**Comparative Functional Anatomy of the Epaxial Musculature of Dogs (*Canis familiaris*) bred for Sprinting versus Fighting**

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**Summary**

The axial musculoskeletal system of quadrupedal mammals is not currently well understood despite its functional importance in terms of facilitating postural stability, and locomotion. Here we examined the detailed architecture of the muscles of the vertebral column of two breeds of dog, the Staffordshire bull terrier (SBT) and the racing greyhound, which have been selectively bred for physical combat and high speed sprint performance respectively. Dissections of the epaxial musculature of nine racing greyhounds and six SBTs were carried out; muscle mass, length, and fascicle lengths were measured and used to calculate muscle physiological cross sectional area (PCSA), and to estimate maximum muscle potential for force, work and power production. The longissimus dorsi muscle was found to have a high propensity for force production in both breeds of dog, however when considered in combination with the iliocostalis lumborum muscle it showed enhanced potential for production of power and facilitating spinal extension during galloping gaits. This was particularly the case in the greyhound, where mm. longissimus dorsi and iliocostalis lumborum were estimated to have the potential to augment hindlimb muscle power by approximately 12 %. Breed differences were found within various other muscles of the axial musculoskeletal system, particularly in the cranial cervical muscles and thoracic muscles which insert on the ribs. These may also highlight key functional adaptations between two breeds of dog which have been selectively bred for particular purposes. Additionally, in both breeds of dog, we illustrate specialisation of muscle function by spinal region, with differences in both mass and PCSA found between muscles at varying levels of the axial musculoskeletal system, and between muscle functional groups.

**Keywords**: *canis;* greyhound; back; muscle; vertebral column; locomotion; axial

**Introduction**

The epaxial spinal muscles have been proposed as important during galloping in quadrupeds, to facilitate coordinated limb movements, and to extend the length of the stride during the lengthened aerial phase (Hildebrand, 1961). Studies of the electromyographic activity of these muscles suggest that their function is somewhat broader than that. Collectively, in addition to mobilising the trunk in extension, torsion and lateral bending, the epaxial muscles are also thought to play a role in controlling or resisting movements of the spine (dynamic stabilisation) as well as ensuring the structural integrity of the vertebral column (local/ static stabilization; English, 1980; Carlson et al. 1979; Ritter et al. 2001; Schilling and Carrier, 2009).

The three main epaxial muscle systems are, from most medial to lateral, the transversospinalis, longissimus and iliocostalis systems (Evans, 1993; Figure 1). The transversospinalis system includes m. spinalis, m. semispinalis, and deep multisegmental muscles such as the mm. multifidi which are considered, based on their activity patterns and fibre metabolic profile, to be equipped for both dynamic spinal stabilisation, as well as producing spinal extension (Carlson et al. 1979; English, 1980; Ritter et al. 2001; Schilling and Carrier, 2009; Schilling, 2009). Similarly the longissimus and iliocostalis systems (which are not easily distinguished from one another in the lumbar region of the dog) are also considered to have multiple roles. They have been implicated in increasing spinal stiffness (Carlson et al. 1979; English, 1980; Schilling and Carrier, 2009), counteracting sagittal flexion (Ritter et al. 2001), as well as in active generation of spinal extension during asymmetric gaits (English, 1980; Schilling and Carrier, 2010) such as the rotary gallop used at high speed by the greyhound. Studies suggest that vertebral level (Wakeling et al. 2007; Schilling and Carrier, 2009) as well as the gait utilised by the animal (English, 1980; Ritter et al. 2001; Schilling and Carrier, 2010) heavily influence the functional role of the various epaxial muscles.

Since the function of the spine and spinal musculature is not consistent along its length, it follows that musculoskeletal anatomy may also vary accordingly. This morphological diversity is well illustrated by variation in the structure of vertebrae (e.g. Kida et al. 1999; Long et al. 1997). Studies of mammalian muscle features such as fibre metabolic profiles also indicate a cranial to caudal differentiation in fibre type distribution along the vertebral column (Moritz et al. 2007; Schilling, 2009) as well as within individual epaxial muscles (Gellman et al. 2002). We may therefore also expect regional variation in the quantitative morphology of muscles along the trunk in quadrupedal mammals. Such regionalisation of muscle architectural characteristics has been illustrated within a single epaxial muscle – m. longissimus dorsi - in the horse (Ritreuchai et al. 2008), however whether regional specialisation in muscle architecture exists in other epaxial muscles and in other quadrupeds is yet to be addressed.

