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RESEARCH ARTICLE

Forelimb muscle activity during equine locomotion

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SUMMARY

Few quantitative data exist to describe the activity of the distal muscles of the equine forelimb during locomotion, and there is an incomplete understanding of the functional roles of the majority of the forelimb muscles. Based on morphology alone it would appear that the larger proximal muscles perform the majority of work in the forelimb, whereas the smaller distal muscles fulfil supplementary roles such as stabilizing the joints and positioning the limb for impact with the ground. We measured the timing and amplitude of the electromyographic activity of the intrinsic muscles of the forelimb in relation to the phase of gait (stance *versus* swing) and the torque demand placed on each joint during walking, trotting and cantering. We found that all forelimb muscles, except the extensor carpi radialis (ECR), were activated just prior to hoof-strike and deactivated during stance. Only the ECR was activated during swing. The amplitudes of muscle activation typically increased as gait speed increased. However, the amplitudes of muscle activation were not proportional to the net joint torques, indicating that passive structures may also contribute significantly to torque generation. Our results suggest that the smaller distal muscles help to stabilize the forelimb in early stance, in preparation for the passive structures (tendons and ligaments) to be stretched. The distal forelimb muscles remain active throughout stance only during canter, when the net torques acting about the distal forelimb joints are highest. The larger proximal muscles activate in a complex coordination to position and stabilize the shoulder and elbow joints during ground contact.

Key words: equine gait, walk, trot, canter, quadrupedal biomechanics, joint torque, EMG.

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INTRODUCTION

Biomechanical experiments and mathematical modelling have contributed significantly to current understanding of muscle function in animal locomotion. The patterns of net muscular torques developed over one gait cycle have been calculated for a wide variety of species using measurements of joint kinematics and ground reaction forces (Clayton et al., 2000; Colborne et al., 1997; Dogan et al., 1991; Fowler et al., 1993; Perell et al., 1993; Pandy et al., 1988; Witte et al., 2002). Individual muscle forces also have been determined, albeit for a smaller selection of animals, using detailed muscle-actuated models of the limbs (e.g. Anderson and Pandy, 2001; Goetz et al., 2008; Harrison et al., 2010; van Antwerp et al., 2007). Some studies have also evaluated the contributions of individual muscles to the angular accelerations of the joints and the acceleration of the whole-body centre of mass, but to our knowledge these analyses have been performed only for locomotion in humans (Anderson and Pandy, 2003; Anderson et al., 2004; Liu et al., 2006; Pandy et al., 2010; Pandy and Andriacchi, 2010) and cats (van Antwerp et al., 2007). Because muscle forces cannot be measured non-invasively in living subjects, muscle electromyographic (EMG) recordings are often used to gain confidence in model predictions of muscle forces.

Locomotion in the horse results from a complex coordination of forces generated by active muscle contraction and passive stretching of tendons and ligaments. During stance, muscles, tendons and ligaments develop substantial torques about the body joints to support the centre of mass against gravity and to propel it forward at a steady speed. These structures also act to accelerate the limb in early swing and to reposition it in late swing prior to ground contact.

Loading of the passive structures of the distal forelimb has been the subject of frequent study (Biewener, 1998; Harrison et al., 2010; Jansen et al., 1993; Meershoek et al., 2001; Swanstrom et al., 2004; Swanstrom et al., 2005; Wilson et al., 2001); however, little is known about the coordination of active muscle contraction (Butcher et al., 2009; Hoyt et al., 2005; Jansen et al., 1992; Tokuriki et al., 1989). Muscle activation patterns have been predicted from calculations of net joint torques using biomechanical models of the forelimb (Harrison et al., 2010; Swanstrom et al., 2005; Wilson et al., 2001), but no study has validated these calculations against direct measurements obtained *in vivo*. The most comprehensive model of the equine forelimb developed to date includes only those muscles distal to the elbow (Harrison et al., 2010), and no complete musculoskeletal model of the proximal limb is currently available.

Differences in morphology between the proximal and distal muscles of the forelimb (Brown et al., 2003; Payne et al., 2004; Watson and Wilson, 2007) suggest the likelihood of significant differences in function (Payne et al., 2004), although this has yet

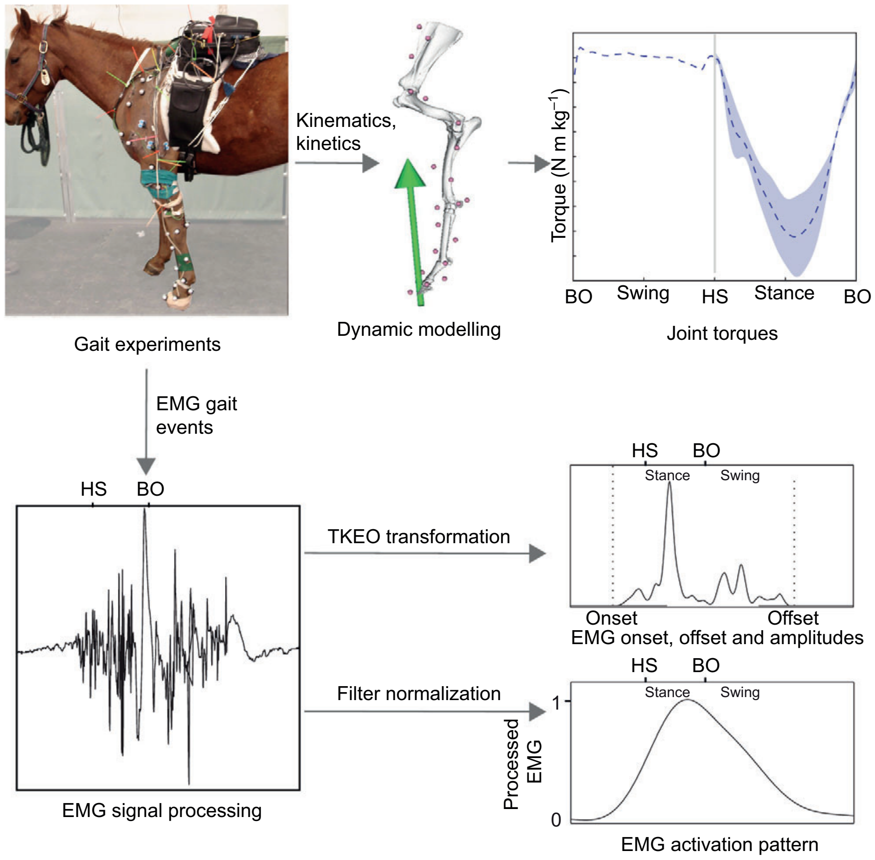


Fig. 1. Schematic diagram of the study method. Gait experiments were used to measure the joint kinematics, ground reaction forces and electromyographic (EMG) activity of the forelimb muscles simultaneously. The kinematics and ground reaction forces (indicated by the green arrow) were applied to subject-specific biomechanical models of the forelimb to calculate the net torque acting about each joint during stance and swing. The EMG signals were digitized and then processed by two methods (see Materials and methods for details). The hoof-strike (HS) and breakover (BO, analogous to toe-off in human gait) of two strides are shown in the EMG results.

to be confirmed by experiment. The proximal muscles [i.e. those inserting proximal to the carpus such as the triceps, supraspinatus (SUP) and infraspinatus (INF)] typically have small pennation angles, are relatively large in volume and, apart from the biceps (BIC), have relatively short tendons (Payne et al., 2004; Watson and Wilson, 2007). In contrast, the distal muscles [i.e. those inserting distal to the carpus such as the superficial digital flexor (SDF)] are typically highly pennated, small in volume, and have long tendons relative to their contractile fibre lengths (Brown et al., 2003). Indeed, the distal muscles constitute only 10% of the muscle mass of the entire forelimb (Brown et al., 2003; Payne et al., 2004; Watson and Wilson, 2007). Thus, on the basis of architecture alone, it would seem likely that the proximal muscles perform most of the work done by the forelimb during locomotion, whereas the distal muscles act mainly in a supporting role.

