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Comparative need for spinal stabilisation between quadrupedal and bipedal locomotion

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Abstract

Sheep are commonly used as an animal model for the human lumbar spine, but similarities in trunk muscle activity of humans and sheep during functional tasks such as locomotion have not been investigated. Therefore, the aim of the study was to evaluate trunk and pelvic limb muscle activity during walk and run/trot gaits in man and sheep. Electromyography of the muscles erector spinae (ES), gluteus maximus (GM), rectus abdominis (RA), obliquus externus (OE) and obliquus internus (OI) were collected in 24 humans and 15 sheep during treadmill walk and run/trot. Kinematic data from the tarsus (human) or metatarsus (sheep) were obtained to define motion cycles and determine stride characteristics. Mean and range of normalised muscle activity were calculated. In phasic muscles, the occurrence of the maximum was reported. At walk, mean activity was greater in humans for all three abdominal muscles (all $p < 0.01$). At the run/trot, mean activity of ES was significantly greater in sheep ($p < 0.05$) and mean activity of right OI was greater in humans ($p = 0.016$). At the walk, range of ES activity was significantly greater in humans compared to sheep ($p < 0.01$), but significantly smaller in humans in RA and right OE ($p < 0.05$). At the run/trot, range of activity was significantly greater in humans compared to sheep in all muscles ($p < 0.05$), except right RA and OI. Compared to humans, occurrence of maximum activity was earlier in sheep for ES right during walk ($p = 0.005$), and later for GM during walk and run/trot ($p < 0.001$). The results suggest that numerous differences in trunk muscle activity exist between man and sheep during treadmill walk and run/trot, and that these differences are muscle- and gait-specific. Trunk muscle activity should therefore be regarded as species-specific which suggests differences in stabilization strategies. This should be taken into consideration when extrapolating animal model findings to the human spine.

Keywords

Thoracolumbar spine; Electromyography; Human; Sheep; Gait

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Conflicts of interest

The authors do not have any conflicts of interest to declare.

Introduction

Quality of life and the ability to perform activities of daily living are commonly investigated in patients with low back pain (i.e. Lidgren 2003, Nolet *et al.*, 2014), although functionality is not evaluated in studies assessing surgical interventions for the lumbar spine using animal models. Rather, animal studies are generally limited to *in vitro* investigations, and findings extrapolated to predict clinical outcomes in a patient population. Currently very little is known about the (dis)similarities in biomechanical behaviour of healthy human and animal spines *in vivo*, and obtaining such information during functional tasks i.e. locomotion could identify to what extent animal to human spine translation is appropriate.

Human walk consists of a combination of double and single leg support phases without a suspension phase, whereas during running, a bilateral leg suspension phase exists at the beginning and end of the swing phase (Novacheck, 1998). Despite the fundamental differences between walking and running mechanics, thoracolumbar spine kinematics during walking and running are very similar, which is probably due to the diagonally reciprocal relationship between upper and lower limb movement evident in both gaits. Terrestrial mammals display a much greater range of gaits compared to man, not limited to walk, trot, run (canter) and gallop. During quadrupedal walk, all four legs move separately with a large overlap in stance phase times without a resultant suspension phase. The quadrupedal trot however is a symmetrical, diagonal gait with suspension phase, where a hindlimb and contralateral forelimb are advanced simultaneously and a suspension phase exists (Starke *et al.*, 2009). The diagonal nature of quadrupedal trotting locomotion may therefore be most similar to the diagonal reciprocal arm swing to leg placement pattern in human locomotion.

Differences in spinal orientation and alignment between humans (vertical orientation with a lumbar lordosis) and quadrupeds (horizontal orientation and lumbar kyphosis) are likely to result in differences in motor control strategies and muscle activation patterns. The human spine experiences a large amount of axial compression (Boszczyk *et al.*, 2001) and due its vertical alignment, requires muscular stabilization against multidirectional forces from the sagittal, frontal and transverse planes. Although the quadrupedal spine experiences considerable axial loading to oppose bending moments (evidenced by vertebral trabecular bone architecture), passive and active structures are also required to counteract moments in particular the ventral trunk muscles (Smit, 2002). Therefore, trunk muscle activity may vary considerably between bipeds and quadrupeds.

