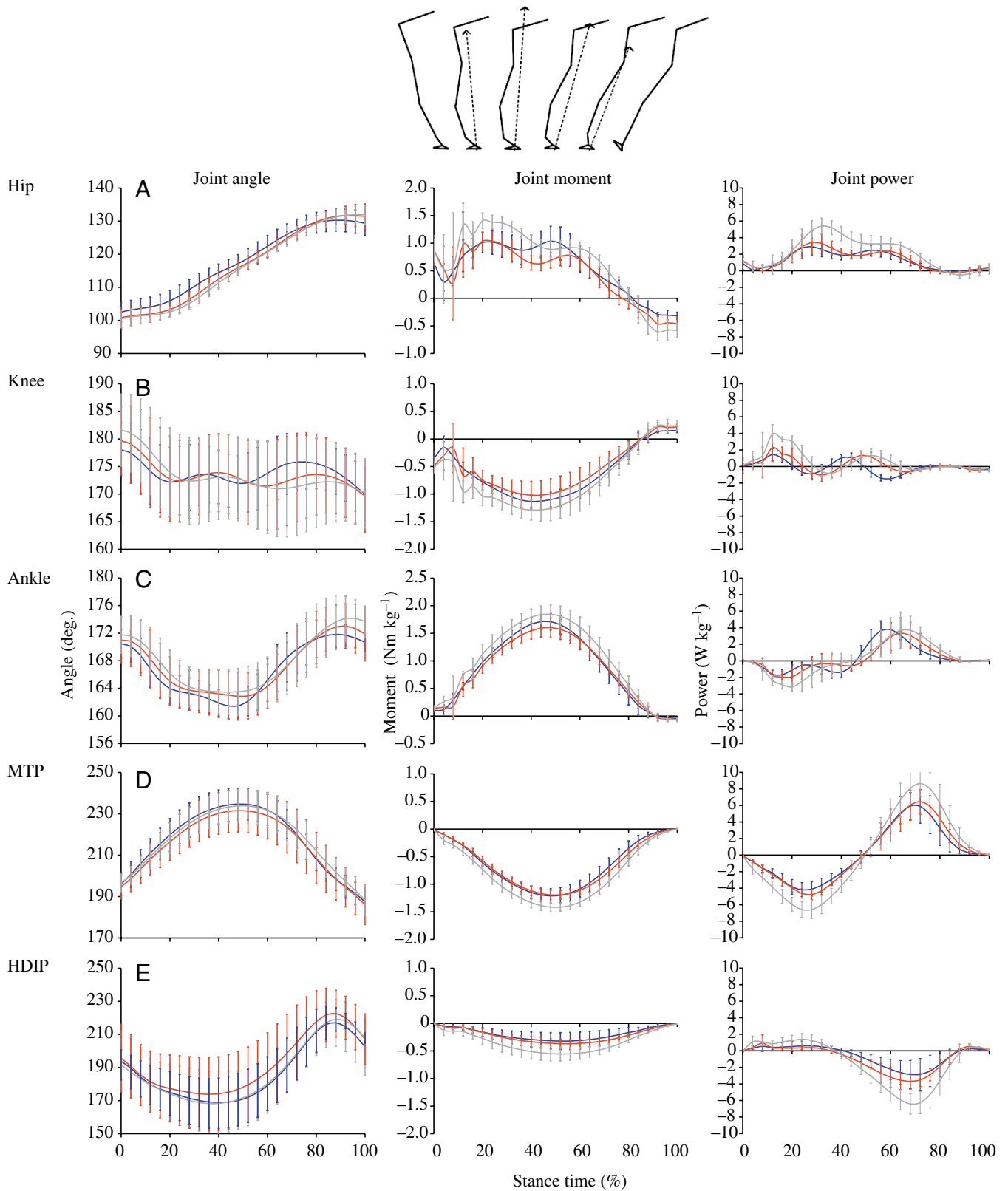


Fig. 4. Joint angles, moments and powers for the hindlimb (hip, A; knee, B; ankle, C; MTP, metatarsophalangeal, D; HDIP, hindlimb distal interphalangeal, E). The blue line represents slow speed ($<3.25 \text{ m s}^{-1}$), the red line medium speed ($3.25\text{--}4.00 \text{ m s}^{-1}$) and the grey line fast speed ($>4.0 \text{ m s}^{-1}$). The error bars on each curve are the standard deviation. The stick figure representations at the top are from every 20% of stance of the hindlimb from one medium speed trial (with the same orientation as the forelimb in Fig. 1) with the ground reaction force included.