EMG measurement is a useful tool for determining the sequence and timing of muscle activity during movement. Numerous equine studies have characterized EMG activity of the hindlimb muscles (Robert et al., 1999; Robert et al., 2000; Tokuriki and Aoki, 1995; Wentink, 1978) and of the intrinsic muscles of the trunk (Licka et al., 2004; Robert et al., 2001), but few data are available to show the activation patterns of the forelimb muscles (Aoki et al., 1984; Hoyt et al., 2005; Jansen et al., 1992; Tokuriki et al., 1989). Thus, little is known about the coordination of the proximal and distal muscles of the equine forelimb across a range of locomotion speeds. Whilst EMG measurements assist in the understanding of muscle function during movement, a complete description of the functional roles of muscles requires quantitative knowledge of muscle–tendon lengths, muscle–tendon contraction velocities and muscle–tendon forces. Nonetheless, the juxtaposition of EMG activity and net joint torques may further illuminate the functional roles of the major muscles of the forelimb during gait.

The overall goal of the present study was to measure the patterns of muscle activity in the equine forelimb and to correlate this information with the net torques developed about the joints during walking, trotting and cantering. We addressed three specific questions. (1) Which forelimb muscles are active under weight-bearing load during stance? (2) Which forelimb muscles are active when the limb is accelerated and repositioned during swing? (3) How do the timing and amplitude of forelimb muscle activity change with gait?

MATERIALS AND METHODS

Subjects

Three Thoroughbred horses (mass 484±13 kg, age 4.3±0.8 years) were used as subjects for this study. All protocols were approved by the Institutional Animal Use and Care Committee at Colorado State University. The horses were exercised for 2 weeks prior to data collection to allow acclimatization to both high-speed treadmill exercise and the gait analysis equipment used in this study.

Gait experiments

Two sets of experiments were performed on each subject. In the first set of experiments, each horse walked ($1.6\,\mathrm{m\,s^{-1}}$) and trotted ($3.4\,\mathrm{m\,s^{-1}}$) overground on a level surface, whereas in the second set each horse walked ($1.6\,\mathrm{m\,s^{-1}}$), trotted ($3.4\,\mathrm{m\,s^{-1}}$) and cantered ($7.5\,\mathrm{m\,s^{-1}}$, left leg leading) on a level treadmill (Equigym, Lexington, KY, USA).

Table 1. Root mean square EMG amplitudes (normalized to mean results at the canter) for the 15 forelimb muscles tested in this study

Muscle	*N*	Condition 1 OG walk	Condition 2 OG trot	Condition 3 TR walk	Condition 4 TR trot	Condition 5 TR canter
Biceps brachii*	3	0.20±0.05	0.27±0.12	$0.17{\pm}0.13^{5}$	0.44±0.45	1^{3}
Brachialis	2	0.14±0.09	0.27±0.13	0.16±0.02	0.26±0.03	1
Common digital extensor*	3	$0.13{\pm}0.04^{2}$	$0.28{\pm}0.07^{1}$	$0.17{\pm}0.02^{4,5}$	$0.28{\pm}0.04^{3,5}$	$1^{3,4}$
Deep digital flexor*	3	$1.00{\pm}0.81^{3}$	$1.50{\pm}0.81^{4}$	$0.40{\pm}0.53^{1}$	$0.43{\pm}0.29^{2}$	1
Deltoideus	3	0.23±0.11	0.35±0.07	$0.30{\pm}0.14^{5}$	$0.32{\pm}0.11^{5}$	$1^{3,4}$
Extensor carpi radialis*	3	$0.25{\pm}0.1^{2}$	$0.70{\pm}0.35^{1}$	$0.28{\pm}0.06^{4,5}$	$0.57{\pm}0.09^{3,5}$	$1^{3,4}$
Flexor carpi radialis	3	0.42±0.26	1.12±0.78	0.27±0.09	0.40±0.16	1
Flexor carpi ulnaris*	3	$0.25{\pm}0.04^{2}$	$0.48{\pm}0.15^{1}$	$0.27{\pm}0.05^{4,5}$	$0.45{\pm}0.09^{3,5}$	$1^{3,4}$
Infraspinatus	1	0.34	0.29	0.11	0.31	1
Lateral digital extensor	1	0.43	1.02	0.57	0.53	1
Superficial digital flexor	3	0.42±0.33	1.96±2.13	0.23±0.15	0.48±0.49	1
Supraspinatus*	3	$0.52{\pm}0.77^{2}$	$1.08{\pm}1.33^{1}$	$0.70{\pm}0.93^{4}$	$1.22{\pm}1.39^{3}$	1
Triceps lateral head*	3	$0.09{\pm}0.03^{2}$	$0.29{\pm}0.15^{1}$	$0.12{\pm}0.02^{4,5}$	$0.19{\pm}0.05^{3,5}$	$1^{3,4}$
Triceps long head*	3	$0.13{\pm}0.03^{2}$	$0.38{\pm}0.18^{1}$	$0.18{\pm}0.04^{4,5}$	$0.31{\pm}0.04^{2,3,5}$	$1^{3,4}$
Ulnaris lateralis*	3	$0.31{\pm}0.03^{2}$	$0.61{\pm}0.14^{1}$	$0.40{\pm}0.08^{4,5}$	$0.50{\pm}0.07^{3,5}$	$1^{3,4}$

Data are means ± s.d. except for infraspinatus and lateral digital extensor, where data were available for only one horse. *N* refers to the number of horses.

OG, overground; TR, treadmill.

*Significant gait effect ($P<0.05$).

Numerical superscripts (1–5) specify significantly different conditions ($P<0.05$), i.e. Condition $1^{2,3}$ is significantly different from Conditions 2 and 3.

In both the overground and treadmill experiments, kinematic, ground reaction force and muscle EMG data were recorded simultaneously. Nineteen retro-reflective markers were placed over the defined bony landmarks of the left forelimb (Fig. 1) to facilitate kinematic measurement using eight optical motion capture cameras (Vicon, Los Angeles, CA, USA) sampling at 200 Hz. A force-measuring horseshoe, or dynashoe (Roland et al., 2005), was fitted to the left forelimb of each horse to record all six components of the ground reaction force and moment, which were then used to compute the centre of pressure. A shoe of similar geometry and mass was fitted to the right forelimb to ensure symmetry during gait. Each of the six channels of the ground reaction force data recorded by the dynashoe were sampled at 1000 Hz. A camera synchronization signal received wirelessly was used to trigger data collection from the dynashoe. Output of the dynashoe was validated during the overground experiments by recording ground reaction forces simultaneously from the dynashoe and a six-component, strain-gauged force platform (Bertec Corporation, Columbus, OH, USA).