There is a general paucity of quantitative comparative information regarding the anatomical structure of the muscles of the trunk of dogs and of quadrupeds in general. To date, only one study has considered muscle architecture in the canine back (Sharir et al. 2006), considering only the neck muscles of mixed-breed dogs. The aim of this study was therefore to provide detailed quantitative and comparative data regarding muscle functional anatomy throughout the axial musculoskeletal system of two breeds of dog bred for contrasting purposes: running versus fighting.

The racing greyhound is an elite sprinting athlete that has been under intense artificial selection for both high speed running and aerobic stamina. It has been shown that these dogs can often reach speeds of 17 ms-1 for short periods during sprinting (Usherwood and Wilson 2005), and can accelerate at 10 ms-2 (Williams et al. 2009a). Laboratory experiments have shown sub-maximally accelerating greyhounds to produce total limb peak powers of approximately 300 Wkg-1 of hindlimb extensor muscle mass (Williams et al. 2009b), and greyhounds during racing to have centre of mass (CoM) powers (over a stride) as high as 60 Wkg-1 (body mass specific; Williams et al. 2009b). These figures are towards the top end of published values for potential maximum muscle power output in mammals (Weis-Fogh and Alexander, 1977) and in the company of animals which show particularly impressive values for maximum muscle power, such as ascending quail (Askew et al. 2001).

In order to achieve such impressive power production, greyhounds might possess superior physiological properties of limb muscles. Greyhounds have a higher proportion of fast muscle fibres than other breeds of dog (Rodriguez-Barbudo et al. 1984). However, even the fastest land mammal the cheetah does not have muscles with extraordinary physiological properties (92.5 Wkg-1 muscle compared to 119.7 Wkg-1 in the rabbit; West et al. 2013). It therefore follows that greyhounds may also possess a multitude of other strategies to enhance power and enable rapid accelerations. Elastic elements within the limbs may act to augment or amplify power production by their muscles (Lichtwark and Wilson, 2005; Peplowski and Marsh, 1997) with such a mechanism proposed to amplify power by up to 15 times (Aerts, 1998). A further and likely possibility is that the greyhound spinal musculature performs mechanical work on the CoM during locomotion, thus supplementing that produced by the limb musculature.

In contrast to greyhounds, Staffordshire bull terriers (SBTs) have historically been subject to selection for bloodsports and physical combat and as such dogs of this type possess substantial specialisations for ﬁghting. Clear adaptations have previously been noted in pit bull terrier limb anatomy; they exhibit relatively more muscle mass in their distal limbs compared to greyhounds, have stronger muscles in their forelimbs than their hindlimbs and a much lesser capacity for elastic storage in the extensor muscle-tendon systems of their ankle joints (Pasi and Carrier, 2003). The limb bones of pit bull terriers also appear well adapted for fighting, demonstrating high resistance of failure compared with the relatively stiff and brittle bones of greyhounds (Kemp et al, 2005). It follows that the spinal musculature of SBT dogs may also be adapted for the enhanced strength and dynamic stability that might be required for physical combat. We hypothesised that whilst the SBT would exhibit adaptations for high muscle strength and postural stability, greyhound epaxial muscles would show a greater specialisation for work and power production and for facilitating a wide range of spinal motion. Additionally, we hypothesised that both breeds may exhibit regional specialisation of muscle function throughout the axial musculoskeletal system, with this being reflected by differences in muscle architecture between regions of the vertebral column and between different functional muscle groups.

**Materials and Methods**

This study was approved by the University of Liverpool Veterinary Research Ethics Committee (Reference number VREC104). Nine mature greyhounds (mass 27.3 + 1.7 kg; mean + SD), euthanised due to traumatic racing injury to a limb, and six mature Staffordshire bull terriers (SBT; 21.4 + 1.6 kg), euthanized for reasons not pertaining to the musculoskeletal system were used for the study. Cadavers were frozen at -20 ° C within 24 hours of euthanasia and removed from the freezer and stored at 4°C no more than 48 hours prior to dissection.