Trunk muscle activity has been evaluated during locomotion in some quadrupeds including the horse (Licka *et al.*, 2004, Licka *et al.*, 2009, Zsoldos *et al.*, 2010), dog (Fischer *et al.*, 2013), cat (Koehler *et al.*, 1984) and rat (Gramsbergen *et al.*, 1999), however no data on trunk muscle activity of the ovine is available. This constitutes a void between the detailed knowledge of human and ovine spinal function which is especially pertinent, as small ruminants and in particular sheep are a commonly used animal model for the lumbar spine due to similarities in skeletal anatomy (Wilke *et al.*, 1997, Sheng *et al.*, 2010). Therefore, the purpose of the present *in vivo* study was to compare the activity of several trunk muscles in man and sheep during walking and running/trotting gaits. It was hypothesized that 1. Abdominal muscle activity in sheep is higher and less phasic compared to that in man, 2.

Erector spinae activity in man is higher compared to sheep due to the need to maintain an upright posture, but similarities in phasic activity will be found, 3. Sheep will require greater flexor muscle activity relative to the extensor muscle activity in comparison to man, 4. Phasic activity of a locomotor muscle of the pelvic limb (human lower limb; ovine hind limb) is similar in man and sheep, and 5. A greater number of differences in muscle activity between the species will be found for the walk rather than the run/trot, due to a greater difference in inter-limb coordination between the species during running/trotting.

Materials and Methods

Study population

Twenty-four healthy male and female participants were recruited. Inclusion criteria were age of 18-25 years (young group, n=12) or 45-60 years (mature group, n=12) and a Body Mass Index (BMI) of 25 or under. Participants were excluded if they had current or a history of low back pain in the last 12 months, previous spinal surgery or fracture, neurological or orthopaedic disease, open abdominal surgery, or were not deemed eligible to undergo magnetic resonance imaging (MRI) as the present study was part of a larger investigation. All participants received an information sheet and gave written informed consent. Ethical approval for the human participants (referred to as humans from here on) was granted by the Medical University of Vienna Ethics Committee (1609/2012). For the ovine aspect of the study, 20 male and female Austrian Mountain sheep were allocated to an immature group (6-9 months, n=6), young group (1-3 years, n=5) or a mature group (6-9 years, n=4). Sheep were assessed by an experienced orthopaedic veterinarian and were deemed free from spinal or neurological disorders. Ethical approval for the sheep was granted from the Austrian Federal Ministry of Science and Research (13/10/97/2011). All sheep were accustomed to wearing a halter and trained to walk and trot in hand.

Data collection

Age, height, and body mass were recorded for the humans. In sheep, height at the withers and body mass were obtained. In humans, reflective markers attached to the skin overlying the bony landmarks of the left and right malleoli were included for data analysis. In sheep, markers were attached laterally over all fetlock joints. Three-dimensional kinematic data were collected using 10 high speed cameras (Eagle Digital Real Time System, Motion Analysis Corp., Santa Rosa, USA) recording at 120Hz using kinematic software (Cortex 3.6.1, Motion Analysis Corp., Santa Rosa, USA).

In humans, the site of EMG electrode placement was prepared by shaving where necessary, followed by gentle abrasion with sand paper and cleaning with alcohol. The sheep were shorn, shaved, and the skin cleaned with alcohol followed by ether to degrease the skin. Surface electromyography (sEMG) electrodes (Delsys Trigno, Boston, USA) were attached to the humans over the left and right sides of the following muscles: gluteus maximus (GM) at the mid-point of an imaginary line between the sacrum and greater trochanter (SENIAM Surface Electromyography for the Non-Invasive Assessment of Muscles guidelines), rectus abdominis (RA) 2cm above the umbilicus and 1cm lateral to midline (Beith et al 2001), external obliquus (EO) midway between the ASIS and ribcage (Ekstrom et al 2007), and