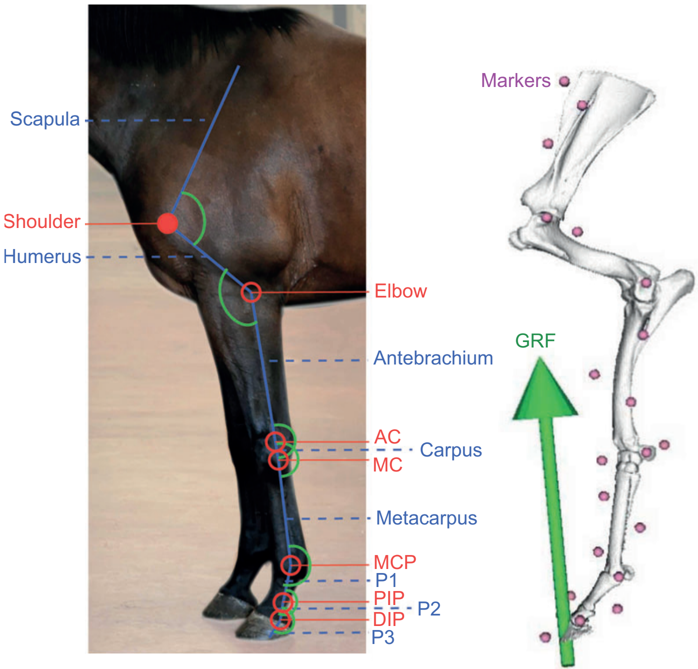
EMG data were recorded from 15 muscles of the left forelimb of each subject (Table 1). Surface EMG electrodes were positioned over the middle portions of 11 muscle bellies: infraspinatus (INF, one animal only), deltoideus (DELT), long head of triceps brachii (TRILONG), brachialis (BRAC, two animals only), lateral head of triceps brachii (TRILAT), extensor carpi radialis (ECR), flexor carpi radialis (FCR), humeral head of flexor carpi ulnaris (FCU), ulnaris lateralis (UL), long digital extensor (LDE, one animal only) and common digital extensor (CDE). Fine-wire EMG electrodes were inserted by a licensed veterinarian into four additional muscles: supraspinatus (SUP), biceps (BIC), superficial digital flexor (SDF) and the radial head of deep digital flexor (DDF). The electrodes for SDF and DDF were inserted under ultrasound guidance into the distal portions of these muscles near the myotendinous junction. Force plate and EMG data were digitized at 3000 Hz and synchronized with the optical motion capture system. Data were collected for 10 s intervals in both sets of experiments.

Calculation of joint torques

Net joint torques were computed using a biomechanical model of the forelimb. The skeleton was represented as a 9 segment, 9 degrees-of-freedom kinematic linkage composed of 7 joints: distal interphalangeal (DIP) joint, proximal interphalangeal (PIP) joint, metacarpophalangeal (MCP) joint, midcarpal (MC) joint, antebrachiocarpal joint (AC), elbow joint and shoulder joint (Fig. 2). All joints were represented as a hinge with one (flexion–extension) joint angle, except the shoulder, which was represented as a ball-and-socket joint with three joint angles. Subject-specific musculoskeletal models were developed in OpenSim software (Delp et al., 2007) with the inertial properties of the segments scaled on the basis of body mass (Buchner et al., 1997). For each subject, marker trajectories were identified from the raw kinematic data using Vicon Motus 9.2 software. A Gait-Extract toolbox (freely available from https://simtk.org/home/c3dtoolbox) was used to extract and process the raw kinematic marker, ground reaction force and muscle EMG data obtained for each trial into a format suitable for input to the musculoskeletal model. Kinematic data were filtered at 6 Hz, whereas ground reaction force data were filtered at 50 Hz (Harrison et al., 2010). Joint angles were determined from marker kinematics using the subject-specific biomechanical model and an inverse kinematics algorithm available in OpenSim. In this algorithm, differences between the experimental markers and virtual markers on the model were minimized, resulting in an optimized set of joint angles at each instant of the gait cycle. Net joint torques were then found using an inverse-dynamics analysis that incorporated the ground reaction forces, gravitational forces and inertial forces as inputs to the model. The resultant joint torques were averaged across the three trials for each gait and then normalized to the durations of stance and swing.

EMG analyses

EMG data were treated in two different ways before normalization to the mean peak amplitude measured for cantering (Fig. 1). In the first method, EMG onset and offset times were identified manually using a custom-written computer program in Matlab. In this program the EMG signals were treated with a density transformation (TKEO) (Hortobágyi et al., 2009) to improve the signal-to-noise ratio. Onset and offset times were recorded relative to hoof-strike and breakover as a percentage of stance or swing.



Equine forelimb

Dynamic model

Fig. 2. Left panel: schematic diagram of the biomechanical model of the equine forelimb used to calculate net joint torques. The limb was represented as a 9 degrees-of-freedom linkage with 7 joints. The shoulder joint (solid red circle) was treated as a 3 degrees-of-freedom ball-and-socket joint. The remaining joints – elbow, antebrachiocarpal (AC) joint, midcarpal (MC) joint, metacarpophalangeal (MCP) joint, proximal interphalangeal (PIP) joint and distal interphalangeal (DIP) joint – were represented as 1 degree-of-freedom hinge joints. The blue lines indicate the forelimb segments represented in the model: scapula, humerus, antebrachium, proximal row of carpal bones, metacarpus (including the distal row of carpal bones), P1 (proximal phalanx), P2 (middle phalanx) and P3 (distal phalanx). The flexion angle of each joint is shown as a green arc. Right panel: 19 markers (pink spheres) were used to determine the positions of the bone segments during the gait experiments. The ground reaction force (GRF, green arrow) was measured using an instrumented shoe.

Within each onset-to-offset period, the mean signal strength was determined by high-pass filtering the signal at 20 Hz and then calculating the root mean square (r.m.s.) amplitude of a 40 ms window passed across the time series (Hortobágyi et al., 2009). In the second method, a representative time series amplitude of each signal (see Fig. 1, 'EMG activation pattern') was separately determined using a four-step algorithm: the data were demeaned, low-pass filtered at 40 Hz, rectified and then high-pass filtered at 10 Hz. The results were normalized to the durations of stance and swing and then averaged across all trials for each gait. For each subject, EMG data were normalized to the mean maximum signal magnitude per stride recorded in the cantering experiments. The first method is better suited to the determination of onset and offset times (Hortobágyi et al., 2009), whereas the second method is commonly used to estimate the amplitude of muscle activation (Lloyd and Besier, 2003).

Statistical analysis

EMG onset times, offset times, and r.m.s. amplitudes were averaged within subjects for each gait and surface (i.e. overground *versus* treadmill). Onset times, offset times and r.m.s. amplitudes were analysed using three-way analyses of variance (ANOVA) that included the effects of animal, gait, surface and the interaction between gait and surface. Comparisons between the surfaces excluded the data recorded for cantering. Comparisons between the walking, trotting and cantering data excluded the overground trials. *Post hoc* comparisons were adjusted using the Sidak method. Level of significance was defined as $P<0.05$.

RESULTS

The durations of the stance and swing phases decreased significantly as gait speed increased (Table 2). The decrease in swing time was smaller than the decrease in stance time. Stance and swing times for walking and trotting were not significantly different in overground and treadmill gait.

All muscles, except the ECR, consistently displayed activity during stance, and were activated either prior to hoof-strike or immediately thereafter (Fig. 3). Deactivation time was muscle dependent and ranged from early to late stance. Apart from intermittent activity of the BIC, SUP and INF, the ECR was the only muscle that was active in the first half of swing when the limb was protracted.

For the majority of the forelimb muscles, the onset of muscle activation was invariant with gait, but muscle de-activation time varied significantly (Fig. 3). Only the CDE, ECR and TRILAT showed significant differences in the onset of muscle activation. As gait speed increased, muscle de-activation occurred later during stance for the DELT, TRILAT, FCR, UL, SDF and DDF, and earlier during swing for the ECR. No significant differences were observed in the timing of muscle activation between overground and treadmill gait. Only the TRILONG displayed a significant difference in de-activation time between overground and treadmill gait. The TRILONG de-activated earlier during stance in treadmill gait.

The EMG amplitudes of all muscles, except the BIC, SUP, DDF, FCR and SDF, were significantly greater in cantering than in walking and trotting (Table 1). The EMG amplitude of the BIC was only significantly greater in cantering than in walking ($P<0.05$). All muscles, except the FCR, SDF and BIC, also showed significant

Table 2. Time periods (s) of the stance and swing phases of gait for each of the five experimental conditions examined in this study

	Gait	Stance	Swing
Condition 1	OG walking	0.74±0.02	0.44±0.01
Condition 2	OG trotting	0.29±0.02	0.39±0.01
Condition 3	TR walking	0.75±0.02	0.44±0.01
Condition 4	TR trotting	0.33±0.00	0.40±0.02
Condition 5	TR cantering	0.16±0.00	0.37±0.02

Data are means ± s.d.
OG, overground; TR, treadmill.