For each dissection, the left hand side of the cadaver was skinned, and the extrinsic muscles of the forelimb removed. Muscles of the vertebral column were systematically isolated and any external tendons associated with the muscle removed. Muscle mass was determined using an electronic balance accurate to 0.01g (Mettler Toledo, Greiffensee, Switzerland), and muscle belly length was measured from origin to insertion using a flexible plastic tape measure accurate to 1 mm. Where a muscle had multiple insertions, this measurement was made to the insertion point furthest from the origin ensuring that muscle belly length reflected the entire line of action of the muscle. A longitudinal incision was made in the muscle belly along the plane of the fascicles, and the lengths of a minimum of five, and up to ten, randomly selected fascicles were measured using a plastic measuring tape. In the case of large muscles, spanning multiple spinal segments, fascicle lengths were sampled along the full length of the muscle belly.

Muscle volume was calculated by dividing muscle mass by muscle density of 1.06 gcm-3 (Mendez and Keys, 1960). Physiological cross sectional area (PCSA) was calculated for each muscle as muscle volume divided by mean fascicle length. Architectural Index (AI), an index normalising fascicle length for muscle length, was calculated for each muscle to allow comparisons of fascicle lengths to be made between muscles of varying sizes. It was calculated as mean fascicle length divided by muscle belly length.

Resulting individual data were scaled in accordance with geometric scaling, with muscle mass scaled in proportion to body mass (g/kg), PCSA scaled to body mass2/3 and muscle belly and fascicle lengths scaled to body mass1/3 (Alexander et al. 1981; Schmidt-Nielsen, 1984). The scaling method utilised in comparative anatomical studies is an important consideration (see Myatt et al. 2011 for a full discussion). To ensure that geometric scaling was the appropriate method for this study, an Independent Samples T-test (significance level of 0.05) was carried out to establish that body mass differed between the two breeds of dog (p < 0.0001). Body mass and muscle parameters (mass, PCSA and fascicle length) were log transformed and linear regression carried out to establish the scaling relationships (exponents) for each parameter. These were not found to be different from geometric scaling relationships (p > 0.05 for all parameters) and therefore given the well recognized sensitivity of allometric scaling methods to low sample sizes (Hui, 2007), it was considered most appropriate to base subsequent analyses on the established geometric scaling relationships.

Scaled muscle architecture variables were compared between greyhound and SBT breeds via Independent Samples Students T –Tests, with a significance level set at 0.05. Muscles were grouped for further analysis based on two features: (i) position along the spine from cranial to caudal (based on location of cranial-most muscle origin: cervical, thoracic or lumbar) and, (ii) muscle system (transversospinalis, iliocostalis, longissimus, and other [predominantly muscles of the neck] muscles). Data were evaluated for normality using a Shapiro-Wilk test and found to be normally distributed (p>0.05). One way analyses of variance (ANOVA) followed by Tukey’s multiple comparisons tests were conducted to determine differences between muscle variables at regions of the vertebral column, and between functional systems of muscles for each of the greyhound and SBT respectively. All statistical procedures were undertaken in GraphPad Prism (Version 6.00 for Windows, GraphPad Software, La Jolla California USA).

**Results**

In total thirteen muscles were considered in this study (see Figure 1 for a representation of their locations along the spine). Muscle architecture parameters for each muscle in both greyhounds and SBTs are provided in Table 1.

*Breed differences*

The longissimus thoracis et lumborum muscle (the thoracic and lumbar portions of which are fused at around the level of the thirteenth rib, and hereafter referred to as m. longissimus dorsi) was the largest muscle in the axial musculoskeletal system of both breeds (Figure 2a; greyhound 351 ± 61 g and SBT 273 ± 39 g ). The longissimus dorsi muscle was over five times the size of the next largest muscle (in the greyhound, m. splenius; 125 + 16 g, and in the SBT, m. iliocostalis lumborum 113 ± 7 g) and accounted for over 50 % of the mass of the epaxial musculature. There was a significant difference in the mass of m. longissimus dorsi between the two breeds of dog, after scaling for body mass, with the greyhound found to have a significantly heavier longissimus dorsi muscle (p = 0.001). This muscle was found in both breeds of dog to be fused with the iliocostalis lumborum muscle caudally; the iliocostalis lumborum muscle was significantly larger in the SBT (p < 0.0001), however combined with the mass of m. longissimus dorsi, the total muscle mass was found to be larger in the greyhound (p = 0.018). Significant differences in mass of other muscles existed between breeds of dog (Figure 2a); a number of muscles in the cervical region, namely m. obliquus capitis cranialis, m. obliquus capitis caudalis, and m. semispinalis capitis were larger in the SBT (p = 0.004, p < 0.0001 and p < 0.0001 respectively), and a number of muscles in the thoracic region of the spine, m. serratus dorsalis, m. scalenus and m. multifidus thoracis, were larger in the greyhound (p = 0.001, 0.009 and 0.005).