reaction force (GRF) (Dutto et al., 2004b; Merken et al., 1993), that the work done by the forelimb would be slightly negative and for the hindlimb would be positive. Observed work done by the forelimb was essentially zero, while the hindlimb did not do quite twice as much work as expected (0.34 J kg^{-1} vs a predicted value of 0.18 J kg^{-1}). The second hypothesis was that the work done by the limbs would not change with speed, and, indeed, total work done by the limbs was independent of speed (Fig. 2). Lastly, it was hypothesized that proximal joints contribute more to net work of the limb than distal joints. Whereas the distal three joints of both limbs produced no net power, as expected of joints acted upon by elastic elements, only the proximal hindlimb joints performed net work as hypothesized.

Work during trotting

Based upon investigations into the horizontal GRF produced during trotting, we would expect the forelimb to absorb energy and the hindlimb to generate energy (Dutto et al., 2004b; Merken et al., 1993). From the current inverse dynamic analysis, the forelimb did not appear to do any work (i.e. it neither absorbs nor generates energy). With a slight horizontal braking force present, it would be expected that the forelimb would absorb energy. The distal joints of the limb have very little capacity to do work because of their collective elastic behavior (see discussion below in *Distal vs proximal limb function*). The triceps muscle has been found to be active during the first 40% of stance, either lengthening slightly (the first 25% of stance) or isometric (Hoyt et al., 2005), resulting in a fairly large joint extension moment. During this time (the first 40% of stance) the elbow is flexing (Fig. 3), and, as results from the inverse dynamics analysis indicate, energy is being absorbed (negative power), resulting in agreement between the observed muscle function and mechanical analysis. Later in stance, there is little work done at the elbow, consistent with observations of triceps function where the muscle became inactive, which resulted in reduced force produced as it shortens (Hoyt et al., 2005). A similar pattern was observed at the shoulder, where the largest moment occurs during periods of relatively little joint motion (Fig. 3); it would be interesting to determine if the shoulder extensors are behaving similarly to the triceps during this time. Any energy absorption by the forelimb must be occurring above the level of the shoulder in the extrinsic muscles that attach the scapula to the torso of the animal. The serratus ventralis thoracis is a large muscle that can serve to absorb this energy, either through its large muscle volume and aponeuroses or by allowing the torso to absorb energy through its attachment to the ribs of the thorax, or some combination of the two (Payne et al., 2005b). Inverse

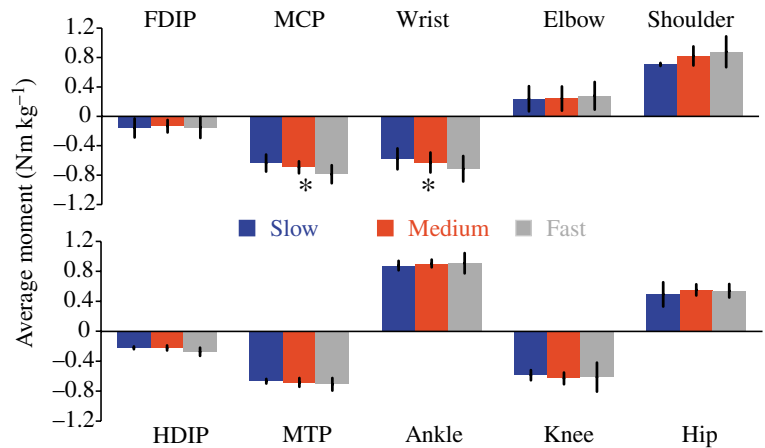


Fig. 5. Average joint moments for each of the three speed ranges. FDIP and HDIP, fore and hind distal interphalangeal, respectively; MCP, metacarpophalangeal, MTP, metatarsophalangeal. Black bars represent the standard deviation. *Significant differences ($P < 0.05$ using repeated-measures ANOVA) with speed.