internal obliquus (IO) 2cm medially in a horizontal plane from the ASIS (Beith et al 2001). For erector spinae (ES) a location 2 fingers width laterally from the thoraco-lumbar junction midline was chosen; this is different from the recommended 2 fingers width laterally from the spinous process of the first lumbar vertebrae (SENIAM), as contact loss was observed at that location in pilot studies. In sheep, the comparable muscles longissimus dorsi and gluteus medius were chosen and comparable locations for EMG electrode placements were selected, as no guidelines or previous sEMG studies exist in sheep. To facilitate inter-species comparison, the sheep longissimus dorsi and gluteus medius are referred to as ES and GM respectively. For all participants, sEMG electrodes and kinematic markers were attached with non-irritant adhesive tape, and an additional drop of glue was used in sheep. Raw sEMG data were sampled at 1200Hz and transmitted via telemetry.

Measurement protocol

An equine treadmill (Kagra, Graber AG, Switzerland) was used for the humans and sheep. All humans had previous treadmill experience and were allowed time to become accustomed to the treadmill used in the present study. A safety rope was attached to the left wrist of the humans which did not interfere with upper body movement and only served to ensure the treadmill would stop if the rope was pulled. The sheep had previously been trained to walk and trot on the treadmill (Valentin *et al.*, 2014). A sheep was considered accustomed to the treadmill when they were able to walk and trot calmly behind a handler for several minutes. The number of training sessions required for each sheep ranged from four to 14 sessions (mean 6.73 ± 3.28). The humans walked and ran at their self-selected speed. A suitable walk and trot speed for each sheep was selected from observation (i.e. sheep not falling behind or rushing forwards, and showing the typical footfall pattern for walk and trot). Kinematic and EMG data were collected synchronously for three sets of 10 seconds for both walk and run/trot.

Data analysis

Kinematic data were smoothed with a 15Hz low pass Butterworth filter. Raw sEMG signals were inspected for obvious contact loss, and these muscles excluded for that trial. From the three trials, the trial which visually showed the most consistent locomotion (i.e. no stumbling or obvious tempo changes in the sheep) and where least EMG contact loss was observed was selected for further analysis. Raw sEMG data were full-wave rectified, mean-offset, re-sampled to match kinematic data sampling and a 4th order 20Hz low pass Butterworth filter applied to obtain linear envelopes using scripts written in MATLAB (2008b). Anterior-posterior displacement of the right malleolus (humans) or right hind fetlock (sheep) was used to identify right lower/pelvic limb stance phase. A motion cycle (MC) was defined to start with the onset of stance phase, i.e. the time when the right malleolus/hind fetlock reached the most forward position. The end of each motion cycle was therefore the last frame prior to the onset of the next stance phase as defined above. Each MC was then normalised to 100%. Stance duration of the right pelvic limb was calculated. The peak EMG amplitude (maximally observed EMG, MOE [mV]) of each muscle was identified from all MCs for walk and run/trot separately. EMG values were then normalised to the MOE of the respective muscle for each gait and reported as percentage (%MOE). The linear envelope of muscle activity throughout each MC is therefore presented in %MOE.

This dynamic peak normalisation method was used as maximum voluntary contractions (MVC) cannot be obtained in sheep.

The average of the normalised linear envelopes of all the MCs of each muscle was obtained for each human participant and sheep at walk and run/trot. From these, the mean %MOE and range %MOE were determined. The mean %MOE was calculated over the 100 data points of the MC. The range of %MOE was calculated by subtracting the minimum %MOE from the maximum %MOE. The flexor-extensor difference (FED) was calculated from the mean %MOE values for each individual at both gaits as follows:

$$((\text{RA left} + \text{RA right} + \text{OE left} + \text{OE right} + \text{OI left} + \text{OI right}) / 6) - ((\text{ES left} + \text{ES right}) / 2)$$

If a muscle was excluded due to contact loss, the data from that muscle was omitted from the equation and the value in the denominator adjusted accordingly. FED is positive with greater relative flexor muscle activity and negative with greater relative extensor muscle activity.