The scaled physiological cross sectional area (PCSA) of some muscles in the neck region was considerably larger in the SBT than in the greyhound (m. obliquus capitis cranialis, . obliquus capitis caudalis; p = 0.003 and 0.004; Figure 2b) as was the iliocostalis lumborum muscle (p < 0.0001). The PCSA of m. iliocostalis thoracis, m. longissimus dorsi, and the combined PCSA of these two muscles were all found to be greater in the greyhound than the SBT (p = 0.0002, p < 0.0001 and p < 0.0001). This difference was particularly large in the longissimus dorsi muscle alone and when this muscle was paired with m. iliocostalis lumborum (58 % and 43 % greater in the greyhound respectively).

Despite the inherent variability of fascicle length within a muscle, the mean scaled fascicle length was found to differ significantly between breeds in a number of muscles (Figure 2c). In the majority of cases (m. longissimus capitis, m. scelenus, m. spinalis et semispinalis thoracis, m. multifidus thoracis, m. iliocostalis thoracis, m. iliocostalis lumborum and the combined iliocostalis lumborum and longissimus dorsi muscle complex), fascicle lengths were found to be longer in the greyhound compared to the SBT (p < 0.05 in all cases), with only the semispinalis capitis muscle exhibiting the opposite trend (p = 0.018). Architectural index (AI) was found to be larger in m. semispinalis capitis, m. spinalis et semispinalis thoracis and m. longissimus dorsi in SBTs (p = 0.0004, 0.02, and 0.049; Figure 2d), and larger in m. longissimus capitis and the combined longissimus dorsi – iliocostalis lumborum muscle complex in greyhounds (p = 0.005 and p = 0.03).

*Regional variation*

Both the greyhound and SBT showed regional variation in the location of muscle mass along the vertebral column (Figures 3 and 4). Both breeds had a higher proportion of muscle mass located in the lumbar region, compared to both the cervical and thoracic regions of the spine (p < 0.0001). Unlike the greyhound however, the SBT had a larger amount of muscle mass located in the cervical region when compared to the thoracic region (p < 0.0001). This trend was mirrored by differences in PCSA between regions. Neither breed showed significant differences in either fascicle length nor AI across regions of the vertebral column, however there was a strong trend for the AI of epaxial muscles to decrease caudally along the spine in the SBT in particular.

The longissimus muscle system was substantially higher in mass and PCSA in both breeds of dog than the other respective muscle systems (p < 0.0001; Figure 3 and 4). Additionally, in both breeds, the transversospinalis system was larger in terms of mass and PCSA than the iliocostalis muscle system (p < 0.0001), and in the SBT also greater than the muscles categorised as ‘other’. No differences were seen between the respective muscle systems in terms of fascicle length or AI (p > 0.05) in either breed of dog.

**Discussion**

*Muscle functional capacity*

Measures of muscle architecture can be utilised to make predictions about a muscle’s maximum functional capacity in terms of force production, performing work and generating power (e.g. Lieber & Friden, 2000; Payne et al. 2005; Smith et al. 2006; Williams et al. 2008a, b; Hudson et al. 2011). Muscle architectural measurements alone cannot generate accurate figures for these parameters; such predictions require additional data, or assumptions to be made regarding muscle physiological properties such as contraction velocity. It is possible however, using basic analytical and graphical procedures, to ascertain broad trends and relationships regarding maximal muscle functional capacity and specialisation within and between species and breeds. Figure 5a illustrates this concept by plotting scaled muscle PCSA against scaled fascicle length for both greyhound and SBT back muscles. Muscles located to the top left of this plot show high maximum capacity for force generation; those to the bottom right show specialisations for performing work across a wide range of motion, and those towards the centre/upper-right of the plot have a high maximum capacity for power production due to their large size and relatively long fascicles.