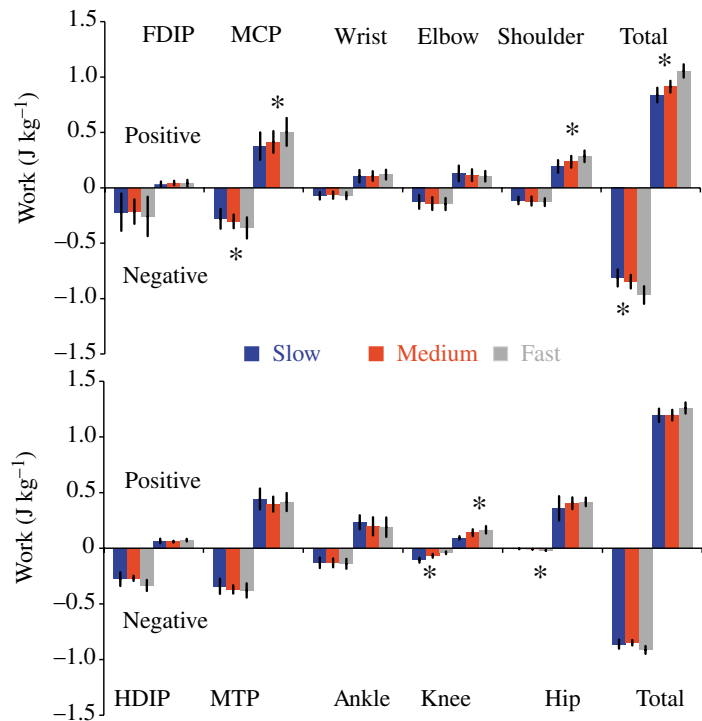


Fig. 6. Net negative and positive work done at each joint, and total limb (forelimb on the top plot and hindlimb on the bottom plot) for each of the three speed ranges (slow $< 3.25 \text{ m s}^{-1}$, medium $3.25\text{--}4.00 \text{ m s}^{-1}$ and fast $> 4.00 \text{ m s}^{-1}$). FDIP and HDIP, fore and hind distal interphalangeal, respectively; MCP, metacarpophalangeal, MTP, metatarsophalangeal. Colored bars indicate the means, and black lines the standard deviation. *Significant differences ($P < 0.05$ using repeated measures ANOVA) with speed. To obtain the total work for each joint and limb (as seen in Fig. 2), the negative and positive work are added together for each joint or for the total limb.