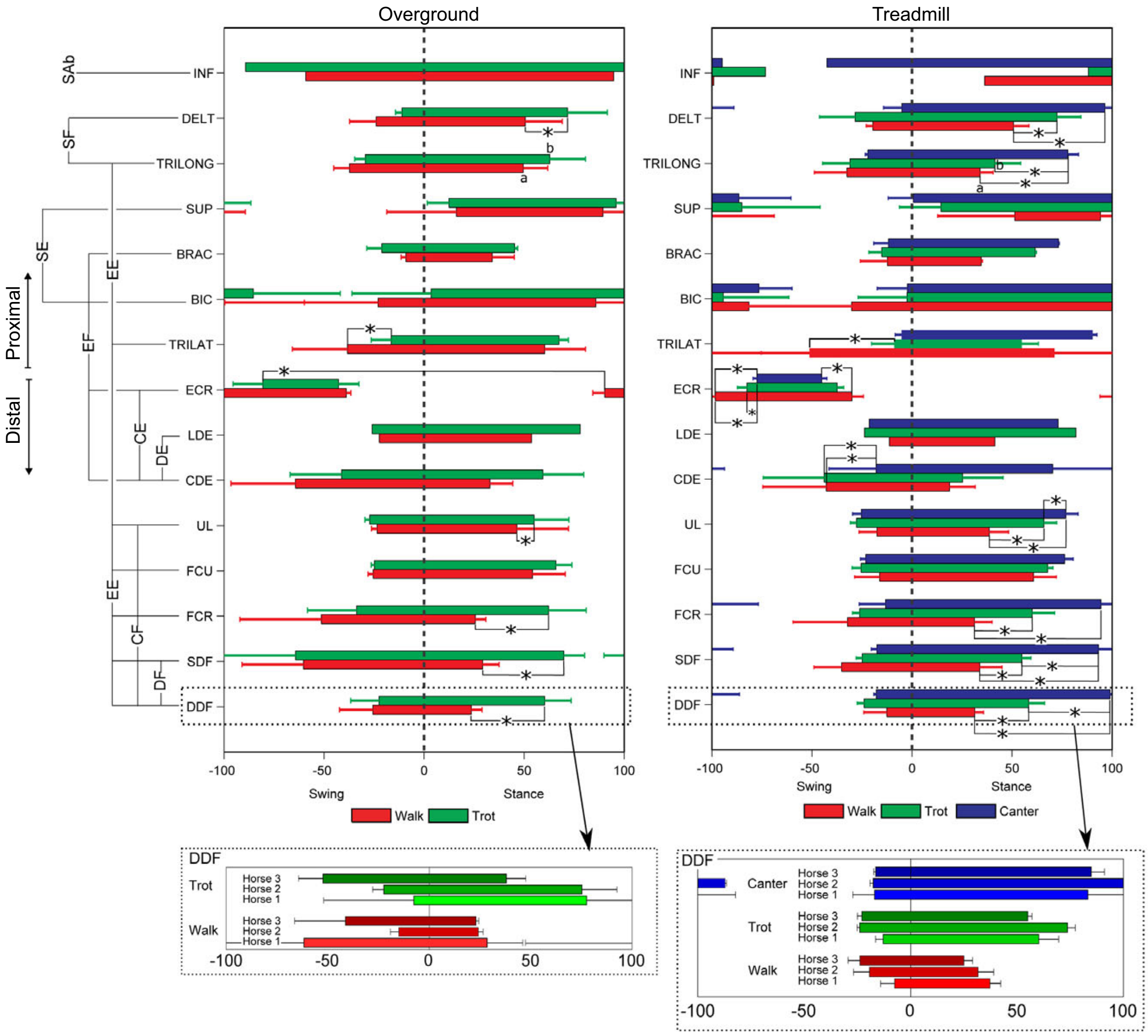


Fig. 3. Onset and offset activation times measured for each muscle during overground and treadmill gait. Data were averaged across subjects and normalized to stance (1 to 100%) or swing (–99 to 0%). Error bars represent 1 s.d. Overground results (left panel) include walk and trot trials, whereas treadmill results (right panel) include walk, trot and canter trials. Muscles are grouped by their action about each joint: digital flexors (DF), digital extensors (DE), carpal flexors (CF), carpal extensors (CE), elbow flexors (EF), elbow extensors (EE), shoulder flexors (SF), shoulder extensors (SE) and shoulder abductor (SAb). Data were collected for the infraspinatus (INF) and lateral digital extensor muscle (LDE) for one horse only, and hence standard deviation bars are not shown for these muscles. Intra-subject variations are indicated in the insets at the base of the figure. Onset and offset activation times for deep digital flexor (DDF) muscles are plotted for each animal. Solid bars indicate the mean over all trials and error bars indicate 1 s.d. Statistically significant ($P<0.05$) differences in onset and offset timings are indicated with an asterisk when between different gaits on the same surface and are indicated with a letter (a or b) when between the same gaits on different surfaces. DELT, deltoideus; TRILONG, long head of triceps brachii; BRAC, brachialis; TRILAT, lateral head of triceps brachii; ECR, extensor carpi radialis; FCR, flexor carpi radialis; FCU, humeral head of flexor carpi ulnaris; UL, ulnaris lateralis; CDE, common digital extensor; SUP, supraspinatus; BIC, biceps; SDF, superficial digital flexor.

differences between walking and trotting. There were no significant differences in the r.m.s. amplitudes of the EMG signals between overground and treadmill gait.

There were clear differences in the magnitude and timing of net joint torque and muscle activation peaks between gaits (Figs 4–8; results for the PIP and MC joints are not shown for brevity). With increasing gait speed the magnitudes of the peak torques during stance phase increased. The peak for the DIP joint torque occurred late in stance for walk and trot and near mid-stance for canter (Fig. 4). For the MCP joint, peak torque occurred before (for walk) or near mid-stance (for trot and canter) (Fig. 5), while for the AC joint peak torque occurred in early stance (Fig. 6). Joint torques during the swing phase were negligible in the distal limb. The distal flexor muscles showed modest activity in swing and peaks of activity just prior to or after hoof-strike. The magnitude of this peak was higher and it occurred later as gait speed increased. The digital extensor muscles (CDE and LDE) were intermittently active during swing, peaking in activity near hoof-strike and with increasing magnitude, and activated later in stance as gait speed increased. The ECR was primarily active in

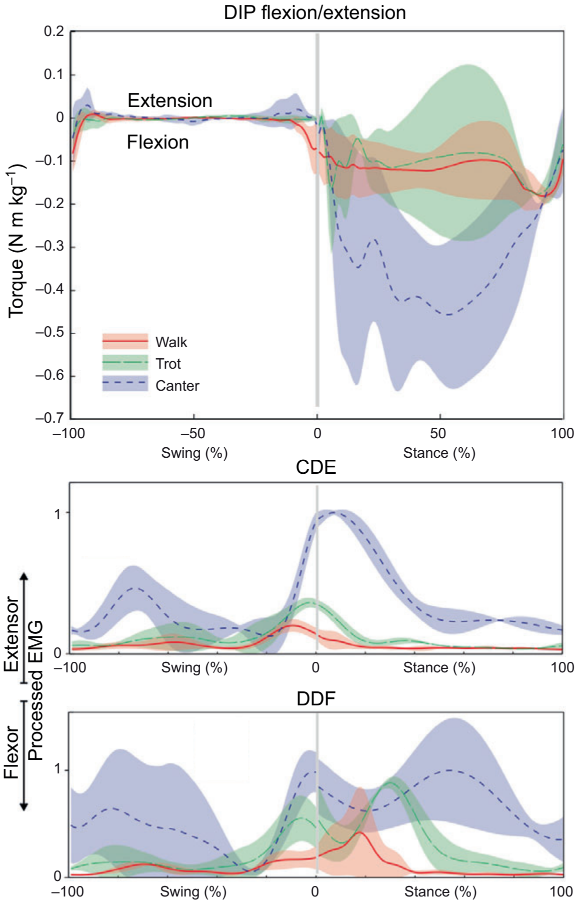


Fig. 4. Flexion–extension torques acting about the distal interphalangeal (DIP) joint during walking, trotting and cantering. Data were normalized temporally to the swing (–99 to 0%) and stance (1 to 100%) phases of each stride. EMG activation patterns for the two muscles that actuate this joint (CDE and the radial head of DDF) are shown in the panels below. Standard deviations are indicated by the shaded areas.

swing; however, during canter, this muscle was intermittently active during early stance.