*The longissimus dorsi muscle*

The longissimus dorsi muscle shows an extremely high capacity for force generation within the axial musculoskeletal system of both breeds of dog (Figure 5a), reflected by its relatively short fascicles and high PCSA. However, when normalised for size differences between breeds, m. longissimus dorsi possesses a far higher propensity for muscle force production (significantly greater PCSA) in the greyhound than in the SBT (Figure 2b; p < 0.05). The two canine breeds show similarity with one another in terms of the relative fascicle lengths of this muscle (p > 0.05). Early studies in cats (Carlson et al. 1976) indicated that the longissimus dorsi muscle is likely to be required to protect the spine from movements that may exceed its range of motion, rather than drive dynamic movements itself. More recent electromyographic studies of vertebral muscles in the dog (Ritter et al. 2001) and horse (Licka et al. 2009; Licka et al. 2004, Robert et al. 2001 and Robert et al. 2002) also lead to the hypothesis that m. longissimus dorsi appears to be geared towards stabilisation of the vertebral column against dynamic forces and limiting hyper-flexion of the spine. Further mass-loading experiments support this, suggesting that m. longissimus dorsi stabilises the back/trunk during trotting locomotion, rather than actively initiating movement (Ritter et al. 2001). These studies support our findings of high propensity for force production in the longissimus dorsi muscle and suggest that this muscle in particular has an important role in support and stability.

The effect of measuring the longissimus dorsi and illiocostalis lumborum muscles (LD&IL) as a whole on the outcome measures of muscle function is highlighted by Figure 5a. In both breeds of dog, combining both muscles into one measurement unit (reflecting the fusion of these two muscle bellies *in situ*) resulted in a right-shift on the graph for the muscle complex. This shift reflects the longer fascicles within the iliocostalis lumborum muscle portion and hence the enhanced potential for power production when these two muscles are considered as a single functional unit. It is notable that the addition of the iliocostalis lumborum muscle results in slightly different alterations in muscle complex function for the two different breeds of dog considered here. The shift towards enhanced power-generating capability is more pronounced in the case of the greyhound, whilst in the SBT, the shift is smaller, and more in the direction of an increase in the force generating capacity of the muscle complex. This may highlight a key functional difference in the more caudal component of this muscle complex in greyhounds compared with SBTs, with the greyhound caudal lumbar musculature more highly specialised toward facilitating rapid powerful extensions of the lumbar spine as might be required for fast running. This may reflect the relative greater specialisation for the use of the galloping gait and high speed locomotion in the greyhound compared to the SBT, historically bred for hunting and later fighting. When galloping the greatest amplitude of sagittal bending occurs in the lumbar region, and the greatest increase in muscle activity of the longissimus lumborum muscle when moving up through the gaits from a walk to trot to gallop occurs at the level of L6 (Schilling and Carrier, 2010). The percentage of glycolytic muscle fibres also increase caudally along the epaxial musculature (Schilling, 2009) indicating a greater potential need caudally for increased muscle fibre contraction velocities and adaptation for muscle activity over a wider range of motion.

*Sources of power for locomotion*

We hypothesised that the greyhound axial musculoskeletal system would be specialised for power production, in order to aid high speed locomotion and rapid accelerations. Many muscles of the greyhound limbs are suited to power production, in particular the large hip extensor muscles (Williams et al. 2008b), however they are unable to match the exceedingly high powers required during rapid accelerations (Williams et al. 2009a; Williams et al. 2009b). Our data suggest that the epaxial muscles of this breed, particularly the combined muscle unit of longissimus dorsi and iliocostalis lumborum, are likely to have the capacity to supplement the power produced by the muscles of the limbs. We can calculate to what extent, since the instantaneous maximum muscle power can be estimated as one tenth of the product of *F*max and maximum fibre contraction velocity, *V*max (Hill, 1938). We assume *V*max to be 3.8 *L*o s–1 (*L*o=muscle fibre resting length; Ameredes et al. 1992). Isometric Fmax can be estimated by multiplying 0.3 MPa – the maximum isometric stress of vertebrate skeletal muscle (Wells, 1965; Medler, 2002) – by PCSA.