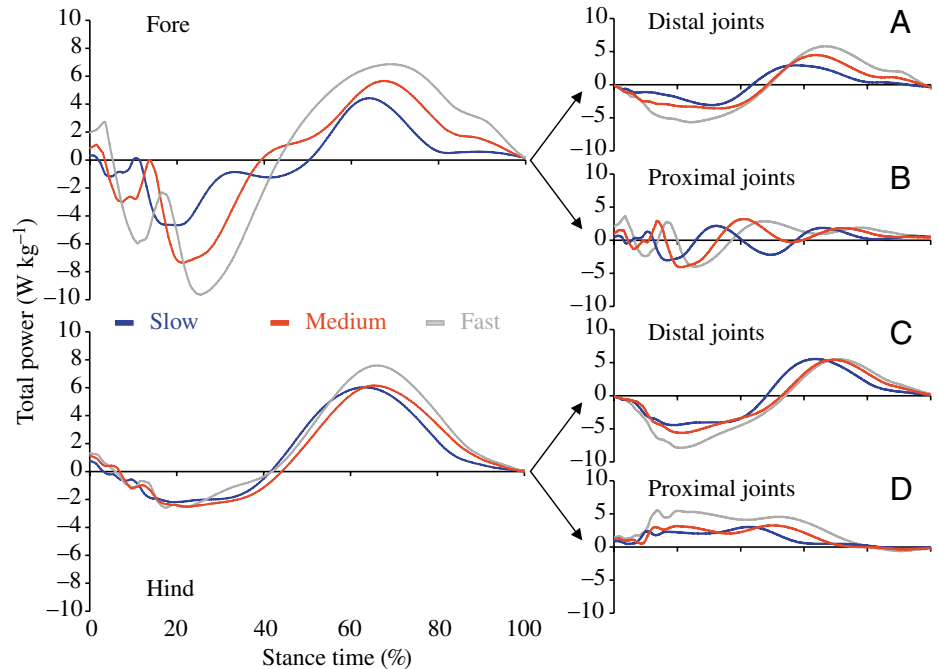


Fig. 7. Total power (sum of the five joints for each limb) during contact, for the fore- and hindlimb. Plots to the right show the total power for the three distal joints (A,C; forelimb: FDIP, MCP, wrist; hindlimb: HDIP, MTP, ankle) and two proximal joints (B,D; forelimb: elbow, shoulder; hindlimb: knee, hip) for each limb. The total power of the limb would be the sum of the proximal and distal power for the limb. FDIP and HDIP, fore and hind distal interphalangeal, respectively; MCP, metacarpophalangeal, MTP, metatarsophalangeal.

dynamics analysis does not allow the assessment of energy absorbed into the trunk without examination of torso, neck and head movement, which was beyond the scope of our study.

Another explanation for a lack of measured energy absorption by the forelimb (beyond those normally associated with inverse dynamics analysis, e.g. the assumption of rigid body segments) may be that the application of skin displacement algorithms outside of their intended speed [3.0 m s^{-1} (van Weeren et al., 1992)] may have incorrectly represented movement of the elbow and shoulder. Shoulder movement was particularly difficult to assess owing to movement of the scapula across the torso (Payne et al., 2005b). At 3.4 m s^{-1} , maximum possible errors in application of skin displacement corrections have been estimated to be 2% (Clayton et al., 1998). However, differences in hip and knee angles have been observed across speeds and on the incline using no skin corrections (Hoyt et al., 2002). It is unlikely that the use of the skin displacement correction algorithms has adversely affected the observed results and subsequent interpretations.

The hindlimb did positive work at all speeds (Fig. 2). Work done by one hindlimb was 0.34 J kg^{-1} , which was greater than that observed during walking [0.16 J kg^{-1} (Clayton et al., 2001)] and less than during jumping [0.71 J kg^{-1} (Dutto et al., 2004b); 1.25 J kg^{-1} (Bobbert and Santamaría, 2005)]. Like the forelimb, the three distal joints of the hindlimb contributed little work to the limb, as it behaved elastically (Fig. 7C). The knee contributed little work as the joint angle did not change very much through much of stance despite having a fairly large flexion moment (Fig. 4). It was not surprising that work was done by the hip. The gluteus medius is capable of better delivering power at the hip over other extensor muscles at the hip and at the knee (Payne et al., 2005b). Similarly in the dog,

the hip musculature does positive work during trotting (Gregersen et al., 1998). The knee has significant extensor musculature (Payne et al., 2005a), however, there was a flexion moment during stance (Fig. 5), indicating that the knee extensor muscles were not acting directly to assist with locomotion, but perhaps to stabilize the knee. The hindlimb has been observed to produce a force such that the GRF was directed anterior to the knee, producing a flexion moment for the majority of stance in several other studies (Biewener et al., 1988; Bobbert and Santamaría, 2005; Dutto et al., 2004a). EMG recordings have shown that gluteus medius, vastus lateralis and biceps femoris (hip extensor/knee flexor) are active for most of the stance phase (Robert et al., 1999). Recently, vastus medialis was observed to be active and shortening for the first 60% of stance, however the knee is flexing during this time (Hoyt et al., 2005). The vastus muscle must be absorbing energy and/or stabilizing the knee through co-contraction of the knee extensors and flexors. It may be that the large extensor muscles of the knee might act to resist gravity as opposed to power locomotion (Hoyt et al., 2005).