In the proximal limb the amplitudes of the net joint torques also increased with increasing gait speed. The elbow torque displayed small peaks of flexion in early swing, late swing and late stance, and a major peak in extension in the second quarter of stance (Fig. 7). The shoulder torque peaked in flexion in early stance and in extension in the third quarter of stance (Fig. 8). Shoulder torques during the swing phase were negligible. Adduction–abduction torque at the shoulder was small compared with those acting about the flexion–extension and internal–external rotation axes, and the variation in the mean amplitudes between subjects was large. During stance the torque was consistently in adduction, whereas during swing the magnitude of adduction–abduction torque was small. The internal–external rotation torque peaked modestly in internal rotation during early stance and displayed a major peak in external rotation after mid-stance. Activation peaks in the proximal muscles increased in magnitude with gait speed apart from SUP, which showed the highest activity during the trot. Most proximal muscles showed one or two peaks in early swing and a larger peak of longer duration in early to mid-stance.

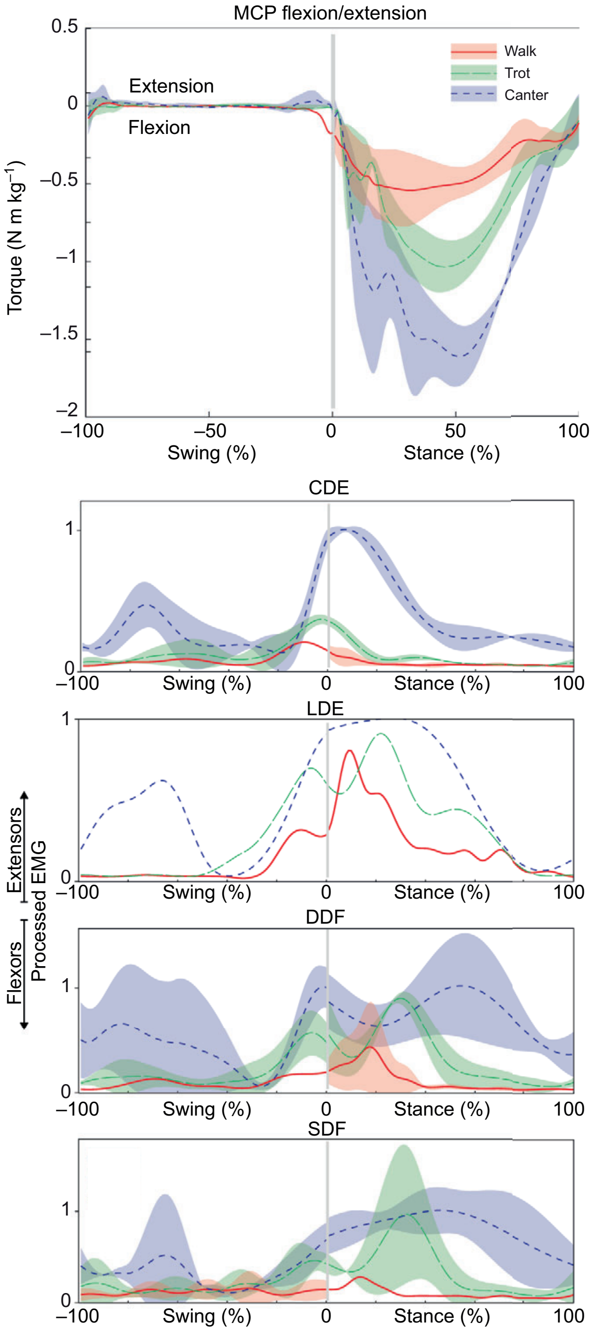


Fig. 5. Flexion–extension torques acting about the metacarpophalangeal (MCP) joint during walking, trotting and cantering. Data were normalized to the swing (–99 to 0%) and stance (1 to 100%) phases of each stride. EMG activation patterns for the two flexor muscles (SDF, DDF) and two extensor muscles (CDE, LDE) are shown in the panels below. Standard deviations are indicated by the shaded areas, except for the LDE, where data were available for only one horse.

DISCUSSION

To our knowledge, this is the first study to report simultaneous measurements of joint kinematics, ground reaction forces and muscle EMG data for a wide range of speeds of equine locomotion.

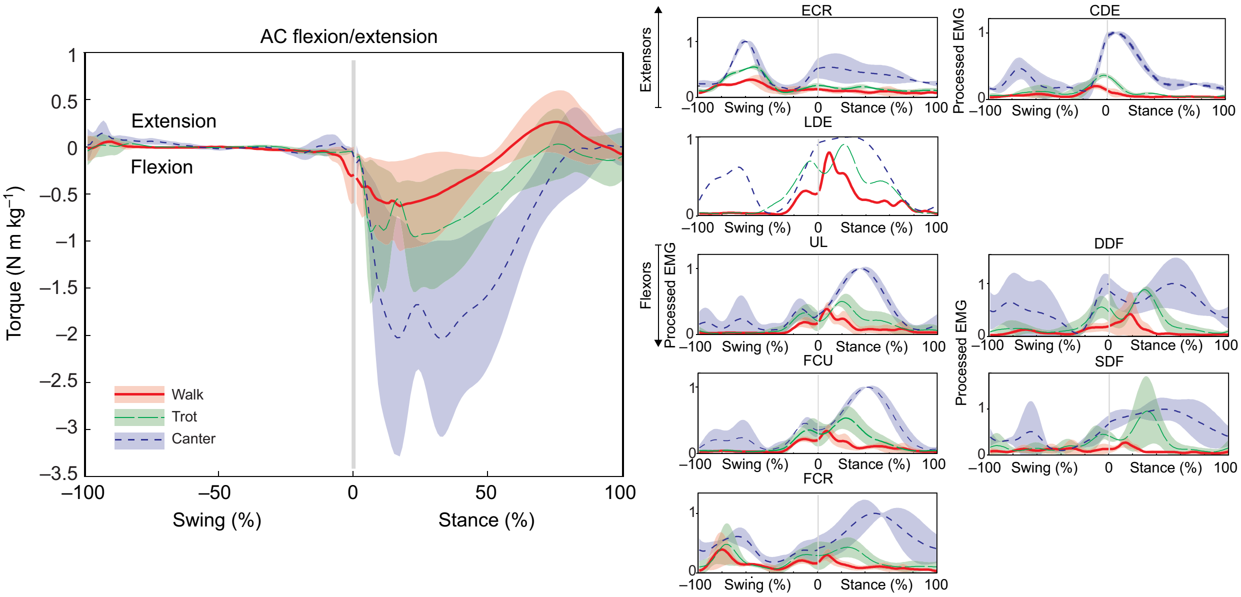


Fig. 6. Flexion–extension torques acting about the antebrachiocarpal (AC) joint during walking, trotting and cantering. Data were normalized to the swing (–99 to 0%) and stance (1 to 100%) phases of each stride. EMG activation patterns for the five flexor and three extensor muscles that actuate this joint (ECR, CDE, LDE, UL, DDF, FCU, SDF and FCR) are shown in the panels to the right. Standard deviations are indicated by the shaded areas, except for the LDE, where data were available for only one horse.

In vivo gait data recorded for walking, trotting and cantering were used to address the following questions. (1) Which forelimb muscles are active under weight-bearing load during stance? (2) Which forelimb muscles are active when the limb is accelerated and repositioned during swing? (3) How do the timing and amplitude of forelimb muscle activity change with gait?

Which forelimb muscles are active under weight-bearing load during stance?