Within each MC the occurrence of the maximum %MOE (percentage of the MC where the maximum %MOE was identified) was calculated for each muscle. Within each muscle and individual, muscles were described as phasic using the following criteria: (1) a range of >15 %MOE in >50% of the MCs, and (2) a standard deviation of <25% across the MCs for the occurrence of the maximum %MOE. A muscle was then globally defined as phasic when >50% of the individuals in each species with measurable sEMG of a muscle met criteria (1) and (2), and the standard deviation of the occurrence of the maximum %MOE was <25% across those individuals. In summary, this approach was used to describe a muscle as phasic when it showed a definite burst in activity, the maximum of which occurred at a consistent location across the study population. Muscles which did not meet the criteria would be considered tonic in nature or too variable within and/or between subjects to be described as phasic.

Statistical Analysis

Normal distribution of the data was investigated using a Shapiro-Wilk test and by assessment of the frequency and Q-Q plots. Height and body mass were compared between age groups for each species using an independent t-test (humans) and one-way ANOVA with Bonferroni post-hoc comparisons (sheep). As a large proportion of the sEMG data was not normally distributed and due to too little data from trotting sheep being available, a two-way ANOVA with species and age as variables could not be performed. Instead, age groups for both species were combined and an independent t-test for normally distributed data and a Mann-Whitney test for non-normally distributed data were used to compare the mean and the range of normalised muscle activity, and FED between sheep and humans at walk and trot separately. Therefore, a combination of parametric and non-parametric testing was used for any one parameter as some muscles were normally distributed and others were not (i.e. for mean %MOE, some muscles were statistically analysed based on the group mean of the individual mean %MOE values [parametric], whereas other muscles were statistically analysed based on the group median of the individual mean %MOE values [non-parametric]). To investigate the influence of age, Pearsons or Spearmans correlation

coefficients were calculated on the mean and range %MOE with age within each species and gait separately. Descriptive statistics on the occurrence of the maximum %MOE for the muscles classed as phasic were calculated for humans and sheep. In cases where a muscle was defined as phasic in both species, inter-species comparisons were performed using an independent t-test or Mann-Whitney test.

Results

Three sheep were excluded due to pregnancy, and two sheep were excluded during the treadmill training phase as they refused to walk or trot on the treadmill after many attempts over several days whilst being tempted by food. Trot data from a further five sheep were excluded as these sheep did not display a correct trot footfall pattern. EMG data from one mature male participant during running was missing due to a technical error. Therefore 24 humans completed the study (data available: walk $n=24$, run $n=23$) and 15 sheep completed the study (data available: walk $n=15$, trot $n=10$).

Mean age of the humans was 22.4 years (± 1.24) in the young group and 50.2 years (± 4.95) in the mature group. There were no significant differences for height and body mass between the human age groups. Combined groups mean height and body mass of the humans was 1.74 m (± 0.11) and 68.85 kg (± 10.87). Mean height and body mass of the sheep was 0.71 m (± 0.04) and 50.33 kg (± 5.59) in the immature group, 0.87 m (± 0.04) and 72.2 kg (± 7.29) in the young group, and 0.91 m (± 0.01) and 99.0 kg (± 20.71) in the mature group. Immature sheep were significantly smaller in height compared to young and mature sheep (both $p<0.05$). Significant differences in body mass were found between all age groups of sheep (all $p<0.05$).

Walking and running/trotting speeds between the humans and sheep were not significantly different. Details of the stride lengths and heights are shown in Table 1 and 2. Stance duration of the right pelvic limb was significantly shorter in the humans compared to the sheep at the walk (humans: $61.23 \pm 1.44\%$; sheep: $64.35 \pm 1.14\%$, $p<0.001$), but were similar for run/trot (humans: $55.06 \pm 2.01\%$; sheep: $56.32 \pm 1.02\%$, $p=0.064$).