Changes in joint mechanics with speed

Net work in both limbs was the same for all speeds (Fig. 2). Forelimb GRF increases with speed, to maintain vertical torso position against the acceleration of gravity (Dutto et al., 2004b), resulting in significantly larger moments at the MCP and wrist (Figs 3, 5). Despite having a larger moment and greater ROM at higher speeds [consistent with previously reported observations (McGuigan and Wilson, 2003)], there were no changes in total work (Fig. 2). Neither the ROM nor moment changed at the elbow and shoulder. However, the shoulder did significantly greater work at the higher speeds (Fig. 2). Non-significant increases in shoulder ROM and joint

moment combined to increase the observed positive work slightly (Fig. 6), thereby increasing the net work done by the joint.

Because both horizontal and vertical GRF of the hindlimb did not change with speed during trotting, unlike the forelimb (Dutto et al., 2004b), we expected there to be no change in joint moments, powers, and work. Indeed, joint motion and average joint moments remained constant across speeds (Figs 4, 5). A previous report of horses trotting on a treadmill observed that the hip ROM increased 6° when increasing speed from $2\text{--}4\text{ m s}^{-1}$ (Hoyt et al., 2002). This was not the case in the present study, perhaps due to the differences in absolute speed. Ankle, knee and hip joint work done by human runners also appeared to increase when increasing running speed from 4.0 m s^{-1} to maximum sprint, particularly for the hip (Belli et al., 2002). However, these changes appeared to be greatest at the hip and when sprinting. Differences appear to be smaller at the lower speeds (Belli et al., 2002).

We assessed (*post hoc*) peak positive and/or negative power and peak joint moments. Peak powers were observed to be greater for many of the joints at higher speeds (Figs 3, 4). Because power was calculated by multiplying the joint moment by the joint angular velocity, one (or both) of these variables had to increase as speed increased. Peak joint moments also tended to be higher at greater increase in speeds, as can be observed in the joint moment plots (Figs 3, 4). Angular velocity must also be higher as joint ROM stayed the same or increased with greater speed. It has been established previously that time of contact decreased at greater speeds (Dutto et al., 2004b; Hoyt et al., 2000; Kram and Taylor, 1990; McLaughlin et al., 1996; Robert et al., 2002). Angular velocities must increase so that the joint can complete the necessary range of motion at higher speeds. Faster motion at the joint requires increased muscle contraction speed. For example, the vastus lateralis has an increased strain rate and integrated EMG with increased speed in the trotting horse (Hoyt et al., 2005) and the semimembranosus has a greater shortening velocity during galloping relative to trotting in dogs (Carrier et al., 1998).

Distal versus proximal limb function

The distal joints of the limb have very little capacity to do work (either absorb or generate energy) because of the small, highly pinnate muscles with long tendons that cross the joints (Biewener, 1998; McGuigan and Wilson, 2003; Payne et al., 2005b). The distal three joints of both limbs behave collectively as elastic systems storing and returning energy (Fig. 7A,C) with the ability to recover up to 40% of energy during the stride (Biewener, 1998). Elasticity was driven primarily by the MCP in the forelimb and the MTP in the hindlimb. Both of these joints are controlled by muscles with long tendons, primarily the superficial and deep digital flexor tendons, and the accessory ligaments. These tendons have been found to be structurally ideal for storing and releasing energy (Batson et al., 2003; Biewener, 1998). As seen in Fig. 3, the MCP behaved in an elastic manner storing and returning energy and increasing ROM with increased speed – a change that was in proportion

to the GRF, similar to previous reported observations (McGuigan and Wilson, 2003). Mechanics of the MTP were the same as those of the MCP, except that ROM remained the same across speeds.

The wrist and the ankle behaved elastically (the ankle more so than the wrist) as evidenced by the small amounts of energy absorption followed by equivalent energy return (Fig. 6). Stabilization of the wrist during stance was done by ulnaris lateralis and flexor carpi ulnaris, both relatively stiff muscle–tendon units (Brown et al., 2003) that have been shown to undergo some strain during trotting (Biewener, 1998). At the ankle, extensor muscles (gastrocnemius, soleus) have the dual capabilities of producing small amounts of work and behaving elastically from the extensive tendinous structure around the muscle fibers (Payne et al., 2005a). The distal hindlimb has been shown to be better than the forelimb at storing and returning energy (Biewener, 1998), even though it appears to be more important for the forelimb to do this during trotting (owing to greater force load and lack of net energy generation). If the distal forelimb was not behaving elastically efficiently, then the torso musculature at the scapula may be more important for absorbing and storing/releasing energy during trotting.