All of the surveyed muscles, except the ECR, were active during stance; specifically, the muscles of the forelimb were activated between late swing and early stance and deactivated only in late stance. This timing of muscle activation did not correspond with the peak joint torques applied to the limb, which typically occurred during mid-stance. While EMG data alone cannot elucidate the force generated by a muscle, we have shown that the flexor and extensor muscles co-contract during stance. Models of the forelimb have generally assumed negligible co-contraction, thereby simplifying muscle force calculations (Meershoek et al., 2001; Merritt et al., 2008; Swanstrom et al., 2005; Wilson et al., 2003). Some co-contraction during stance was predicted in a musculoskeletal model of the distal forelimb (Harrison et al., 2010), but these findings were not directly validated against EMG measurements. Our EMG data indicate that future modelling studies ought to include the effects of muscle co-contraction.

Although co-contraction may reduce the torque-generating capacity of muscles, it can also provide added stability to the joints. When antagonistic muscles develop forces simultaneously, the contribution to the net joint torque that is generated by one muscle (equal to the muscle force multiplied by its moment arm) is mitigated by the torque of its paired antagonist. However, the superposition of agonist and antagonist muscle forces adds to the compressive joint force by pulling together the bones that meet at a joint. Compressive forces can reduce the net shear or tensile loads on the joint that contribute to injury [as has been illustrated at the human shoulder (see Ackland and Pandy, 2009)]. Our results show that muscle co-contraction is most prevalent when the limb makes contact with the ground prior to the development of large joint torques. The presence of muscle co-contraction at this time may serve not only to mitigate the shear loads induced at the forelimb joints by ground impact but also to promote positional control of the limb.

This study reinforces findings from a recent modelling study (Harrison et al., 2010) by demonstrating that the passive stay apparatus generates a large proportion of the joint torques developed during stance, especially during the slower gaits. The net torques developed about the DIP, PIP, MCP and AC joints are generated mainly by the SDF, DDF and suspensory apparatus (Harrison et al., 2010; Meershoek et al., 2001; Swanstrom et al., 2005). Stretching of the accessory ligaments of the SDF and DDF increases tendon force, and therefore limits the need for active muscle contraction. This passive storage of strain energy improves gait efficiency. However, the accessory ligaments are only loaded in mid- to late stance (Harrison et al., 2010; Riemersma et al., 1996). Therefore, activation of the SDF and DDF prior to hoof-strike may contribute to joint compression and stability during ground contact, and in early stance may be necessary to generate the torques we observed about the distal joints prior to loading of the passive structures. The SDF and DDF muscles were active in mid-stance during canter, which, in agreement with our previous findings (Harrison et al., 2010), suggests that passive force generation alone is not sufficient to develop the high joint torques generated during faster gaits. Pfau and colleagues suggested that elastic energy storage in the limbs is small compared with total mechanical energy expenditure during galloping (Pfau et al., 2006), implying that muscle work is dominant at the fastest gaits. Work done on the centre of mass and limbs was most significant during the stance phase of gallop, and was approximately an order of magnitude larger than the elastic energy

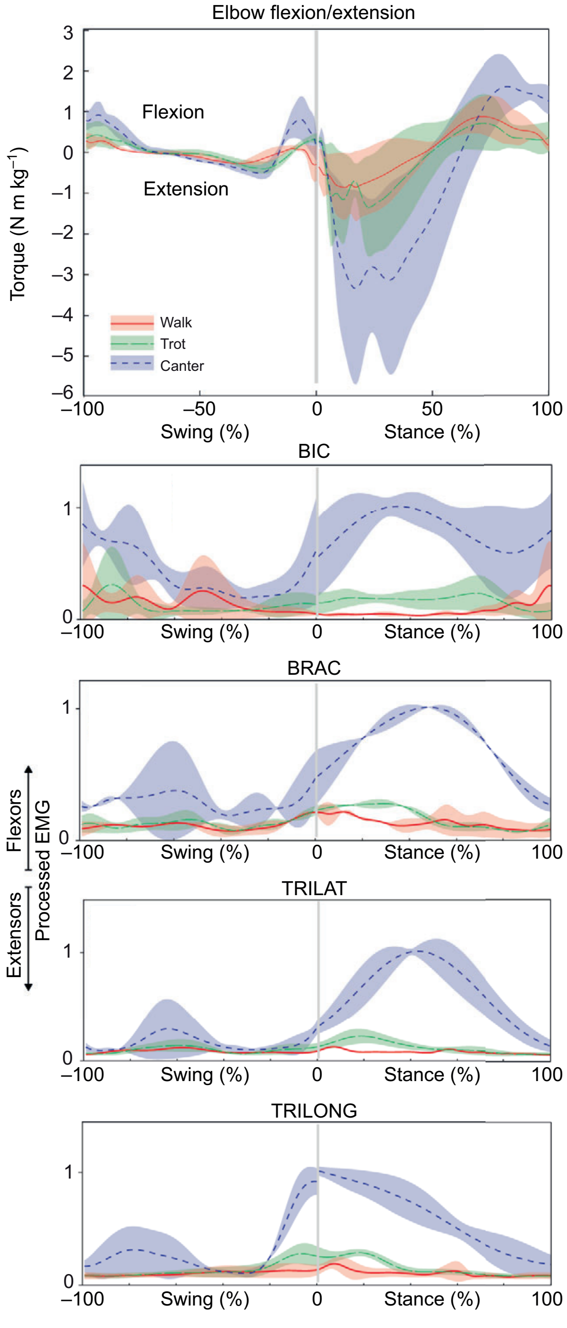


Fig. 7. Flexion–extension torques calculated for the elbow joint during walking, trotting and cantering. Data are normalized to the swing (–99 to 0%) and stance (1 to 100%) phases of each stride. EMG activation patterns for two flexor and two extensor muscles that actuate this joint (BIC, BRAC, TRILAT and TRILONG) are shown in the panels below. Note that all of the muscles shown in Fig. 6, except LDE, also actuate the elbow. Standard deviations are indicated by the shaded areas.

stored by passive stretching of the muscles and tendons. However, a whole-body musculoskeletal model is needed to determine the relative contributions of muscle work and elastic energy storage to the overall mechanical energy of the body during gait. Analogous to the behaviour of the SDF and DDF muscles, the human gastrocnemius muscle also activates prior to heel strike in activities where passive strain energy utilization is significant; for example, in hopping (Funase et al., 2001) and stair descent (Spanjaard et al., 2007), but not in stair ascent (Spanjaard et al., 2007) or walking (Murray et al., 1984), where passive strain energy utilization is presumably less important.

Positional control of the joints may be another reason for muscle co-contraction in late swing and early stance. Limb protraction in early swing is largely a passive process (Wilson et al., 2003), but in late swing the limb must decelerate and be positioned accurately prior to impact, which may not be easily achieved passively. Following impact, the carpal and MCP joints must maintain extension to allow the development of passive loads in the tendons of SDF, DDF and the suspensory apparatus. The CDE and LDE, the only muscles that can induce extensor torques about the carpus and MCP joints, were active in late stance and early swing (Figs 3–5). The absence of an extensor moment during early stance would allow a joint to flex inappropriately. This occurs at the MCP joint when the CDE and LDE tendons are severed (Mespoulhès-Rivière et al., 2008). Animals with severed digital extensor tendons can learn to accelerate their limbs to avoid flexion early in stance (Mespoulhès-Rivière et al., 2008), but it is clearly more advantageous for the animal to activate the digital extensors and forcibly extend the limb. Thus, co-contraction of the muscles of the distal limb may position the limb in late swing, stabilize the limb at hoof-strike, and prevent flexion of the MCP and carpal joints in early stance.