The mean linear envelopes of muscle activity of the humans and sheep are shown in Figure 1. The mean %MOE and range %MOE are displayed in Figures 2 and 3. The occurrence (%MC) of the maximum %MOE for the muscles classified as phasic is shown in table 3.

Relative mean FED was significantly different between humans and sheep at both gaits, with sheep showing greater relative extensor activity (walk: humans = 7.78 ± 7.73 , sheep = -2.14 ± 11.79 , $p=0.003$; run / trot: human = 4.97 ± 8.68 , sheep = -6.52 ± 9.28 , $p=0.002$). The linear envelope of ES displayed a singular burst in all sheep and in the majority of humans ($n=18/24$). In the remaining human ES traces, a double-burst (large and small, or both of equal amplitude) was noted.

Age was significantly correlated to mean %MOE of ES left ($r=0.465$, $p=0.022$) and RA right ($r=0.517$, $p=0.010$) at the walk, and to ES left ($r=0.624$, $p=0.003$) and OE left ($r=0.433$, $p=0.044$) at the run in humans. In sheep, age was only correlated to mean %MOE of ES right ($r=0.578$, $p=0.024$) at the walk. In the humans, only the range of %MOE of RA right at

walk was significantly correlated with age ($r=-0.539$, $p=0.007$). In sheep at the walk, range of %MOE of GM right was significantly correlated with age ($r=0.575$, $p=0.025$), and at the trot, right RA and left OE were significantly positively correlated with age (RA right $r=0.822$, $p=0.007$, OE left $r=0.75$, $p=0.049$).

Discussion

The results of this study should be considered in light of several study limitations. Normalization of EMG data is crucial in obtaining meaningful information on the relative activity of a muscle (Hsu *et al.*, 2006). Furthermore, in order to reduce the likely effects of differences in skin properties and subcutaneous fat between humans and sheep, EMG normalization is vital to reduce these errors and allow meaningful comparisons between species to be made. An isometric maximum voluntary contraction (MVC) is the most commonly accepted method of EMG normalization in man (Burden, 2010). As it is not possible to apply this method in animal studies, the results of this study cannot be directly compared to studies using MVC normalization methods. Besides animals, there are other population groups where MVCs may not be possible or less reliable, such as patients with low back pain (Dankaerts *et al.*, 2004, Dufour *et al.*, 2013) or neurological conditions, or in the elderly (Hsu *et al.*, 2006). Studies investigating such populations have resorted to using a submaximal voluntary contraction (Dankaerts *et al.*, 2004) or using non-standardized isometric contractions at maximum effort (Hsu *et al.*, 2006). As gait was compared between species in the present study, it was felt that the task-specific maximal peak method of normalization used here was the most appropriate approach; it also preserved a maximum number of participants for each gait. Guidelines are available by SENIAM for sEMG placement in man, but no guidelines or previous studies are available on sEMG placement in sheep. This would be required to create more reliable and comparable EMG data in this species. As a result, anatomically comparable sites were selected and tested in pilot studies (unpublished). Lastly, the amount of skin displacement during functional tasks in sheep have not been quantified which is recommended for future studies, as skin displacement can influence signal output due to a relative shift in location of the motor points from the EMG electrode (Hermens *et al.*, 2000).

In both species, the GM muscle showed similar phasicity in both gaits, suggesting a similar locomotor function of this muscle. Furthermore, no differences in mean or range of activity were found for this muscle between the species during walk. However, maximum amplitude was reached later in the MC in sheep at the walk, which is likely to be due to the difference in footfall pattern between bipeds and quadrupeds. Interestingly though, a significantly smaller range of activity was found in this muscle for sheep in trot compared to the humans during running. The reason for this may be that the thoracic limbs contribute relatively more to propulsion during sheep trot than walk. This would require further investigation of front and hind limb muscles to explore the relative contribution of muscles to the combined task of propulsion at faster gaits.