Although the distal fore- and hindlimbs behaved similarly during trotting, the proximal limbs did not (Fig. 7B,D). Both the elbow and shoulder had extensor moments (Fig. 5), but when the moments were largest there was little joint movement (Fig. 3). These joints were relatively rigid to allow the more proximal scapular and torso musculature to absorb and/or return energy. Modeling the proximal limb as a stiff spring seems to be appropriate, as a stiffer spring will allow forces to be transmitted through it to extrinsic musculature (McGuigan and Wilson, 2003). This would be consistent with the observation that neither joint changed limb energy by appreciable amounts. The proximal hindlimb functioned as a motor. Energy was provided by the hip, consistent with anatomical measurements of musculature at the hip (Payne et al., 2005a). Transfer of energy from the hip to the distal limb and ground or to the torso was facilitated by the knee, as the knee was stable (no movement) when the hip was producing the greatest power. Thus, although the knee did little work, maintaining stability was important for hip function.

Conclusion

In this study, three hypotheses regarding limb function during the stance phase of trotting were tested. The first proposed that the forelimb absorbed energy (did negative work) and the hindlimb generated energy (did positive work). Indeed the hindlimb did positive work, primarily by the hip. However, the forelimb did no work, leading to the observation that more proximal structures are absorbing energy, which are more difficult to measure with inverse dynamic analysis. The second hypothesis speculated that work would not change as trotting speed increased. Work done by both limbs was consistent across speeds. More work was done by the shoulder at greater speeds, but this had no effect on net work done by the forelimb. Work done at the knee increased at higher speeds, but this was

offset by reduced work done at the ankle. Finally, the distal joints of both limbs behave elastically, but the proximal forelimb remained fairly rigid and the proximal hindlimb powered locomotion.

We gratefully acknowledge the assistance of Devin Johnson, Jessica Schreiber, Gwenn Catterfeld and Carmen Lopez for data collection. This study was funded by N.I.H. grant no. S06 GM53933 to D.F.H. and S.J.W. Horses were trained and led during testing by Deborah Mead with the help of Shannon Garcia. Kinematic and inverse dynamic data processing was performed by Joel Lanovaz at the McPhail Equine Performance Center, College of Veterinary Medicine, Michigan State University. We would also like to acknowledge Holly M. Greene, MS, Equine Research Technician, for providing technical support.