The instantaneous maximum muscle power of the combined longissimus dorsi and iliocostalis lumborum muscles was calculated using the above method. When considered as a proportion of the total summed instantaneous maximum power of all the hindlimb muscles (564 W from Williams et al. 2008b) this suggests that the combined longissimus dorsi and iliocostalis muscle unit has the capacity to augment the power produced by the combined hindlimb musculature by 12%. A simpler estimation based on augmentation of simply muscle mass alone (summed total of hindlimb muscle mass is 5.42 kg taken from Williams et al. 2008b) provides a similar figure (11.7 %). The total combined power producing capability of the major epaxial muscle and hindlimb musculature therefore equals 106 W kg-1 muscle mass – a figure just below the maximum estimated operating power of greyhound muscles during maximal accelerations (120 W kg-1; Williams et al. 2009b). This latter value was calculated from the measured body mass specific power of 60 W kg-1 during maximal accelerations (Williams et al. 2009b), doubled to express in muscle mass specific terms, since 50 % of greyhound body mass is muscle (Williams et al. 2008ab). Elastic elements within the limbs, or indeed the back, may play a role in amplification of muscle power in order to reach these high values, as has been illustrated in specific circumstances (e.g. Wilson et al. 2003). There is certainly compelling evidence to suggest that aponeuroses can act as efficient springs for storing and releasing energy (Azizi et al. 2009), and thus the thick thoracolumbar fascia that overlies m. longissimus dorsi may well play such a role within the back during locomotion (Alexander et al. 1985). Equally, we have not included the forelimbs in our calculations above, and these may contribute somewhat to powering accelerations.

*Breed differences*

Aside from differences between breeds in m. longissimus dorsi and m. iliocostalis lumborum, other muscles also showed significant architectural differences between SBTs and greyhounds (Figure 2). A number of muscles in the cervical region, namely m. obliquus capitis cranialis, m. obliquus capitis caudalis, and m. semispinalis capitis were larger in the SBT (p < 0.05) with considerably higher PCSAs. Of these muscles, m. semispinalis capitis appears to be suited to generating reasonably high forces within the vertebral column (Figure 5b). Head and neck motions are important for effective locomotor function, but also imperative for a range of other behaviours: feeding, orientation (through visual, auditory and vestibular means), and defence amongst others. The relative difference in size and morphology of these cranial neck muscles between breeds of dog may be reflective of selective breeding for rather different skull and neck conformations that facilitate rapid running versus fighting in the greyhound and SBT respectively.

A number of muscles of the thoracic region of the spine, m. serratus dorsalis, mm. scaleni and m. multifidus thoracis, were larger in the greyhound (p < 0.05), with m. scaleni and m. multifidus thoracis also possessing relatively longer fascicles in the greyhound with respect to the SBT. These three muscles all have origins/ insertions upon the ribs, and as such function not only to facilitate locomotion, but are involved to varying extents in ventilation. Based upon gross morphological and experimental studies, these muscles can contribute to inspiration via expansion of the thoracic cavity by rotating the ribs cranially and laterally (e.g., Raper et al. 1966; De Troyer and Kelly, 1984; De Troyer et al. 1994). Locomotion and ventilation are intrinsically linked during galloping gaits (Bramble and Carrier, 1983), and it follows to reason that an animal highly specialised for rapid sprinting may need to possess enhanced adaptations of musculature used to facilitate ventilation during galloping.

Studies such as this, which infer adaptation from direct comparisons between two species, are subject to well recognised limitations (Garland and Adolph, 1994), since this process involves the confounding of independent variables (the environmental factor, i.e. selective ‘regime’, and species membership). The specific choice of greyhound and SBTs as comparator breeds in this study however goes some way to placate some of these concerns, and has been discussed at length elsewhere (Pasi and Carrier, 2003; Kemp et al. 2005). The type of selection undergone by these two breeds has been very specific and extreme, whilst their environments (domestic, and influenced by a desire for the dog to be well housed, fed, and in good condition for running or fighting) have been highly controlled. Thus, although it is plausible that differences between the two breeds seen in this study may exist due genetic drift, it is more likely that the adaptive differences indicated are caused directly by selection for fighting or running.

*Regional Specialisation*

Both the greyhound and SBT showed regional variation in the location of muscle mass along the vertebral column (Figures 3 and 4). Both breeds had a higher proportion of muscle mass located in the lumbar region, compared to both the cervical and thoracic regions of the spine. This trend was mirrored by differences in PCSA between regions. Our hypothesis, that location along the vertebral column influences muscle architecture parameters, appears to be supported by these data. Such regional specialisation of epaxial muscle architecture has been seen in other species, notably the horse. Studies have indicated that in addition to variation between muscles along the length of the axial musculoskeletal system, an individual muscle also has the potential to perform varying functions along its length (Wakeling et al. 2007; Ritruechai et al. 2008). PCSA in the equine longissimus dorsi muscle increased caudally (Ritruechai et al. 2008), along with the apparent force generating capacity of the muscle. It was not possible to segment m. longissimus dorsi in this way (by vertebral level) in our study since the relatively longer fascicle lengths and different orientation in the canine specimens meant that fascicles spanned across many spinal segments. Standardisation of any muscle segmentation would therefore have been problematic and was avoided.