Trunk muscle use and thoracolumbar motion during walking and running are intricately linked in all species, and therefore in-depth interpretation of the differences in sEMG activities between two species also requires adequate information on the differences in the

thoracolumbar motion. This was not quantified, however a difference between bi- and quadrupedal thoracolumbar motion is expected due to the different functions of the thoracic limbs (upper limbs, fore limbs), which in quadrupeds experience a braking (decelerating) force with each ground contact, whereas in bipeds, the upper limbs swing relatively freely in an alternating pendular manner. This potentially creates a much larger trunk rotation whereas the sheep might experience more lateral flexion as the propulsive input of the pelvic limb onto the thoracolumbar spine is acting simultaneously to the braking input of the forelimb. In support of this proposition, one would expect the oblique muscles of the trunk in man to be more active compared to the sheep, in order to control the rotation moments, which we have shown in the present study. Moreover, sheep might need greater activation in the dorsal spinal muscles to stabilize against the lateral motion of the spine, which was also demonstrated in the majority of conditions and outcomes explored in the present study. At faster gaits, movements outside the sagittal plane reduce motion efficiency considerably more, so that both thoracolumbar lateral bending (sheep) and rotation (humans) is expected to be reduced by an increase in muscle activity. Fittingly, trunk muscle activity has been shown to increase with increasing speed of locomotion in man (Anders *et al.*, 2007, Anders *et al.*, 2009, Capellini *et al.*, 2006) and in equids (Robert *et al.*, 2001, Robert *et al.*, 2002). It has been demonstrated that in man, the relative timing in muscle activity does not change considerably with increasing speed, although muscle-dependent changes in phasic behavior can be observed (Anders *et al.*, 2007, Saunders *et al.*, 2004). The humans in this study were able to select a speed of locomotion which was comfortable to them, and an appropriate locomotion speed was selected for each individual sheep based on observation. This resulted in similar speeds of locomotion between man and sheep in the present study. Therefore, the influence of speed on measured muscle activity between man and sheep investigated here is considered negligible.

We also hypothesized that a greater number of differences in muscle activity between the species would be found for the walk rather than the run/trot, because of a greater difference in inter-limb coordination and gait mechanics at the walk between bipeds and quadrupeds. A considerable number of differences were found between humans and sheep overall, with as many of these differences at walk and at run/trot. This may be because, despite the complexity of inter-limb coordination, only five temporal activation components are required to describe muscle activity during both walking and running in man, based on a principal component analysis method to evaluate EMG wave forms (Capellini *et al.*, 2006, Ivanenko *et al.*, 2004). However, a phase-shift was seen during the stance phase in one component when walking and running were directly compared (Capellini *et al.*, 2006). Furthermore, increasing speeds were also shown to result in the earlier occurrence of the components peaks (Capellini *et al.*, 2006), these shifts being closely related to stance duration (Ivanenko *et al.*, 2004). It is thought that this small number of temporal activation components is a management strategy of the neural system to reduce the possible degrees of freedom in order to produce targeted and controlled movements (Ivanenko *et al.*, 2005, Tresch *et al.*, 2002). Simplification of muscle activation has also been found in the frog (d'Avella *et al.*, 2003, Hart and Giszter, 2004) and the cat (Torres-Oviedo *et al.*, 2006). In addition, the importance of sensory feedback in this system has been demonstrated in cats (Lemay *et al.*, 2004). To our knowledge, these neural control strategies during locomotion

have not been compared between bipeds and quadrupedal species. However, due to the narrow range of activation strategies being reported within individual species, one might suggest that similarities in muscle activation may also be found across species, which would explain that a greater complexity of inter-limb coordination during quadrupedal locomotion does not necessitate substantial differences in motor control. As a result, it is likely that the differences found in the present study are explained by biomechanical factors.