References

- Abourachid, A.** (2001). Kinematic parameters of terrestrial locomotion in cursorial (ratites), swimming (ducks), and striding birds (quail and guinea-fowl). *Comp. Biochem. Physiol.* **131A**, 113-119.
- Aerts, P.** (1998). Vertical jumping in *Galago senegalensis*: the quest for an obligate mechanical power amplifier. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **353**, 1607-1620.
- Batson, E. L., Paramour, R. J., Smith, T. J., Birch, H. L., Patterson-Kane, J. C. and Goodship, A. E.** (2003). Are the material properties and matrix composition of equine flexor and extensor tendons determined by their functions? *Equine Vet. J.* **35**, 314-318.
- Belli, A., Kyrolainen, H. and Komi, P. V.** (2002). Moment and power of lower limb joints in running. *Int. J. Sports Med.* **23**, 136-141.
- Biewener, A. A.** (1998). Muscle-tendon stress and elastic energy storage during locomotion in the horse. *Comp. Biochem. Physiol.* **120B**, 73-87.
- Biewener, A. A. and Roberts, T. J.** (2000). Muscle and tendon contributions to force, work, and elastic energy savings: a comparative perspective. *Exerc. Sport Sci. Rev.* **28**, 99-107.
- Biewener, A. A., Thomason, J. J. and Lanyon, L. E.** (1988). Mechanics of locomotion and jumping in the horse (Equus): in vivo stress in the tibia and metatarsus. *J. Zool.* **214**, 547-565.
- Biewener, A. A., McGowan, C., Card, G. M. and Baudinette, R. V.** (2004). Dynamics of leg muscle function in tammar wallabies (*M. eugenii*) during level versus incline hopping. *J. Exp. Biol.* **207**, 211-223.
- Bobbert, M. F. and Santamaría, S.** (2005). Contribution of the forelimbs and hindlimbs of the horse to mechanical energy changes in jumping. *J. Exp. Biol.* **208**, 249-260.
- Brown, N. A., Kawcak, C. E., McIlwraith, C. W. and Pandey, M. G.** (2003). Architectural properties of distal forelimb muscles in horses, *Equus caballus*. *J. Morphol.* **258**, 106-114.
- Buchner, H. H. F., Savelberg, H. H. C. M., Schamhardt, H. C. and Barneveld, A.** (1997). Inertial properties of Dutch warmblood horses. *J. Biomech.* **30**, 653-658.
- Carrier, D. R., Gregersen, C. S. and Silverton, N. A.** (1998). Dynamic gearing in running dogs. *J. Exp. Biol.* **201**, 3185-3195.
- Clayton, H. M., Lanovaz, J. L., Schamhardt, H. C., Willemen, M. A. and Colborne, G. R.** (1998). Net joint moments and powers in the equine forelimb during the stance phase of the trot. *Equine Vet. J.* **30**, 384-389.
- Clayton, H. M., Hodson, E. F., Lanovaz, J. L. and Colborne, G. R.** (2001). The hind limb in walking horses: 2. Net joint moments and joint powers. *Equine Vet. J.* **33**, 44-48.
- Colborne, G. R., Lanovaz, J. L., Springings, E. J., Schamhardt, H. C. and Clayton, H. M.** (1998). Forelimb joint moments and power during the walking stance phase of horses. *Am. J. Vet. Res.* **59**, 609-614.
- Daley, M. A. and Biewener, A. A.** (2003). Muscle force-length dynamics during level versus incline locomotion: a comparison of *in vivo* performance of two guinea fowl ankle extensors. *J. Exp. Biol.* **206**, 2941-2958.
- Dutto, D. J., Hoyt, D. F., Clayton, H., Cogger, E. A. and Wickler, S. J.** (2004a). Moments and power generated by the horse (*Equus caballus*) hind limb during jumping. *J. Exp. Biol.* **207**, 667-674.
- Dutto, D. J., Hoyt, D. F., Cogger, E. A. and Wickler, S. J.** (2004b). Ground reaction forces in horses trotting up an incline and on the level over a range of speeds. *J. Exp. Biol.* **207**, 3507-3514.
- Gabaldón, A. M., Nelson, F. E. and Roberts, T. J.** (2004). Mechanical function of two ankle extensors in wild turkeys: shifts from energy production to energy absorption during incline versus decline running. *J. Exp. Biol.* **207**, 2277-2288.
- Gillis, G. B. and Biewener, A. A.** (2001). Hindlimb muscle function in relation to speed and gait: *in vivo* patterns of strain and activation in hip and knee extensor of the rat (*Rattus norvegicus*). *J. Exp. Biol.* **204**, 2717-2731.
- Gregersen, C. S., Silverton, N. A. and Carrier, D. R.** (1998). External work and potential for elastic storage at the limb joints of running dogs. *J. Exp. Biol.* **201**, 3197-3210.