Neither breed of dog showed a significant difference in fascicle length nor AI between regions of the vertebral column, however there was a strong trend for the AI of epaxial muscles to decrease caudally along the spine in the SBT in particular. A trend for a caudal decrease in AI equates to the presence of shorter, more oblique muscle fibres in the caudal axial musculature. An oblique fibre orientation allows for both mobility and stability in all planes of the body simultaneously and thus better meets the complex needs for multiple diverse functions of the trunk in mammals (Schilling and Carrier, 2010). This appears to be particularly important towards the caudal end of the trunk, likely due to the requirement of this region to facilitate stabilization but also sagittal mobilisation during high speed asymmetrical gaits. An oblique fibre orientation likely provides an advantage in the shortening velocity of the entire muscle (Brainerd and Azizi, 2005). This is since when fibers in a pennate muscle shorten, they rotate to greater angles of pennation (Maganaris et al. 1998) meaning that the muscle's velocity along its line of action can exceed the velocity of the contracting fibers themselves. This suggests that despite their apparent adaptation for generation of force, the caudal epaxial muscles may still be capable of fast contraction and hence mobilisation. This is also supported by the presence of high proportions of glycolytic muscle fibres within caudal regions of the iliocostalis lumborum and longissimus dorsi muscles in some mammals (Schilling, 2009).

*Limitations*

Some muscle parameters in our data showed reasonably high standard deviations (Table 1), particularly for certain muscles, parameters (especially fascicle length, and thus PCSA since it is derived from this) and in the greyhound. Fascicle lengths are inherently variable throughout a muscle belly, and therefore this variation is somewhat expected in the average values presented. Other sources of this variation include differences in the mass and size of our specimens: for greyhounds, the largest dog was 7 % heavier than the mean body mass, and the smallest, 11 % lighter; for SBTs the largest dog was 8 % heavier than the mean and the smallest, 7 % lighter. We were restricted in our use of cadavers to those donated or sourced opportunistically, meaning that inevitably dogs used in the study will introduce some level of variation due to their wide range of backgrounds, age, training and exercise histories. We were unable to control for this variation in lifestyle features, however our data remain representative of the wider domestic populations of these two breeds of dog.

**Conclusion**

Here we presented quantitative anatomical data for the epaxial trunk muscles of dogs bred for sprinting (the racing greyhound) versus fighting (the Staffordshire bull terrier) in a comparative context. We highlight that some greyhound epaxial muscles – m. longissimus dorsi and m. iliocostalis lumborum in particular - appear to show specialisation for power production, when compared to the SBT. We estimate that these two epaxial muscles alone could augment hindlimb power production during locomotion by around 12 % in the greyhound if used to facilitate lumbar extension during galloping gaits. Breed differences were found within various other muscles of the axial musculoskeletal system, particularly in the cranial cervical muscles and thoracic muscles which insert on the ribs. These may also highlight key functional adaptations between two breeds of dog which have been selectively bred for particular purposes. Additionally, we illustrate specialisation of muscle function by region of the trunk, with differences found in both mass and PCSA of muscles at varying levels of the trunk, and in different muscle functional groups.

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**Author Contributions**

EW was involved with data collection and analysis, and wrote the draft manuscript; PH was involved in data collection and editing of the manuscript; SBC was involved with data collection, analysis, interpretation, and editing of the manuscript.