In the present study, it was shown that sheep do not require greater tonic activity of the abdominal muscles to support the trunk, contrary to what was hypothesised. In order to counteract the extensor moments, it may be that other structures (active or passive), or alternative motor control strategies not identified in the present study are in place to support the horizontally orientated spine in quadrupeds. It may be that the ovine spine is inherently stiffer *in vivo*, requiring less work from the abdominal muscle group during walking, aiding locomotor efficiency. At the trot, abdominal muscle activity in sheep was more tonic, possibly as the movement of the heavy abdomen can become increasingly pendulous if moving at a reference frequency to the stride and swinging viscera may create the need for continuous muscular stabilisation of the spine. This is particularly relevant as herbivores have a large fluid-filled rumen. Daley and Usherwood (2010) have described the effects of the visceral mass on limb mechanics and cost of locomotion in quadrupeds. It is therefore likely that spinal mechanics and motor control of the trunk will be influenced more by a large swinging abdomen at faster speeds and gaits in quadrupeds.

In contrast to what was hypothesised at the outset of the study, humans displayed a greater phasic behaviour of ES compared to sheep. It might be that greater ES activity of a less phasic nature is required in quadrupeds to control the amount of lateral bend of the thoracolumbar spine. The stabilising role of the longissimus dorsi muscle to lateral spinal movements in the horse during locomotion has already previously been discussed (Licka *et al.*, 2009). The effects of the pendulous abdomen described earlier may also play an integral part in the differences in ES activity observed between the species. Furthermore, the location of the large rumen on the left side of the body may explain the unilateral finding in the phasic nature of ES in sheep. Sheep ES reaches its maximal amplitude earlier in the MC compared to humans. This may also be related to the pre-emptive activation to control the lateral bend in the spine, but it also is likely to be related to the difference in footfall pattern between bipeds and quadrupeds.

A further qualitative difference in ES activity was noted between humans and sheep. Although all the EMG traces of this muscle displayed a singular burst in all sheep and the majority of humans during walk, a distinct double burst separated by a period of low activity was seen in some humans. This double-burst was not observed during running in either species. Other authors have also described a double-burst (large and small) in ES activity during human walking (Anders *et al.*, 2007, Capellini *et al.*, 2006). Although Capellini and colleagues (2006) identified this pattern at all walking speeds, others have found this more at higher walking speeds (Anders *et al.*, 2009). In our humans, two mature participants showed an equally-sized double burst rather than the previously described large and small burst, and only on one side of ES. Although neither of these participants reported having had back pain, these less commonly noted traces may indicate either asymmetry in muscle use with

age or underlying (non-painful) degeneration, as these traces were not seen in our younger humans. Differences in left to right ES muscle volumes in the mature humans, but not the young humans, have previously been described based on MRI data from the humans in the present study (Valentin *et al.*, 2015), which also points to a potential difference in ES use with age.

In conclusion, the results from the present study suggest that large and numerous differences in trunk muscle activity exist between man and sheep during treadmill walk and run/trot, and that these differences were muscle- and gait-specific. The differences in trunk control required during walking and running/trotting as a result of spinal posture and alignment, and additionally the pendular movements of the viscera in sheep at higher locomotion speeds, are potential explanations for this. As a result of these differences in trunk muscle activities, muscular stabilization strategies are probably species-specific. This should be taken into consideration when extrapolating animal model findings to the human spine.

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Figure 1.

Linear envelope of normalised activity of the muscles erector spinae left (ESL), erector spinae right (ESR), gluteus maximus left (GML), gluteus maximus right (GMR), rectus abdominis left (RAL), rectus abdominis right (RAR), obliquus externus left (OEL), obliquus externus right (OER), obliquus internus left (OIL) and obliquus internus right (OIR) in all humans during walk (column 1), all sheep during walk (column 2), all humans during run (column 3) and all sheep during trot (column 4). The black lines indicate the mean normalised activity and the grey areas the standard deviation. The mean stance duration for

the right lower limb in humans (R stance) and the right hind limb in sheep (RH stance) are indicated.

Figure 2.