Muscle activation patterns of the shoulder and elbow are complex and few modelling studies exist to assist in the interpretation of our results. We found that co-contraction is prevalent at the elbow and shoulder, suggesting that stability and positional control are conferred by the muscles of these joints; notably, there are no substantial collateral ligaments at the shoulder, so this joint must be stabilized by muscle action. It is not yet known how the muscles of the shoulder actuate the three rotational degrees of freedom of this joint. The activation patterns of the deep and medial muscles of the proximal limb have yet to be measured, and further work is needed to better understand how the shoulder and elbow muscles coordinate joint motion. The proximal limb is further complicated by the behaviour of the significant biceps tendon (Nevens et al., 2005; Wilson et al., 2003), which links the flexion–extension rotations of the shoulder and elbow joints when the tendon is placed in tension.

Which forelimb muscles are active when the limb is accelerated and repositioned during swing?

The ECR is the only intrinsic forelimb muscle that is clearly activated from early to mid-swing (Fig. 3). This finding is consistent with the small magnitudes of torques exerted about the joints during swing. The ECR is small in size compared with the total muscle mass of the forelimb (Brown et al., 2003; Payne et al., 2004; Watson and Wilson, 2007), suggesting that protraction and forward acceleration of the distal forelimb are largely achieved through the recovery of elastic strain energy stored in the tendons and ligaments. Using a musculoskeletal model of the distal forelimb, we (Harrison et al., 2010) predicted that the elastic energy stored in these structures is at least 0.03 $\mathrm{J\,kg^{-1}}$ of body mass prior to limb protraction. A passive means of limb protraction has been suggested by others (Lichtwark et al., 2009; Wilson et al., 2003) based on data obtained for walking and trotting. We note here that the BIC shows intermittent activity during the swing phase of cantering, which has not previously been reported. The BIC has an insertion *via* the lacertus fibrosus on the

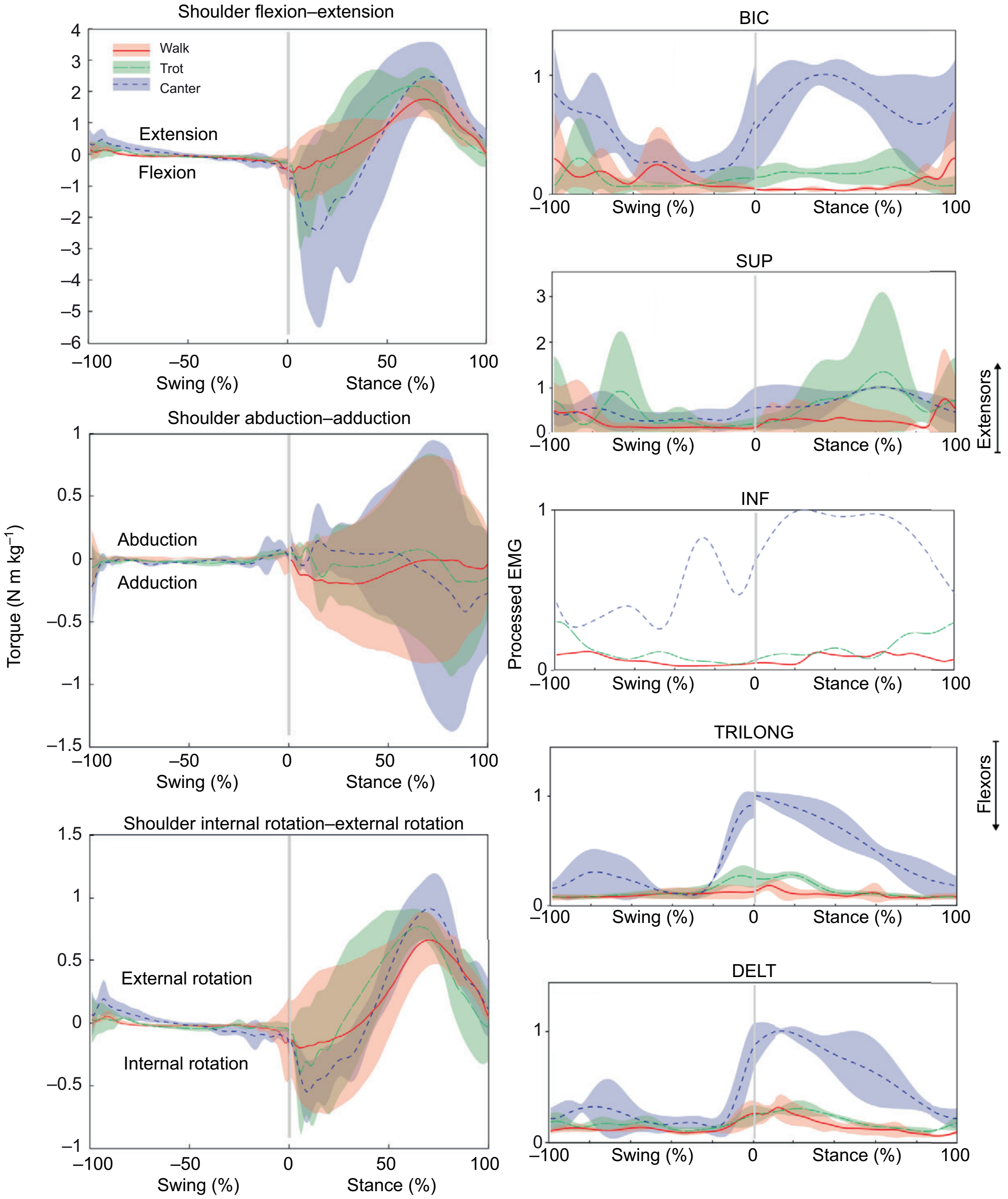


Fig. 8. Flexion–extension, abduction–adduction and internal rotation–external rotation torques calculated for the shoulder joint during walking, trotting and cantering. Data were normalized to the swing (–99 to 0%) and stance (1 to 100%) phases of each stride. EMG activation patterns for five of the muscles that actuate this joint (BIC, SUP, INF, TRILONG and DELT) are shown in the panels on the right. Standard deviations are indicated by the shaded areas, except for the INF, where data were available for only one horse.

external fascia of the ECR, and thus can contribute to carpal extension. We also note that a number of the distal muscles display a small and variable amount of co-contraction in early swing (Figs 4–6), which may be needed for positional control of the limb once the strain energy stored during stance has been recovered. Because protraction of the forelimb requires a considerable amount of mechanical work (Wilson et al., 2003), locomotor efficiency may be enhanced by the recovery of stored elastic energy. However, this feature may place an upper limit on performance: if protraction is predominantly achieved through this passive mechanism, then the maximum speed of protraction may be limited by the properties of the tendons. Further work is needed to confirm this postulation.

If protraction is achieved primarily by passive means (apart from any work done by the trunk muscles), then why does the ECR activate in early swing? Nevens and colleagues showed that the BIC tendon links the motion of the shoulder and elbow joints (Nevens et al., 2005); specifically, shoulder flexion will induce elbow flexion in the absence of overriding external forces. The lacertus fibrosus is a fibrous link between the BIC tendon and the fascia of the ECR, which can transmit a portion of the load in the BIC tendon to the carpus. Therefore, it is possible for the carpus to be extended passively when the shoulder is flexed. However, because the shoulder is extended in early swing, the load in the lacertus fibrosus may be significantly diminished. Thus, active contraction of the ECR may be needed to control the extent of carpal flexion during early swing and to also extend this joint in late swing.

How do the timing and amplitude of forelimb muscle activity change with gait?

For many muscles, EMG activity spanned larger portions of the stance phase as gait speed increased. However, because the leg spent less time in contact with the ground during the faster gaits, the absolute time during which muscles were activated actually decreased as speed increased. The onset timing of most muscles did not vary significantly with gait, but the deactivation timing of many muscles was delayed (as a percentage of stance) as gait speed increased. This suggests that muscles may play similar roles for each gait in late swing to early stance and that the functional roles of muscles later in stance may vary with the speed of gait.