- Herr, H. M. and McMahon, T. A.** (2000). A trotting horse model. *Int. J. Robot. Res.* **19**, 566-581.
- Hoyt, D. F., Wickler, S. J. and Cogger, E. A.** (2000). Time of contact and step length: the effect of limb length, running speed, load carrying and incline. *J. Exp. Biol.* **203**, 221-227.
- Hoyt, D. F., Molinari, M., Wickler, S. J. and Cogger, E. A.** (2002). Effect of trotting speed, load and incline on hind limb stance-phase kinematics. *Equine Vet. J. Suppl.* **34**, 330-336.
- Hoyt, D. F., Wickler, S. J., Biewener, A. A., Cogger, E. A. and De La Paz, K. L.** (2005). In vivo muscle function vs speed. I. Muscle strain in relation to length change of the muscle-tendon unit. *J. Exp. Biol.* **208**, 1175-1190.
- Jacobs, R., Bobbert, M. F. and Vaningenschenau, G. J.** (1996). Mechanical output from individual muscles during explosive leg extensions – the role of biarticular muscles. *J. Biomech.* **29**, 513-523.
- Ker, R. F., Alexander, R. M. and Bennett, M. B.** (1988). Why are mammalian tendons so thick? *J. Zool.* **216**, 309-324.
- Khumsap, S., Lanovaz, J. L., Rosenstein, D. S., Byron, C. and Clayton, H. M.** (2003). Effect of induced unilateral synovitis of distal intertarsal and tarsometatarsal joints on sagittal plane kinematics and kinetics of trotting horses. *Am. J. Vet. Res.* **64**, 1491-1495.
- Kram, R. and Taylor, C. R.** (1990). Energetics of running: a new perspective. *Nature* **346**, 265-267.
- McGowan, C. P., Baudinette, R. V. and Biewener, A. A.** (2005). Joint work and power associated with acceleration and deceleration in tammar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **208**, 41-53.
- McGuigan, M. P. and Wilson, A. M.** (2003). The effect of gait and digital flexor muscle activation on limb compliance in the forelimb of the horse *Equus caballus*. *J. Exp. Biol.* **206**, 1325-1336.
- McLaughlin, R. M., Gaughan, E. M., Roush, J. K. and Skaggs, C. L.** (1996). Effects of subject velocity on ground reaction force measurements and stance times in clinically normal horses at the walk and trot. *Am. J. Vet. Res.* **57**, 7-11.
- Merkens, H. W., Schamhardt, H. C., Van Osch, G. J. V. M. and Van Den Bogert, A. J.** (1993). Ground reaction force patterns of Dutch Warmblood horses at normal trot. *Equine Vet. J.* **25**, 134-137.
- Payne, R. C., Hutchinson, J. R., Robilliard, J. J., Smith, N. C. and Wilson, A. M.** (2005a). Functional specialisation of pelvic limb anatomy in horses (*Equus caballus*). *J. Anat.* **206**, 557-574.
- Payne, R. C., Veenman, P. and Wilson, A. M.** (2005b). The role of the extrinsic thoracic limb muscles in equine locomotion. *J. Anat.* **206**, 193-204.
- Robert, C., Valette, J. P., Degueurce, C. and Denoix, J. M.** (1999). Correlation between surface electromyography and kinematics of the hindlimb of horses at trot on a treadmill. *Cells Tissues Organs* **165**, 113-122.
- Robert, C., Valette, J. P., Pourcelot, P., Audigié, F. and Denoix, J. M.** (2002). Effects of trotting speed on muscle activity and kinematics in saddlehorses. *Equine Vet. J. Suppl.* **34**, 295-301.
- Roberts, T. J. and Belliveau, R. A.** (2005). Sources of mechanical power for uphill running in humans. *J. Exp. Biol.* **208**, 1963-1970.
- Roberts, T. J. and Scales, J. A.** (2004). Adjusting muscle function to demand: joint work during acceleration in wild turkeys. *J. Exp. Biol.* **207**, 4165-4174.
- van Weeren, P. R., van den Bogert, A. J. and Barneveld, A.** (1992). Correction models for skin displacement in equine kinematic gait analysis. *Equine Vet. Sci.* **12**, 178-192.
- Wickler, S. J., Hoyt, D. F., Biewener, A. A., Cogger, E. A. and De La Paz, K. L.** (2005). In vivo muscle function vs speed. II. Muscle function trotting up an incline. *J. Exp. Biol.* **208**, 1191-1200.
- Wilson, A. M., McGuigan, M. P., Su, A. and van den Bogert, A. J.** (2001). Horses damp the spring in their step. *Nature* **414**, 895.
- Winter, D. A.** (1990). *Biomechanics and Motor Control of Human Movement*. New York: John Wiley.