Mean muscle activity normalised to the maximally observed EMG (%MOE) of the left and right sides of erector spinae (ES), gluteus maximus (GM), rectus abdominis (RA), obliquus externus (OE), and obliquus internus (OI) in all humans (H) and all sheep (S) during walk (left column) and run/trot (right column). Each data point indicates an individual human/sheep. Significant between-species differences are indicated with an asterisk (*).

Figure 3.

Range of muscle activity normalised to the maximally observed EMG (%MOE) of the left and right sides of erector spinae (ES), gluteus maximus (GM), rectus abdominis (RA), obliquus externus (OE), and obliquus internus (OI) in all humans (H) and all sheep (S) during walk (left column) and run/trot (right column). Each data point indicates an individual human/sheep. Significant between-species differences are indicated with an asterisk (*).

Table 1

Stride length, height and speed during walking and running in humans

Human		stride length (mm)		step height (mm)		speed m/s	speed km/hr
		right	left	right	left		
walk	mean	1213.91	1212.63	167.75	165.42	1.10	3.97
	stdev	186.34	186.61	24.40	20.31	0.20	0.72
run	mean	1485.81	1484.63	247.37	236.97	1.87	6.74
	stdev	321.52	321.57	69.92	66.92	0.37	1.35

Table 2

Stride length, height and speed during walking and trotting in sheep

Sheep		stride length (mm)				step height (mm)				speed m/s	speed km/hr
		HR	HL	FR	FL	HR	HL	FR	FL		
walk	mean	988.42	991.56	992.80	982.71	49.34	46.68	48.10	47.86	1.16	4.16
	stdev	133.14	144.94	129.02	132.29	14.49	11.12	8.74	18.21	0.12	0.43
trot	mean	1068.43	1068.70	1067.88	1064.12	57.38	53.86	57.06	60.15	1.82	6.56
	stdev	109.46	110.11	111.04	104.64	19.28	21.74	15.08	20.93	0.11	0.39

Table 3

Occurrence of the maximum muscle activity normalised to the maximally observed sEMG (%MOE) and reported as a percentage of the motion cycle (%MC) for the muscles classified as phasic. The muscles erector spinae left (ESL), erector spinae right (ESR), gluteus maximus left (GML), gluteus maximus right (GMR), rectus abdominis left (RAL), rectus abdominis right (RAR), obliquus externus left (OEL), obliquus externus right (OER), obliquus internus left (OIL) and obliquus internus right (OIR) are included. The number of subjects where a particular muscle was phasic is indicated by n. Significant differences between species are indicated by matching superscripts (^a p=0.005; ^{b-d} p<0.001).

Muscle	Human		Sheep	
	Walk	Run	Walk	Trot
ESL	10.09 ± 6.88 (n=15/24)	10.16 ± 17.41 (n=20/21)	Not phasic	Not phasic
ESR	59.09 ± 9.52 (n=16/24) ^a	58.86 ± 7.30 (n=22/22)	42.30 ± 15.08 (n=8/15) ^a	Not phasic
GML	61.31 ± 10.77 (n=23/24) ^b	50.71 ± 13.74 (n=22/22) ^c	75.49 ± 13.73 (n=13/15) ^b	78.02 ± 2.28 (n=5/8) ^c
GMR	10.11 ± 3.15 (n=22/24) ^d	6.79 ± 7.49 (n=20/23)	30.62 ± 18.34 (n=13/15) ^d	Not phasic
RAL	Not phasic	Not phasic	Not phasic	Not phasic
RAR	Not phasic	Not phasic	34.73 ± 17.81 (n=8/15)	Not phasic
OEL	Not phasic	Not phasic	Not phasic	Not phasic
OER	Not phasic	Not phasic	60.38 ± 17.95 (n=8/14)	Not phasic
OIL	Not phasic	Not phasic	56.18 ± 22.67 (n=10/13)	Not phasic
OIR	Not phasic	46.64 ± 13.35 (n=19/23)	Not phasic	Not phasic