In general, the amplitudes of the muscle EMG signals were statistically different for walking, trotting and cantering (Table 1). The SDF and FCR were the only muscles that did not show significant differences between gaits. It is not surprising that EMG amplitudes increase with gait speed given that whole-body metabolic energy consumption increases significantly when the gait changes from walking to trotting and from trotting to cantering (Minetti et al., 1999). It is worth noting that the bouncing gaits (i.e. trotting and cantering) enable the animal to utilize a greater amount of strain energy stored in the tendons of the forelimb compared with walking (Biewener, 1998; Harrison et al., 2010), Thus, both the active structures (muscle contractile elements) and passive structures (tendons and ligaments) are likely to perform more mechanical work in cantering and trotting than in walking.

The time series traces of muscle activation show further evidence of a difference in the levels of muscle utilization between canter and the slower gaits. The majority of the muscles show peaks centred on hoof-strike for walking and trotting, but two different peaks are usually evident for cantering, specifically during mid-stance and in early swing. As noted previously, it is likely that muscles function during walking and trotting primarily to reposition and stabilize the limb before the stay apparatus is loaded, in contrast to the canter where muscle action complements the passive forces generated by the stay apparatus to generate the much larger joint torques needed to maintain steady locomotion. The larger magnitudes of EMG activation during canter may also suggest a greater need to stabilize the limb during locomotion.

Limitations of the findings

There are a number of limitations associated with the present study. First, not all forelimb muscles were surveyed by EMG because of the difficulty in accessing some of the muscles, most notably the medial muscles of the shoulder such as the teres major and subscapularis. Measurement of the activity of these muscles may better elucidate the roles of the proximal muscles of the forelimb. Second, only three horses were used in the gait experiments. Whilst the error bars associated with some of the data appear to be relatively large, the regularity of most joint torque and EMG results (e.g. Figs 5, 6) suggests that our findings may apply to the broad equine population. Third, only one speed was employed for each of the three gaits. Dutto and colleagues showed that the magnitudes of torques and power developed about the joints vary considerably with the speed of trotting (Dutto et al., 2006). It is therefore likely that muscular activity also varies with speed for each gait. Fourth, EMG signals were not normalized to a maximum voluntary contraction, as maximum isometric contractions cannot easily be elicited in live horses. Instead, results were normalized to the most demanding task investigated in this study: treadmill cantering. Nevertheless, the peak EMG amplitudes appear to correlate between animals across the different gaits (Figs 4–8). Fifth, a number of muscles have multiple sub-regions as well as variable morphologies within each muscle sub-region. For example, the FCU has ulnar and humeral heads, while the DDF has ulnar, humeral and radial heads. Within the humeral head of the DDF, there are sections with long muscle fibres and others with very short muscle fibres (Brown et al., 2003). There is therefore the potential within each muscle for independent activation of muscle fibre regions. Sixth, cross-talk caused by skin and electrode movement during locomotion may have affected our measurements of muscle EMG activity, particularly at the canter. Finally, EMG measurements can only give an indication of muscle activity local to the electrode, which may not reflect the averaged activity of the entire muscle. This effect is likely to be significant when fine-wire electrodes were used to record activity from the BIC, SUP, SDF and DDF. Further studies may show different activity profiles if the EMG electrodes are placed differently.

Comparison with literature studies

Jansen and colleagues presented EMG data for the ECR, CDE, FCU, FCR and UL of ponies during walking (Jansen et al., 1992). Our results are consistent with their findings for the carpal flexors (FCU, FCR and UL) and the CDE: muscle activity begins in late swing and concludes in early stance. However, Jansen and colleagues reported two periods of activity for the ECR: one in early swing and the other in late swing (Jansen et al., 1992). Our results showed the same timing of ECR activity in early swing, but we did not record significant activity in late swing, although a small peak in the EMG activity of the ECR was evident at this time (Fig. 6).

Similar comparisons are available for the proximal muscles of the forelimb. Tokuriki and colleagues presented muscle activation timings relative to the stance and swing phases of gait for the BIC, BRAC, TRILONG and TRILAT for overground walking, trotting and cantering (Tokuriki et al., 1989). The gait speeds adopted in their experiments (i.e. walking, 1.42–1.63 $\mathrm{m\,s^{-1}}$; trotting, 3.32–4.03 $\mathrm{m\,s^{-1}}$; cantering, 4.93–5.88 $\mathrm{m\,s^{-1}}$) were similar to those used in the present study. These researchers found that the BIC was active during mid-stance regardless of the gait, and that the BRAC, TRILONG and TRILAT activated prior to hoof-strike and remained active during the first half of stance. Our findings are consistent with these results (Figs 3, 7, 8), except that the BIC was found to be active either in early stance or in late swing (Fig. 3). Because EMG activity of this muscle was measured using fine-wire electrodes, this disparity may be due to differences in electrode placement. Other studies have shown that the TRILAT activates during late swing and deactivates anywhere from early stance to mid-stance (Hoyt et al., 2005; Robert et al., 2002). The SUP and INF have previously been shown to activate from early to mid-stance and to deactivate in late stance during walking, trotting and cantering (Aoki et al., 1984). Again, our findings are in general agreement with these results (Figs 3, 7, 8), although our EMG measurements for the INF (recorded from one horse only) varied between overground and treadmill gait.

Despite obvious differences in anatomy, size and muscle morphology, similar observations have been made for the forelimbs of other quadrupeds, such as cats (English, 1978) and dogs (Tokuriki, 1973a; Tokuriki, 1973b; Tokuriki, 1974) during walking, trotting and galloping. Using similar procedures to those employed in the present study, English proposed that the muscles of the feline shoulder function to provide stability of this joint (English, 1978). Furthermore, the muscles of the distal limb were primarily responsible for providing support during early stance and facilitating strain energy utilization in the period from late stance to early swing. In the canine, Tokuriki observed co-contraction between the TRILONG, a shoulder flexor and elbow extensor, the BIC, a shoulder extensor and elbow flexor, and the BRAC, an elbow flexor (Tokuriki, 1973a; Tokuriki, 1973b; Tokuriki, 1974). Tokuriki suggested that the BIC works synergistically with the TRILONG to achieve stability of the elbow, whereas the BRAC works against the TRILONG to achieve elbow flexion. Similar to our results for the distal muscles of the equine forelimb, Tokuriki found that the canine carpal muscles, such as the ECR, FCR and FCU, are activated prior to foot strike to decelerate the paw and stabilize the carpus prior to ground contact; and that the extensor muscles, such as the ECR, are activated in early swing to achieve limb protraction.

CONCLUSIONS

Widespread co-contraction of the forelimb muscles prior to hoof impact was observed during walking, trotting and cantering. As co-contraction reduces the net torque-generating capacity of the musculature, other outcomes such as joint stability (through increased compressive forces) and positional control of the limb may result. The ECR is the only muscle to show a significant amount of activation during swing, consistent with limb protraction being achieved primarily through the recovery of elastic energy stored in the passive structures (tendons and ligaments) during stance. The coordination of the proximal limb musculature is complex, and further work is needed to correlate muscle activity with the net torques developed about the elbow and shoulder joints. A more detailed investigation of the forelimb musculature is needed to quantify the functional roles of these muscles during gait. Musculoskeletal modelling of the entire forelimb, especially when coupled with induced acceleration analyses (e.g. Pandy and Zajac, 1991; Anderson and Pandy, 2003; Yu et al., 2011), has the potential to further enhance our understanding of muscle function during equine locomotion.

LIST OF ABBREVIATIONS

BIC	biceps muscle
BRAC	brachialis muscle
CDE	common digital extensor muscle
DDF	deep digital flexor muscle
DELT	deltoideus muscle
ECR	extensor carpi radialis muscle
FCR	flexor carpi radialis muscle
FCU	flexor carpi ulnaris muscle
INF	infraspinatus muscle
LDE	lateral digital extensor muscle
SDF	superficial digital flexor muscle
SUP	supraspinatus muscle
TRILAT	lateral head of triceps brachii muscle
TRILONG	long head of triceps brachii muscle
UL	ulnaris lateralis muscle

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