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**Supplementary Material**

**Tables**

Table 1. Quantitative muscle data (unscaled) from the epaxial musculature of the greyhound (GH) and Staffordshire bull terrier (SBT). Values indicate means. Values in brackets indicate standard deviation. \* indicates significant difference after scaling for body mass (p < 0.05)

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Muscle | Abbv. | Mass (g) | Length (mm) | Fascicle length (mm) | PCSA (mm2) |
| GH | SBT |  | GH | SBT |  | GH | SBT |  | GH | SBT |  |
| Obliquus capitis cranialis | OCCr | 9.4 | (4.9) | 7.8 | (1.2) | \* | 97 | (2) | 70 | (3) | \* | 89 | (6) | 54 | (10) |  | 102 | (59) | 129 | (17) | \* |
| Obliquus capitis caudalis | OCCa | 32.2 | (1.4) | 34.8 | (4.7) | \* | 81 | (24) | 72 | (5) |  | 72 | (31) | 50 | (2) |  | 463 | (181) | 608 | (42) | \* |
| Splenius | Sp | 124.8 | (16.2) | 87.6 | (10.6) |  | 342 | (28) | 249 | (13) | \* | 227 | (64) | 188 | (8) |  | 550 | (156) | 442 | (64) |  |
| Semispinalis capitis | SSC | 86.9 | (13.8) | 103.8 | (13.4) | \* | 366 | (30) | 238 | (12) | \* | 50 | (12) | 84 | (25) | \* | 1715 | (391) | 1577 | (330) |  |
| Longissimus capitis | LCa | 24.9 | (5.3) | 21.5 | (3.8) |  | 270 | (36) | 187 | (21) | \* | 174 | (68) | 55 | (9) | \* | 166 | (95) | 382 | (110) | \* |
| Longissimus cervicis | LCe | 53.0 | (9.8) | 37.1 | (7.5) |  | 252 | (33) | 161 | (18) | \* | 110 | (37) | 87 | (6) |  | 504 | (205) | 397 | (64) |  |
| Spinalis et semispinalis cervicis | SetSC | 33.5 | (22.4) | 14.4 | (3.2) |  | 222 | (54) | 140 | (24) | \* | 118 | (66) | 103 | (27) |  | 441 | (514) | 146 | (69) |  |
| Serratus dorsalis | SD | 42.4 | (11.3) | 22.2 | (2.3) | \* | 222 | (80) | 188 | (30) |  | 80 | (25) | 61 | (1) |  | 501 | (191) | 351 | (44) |  |
| Scalenus | Sc | 36.4 | (4.4) | 24.5 | (2.9) | \* | 273 | (24) | 169 | (15) | \* | 171 | (28) | 128 | (12) | \* | 206 | (50) | 190 | (44) |  |
| Spinalis et semispinalis thoracis | SetST | 67.6 | (11.3) | 48.6 | (7.0) |  | 271 | (16) | 202 | (38) | \* | 86 | (22) | 92 | (14) | \* | 802 | (293) | 506 | (105) |  |
| Multifidus thoracis | MT | 62.9 | (32.3) | 32.2 | (6.1) | \* | 304 | (67) | 200 | (23) | \* | 49 | (15) | 27 | (17) |  | 1346 | (920) | 1178 | (446) |  |
| Iliocostalis thoracis | ILT | 35.2 | (6.7) | 25.3 | (2.3) |  | 332 | (41) | 273 | (50) | \* | 44 | (10) | 69 | (20) | \* | 778 | (149) | 358 | (88) | \* |
| Longissimus dorsi | LD | 680.6 | (218.3) | 272.8 | (39.3) | \* | 652 | (92) | 422 | (20) | \* | 89 | (28) | 68 | (15) |  | 8139 | (3700) | 3923 | (1080) | \* |
| Iliocostalis lumborum | ILL | 37.9 | (17.4) | 113.2 | (7.2) | \* | 335 | (54) | 209 | (9) | \* | 184 | (84) | 93 | (3) | \* | 209 | (101) | 1178 | (104) | \* |

**Figure legends**

Figure 1. Diagrammatic representation of muscles of the vertebral column coloured by muscle group: red- longissimus; blue – transversospinalis; green – iliocostalis; orange – other

Figure 2. (a) Scaled muscle mass, (b) Scaled PCSA (physiological cross sectional area), (c) Scaled fascicle length and (d) Architectural Index for muscles of the vertebral column. Bars represent mean + 95 % Confidence Intervals for Staffordshire bull terriers (dark red; n=6) and Greyhounds (red; n= 9). Muscles are arranged from cranial to caudal along the vertebral column. Significant differences (p < 0.05) between dog breeds are indicated by asterisks. Muscle abbreviations are given in Table 1.

Figure 3. Functional regionalisation of greyhound muscle architecture by region of the vertebral column [cervical - dark, thoracic - pale and lumbar - mid] and by muscle functional group [red- longissimus; blue – transversospinalis; green – iliocostalis; orange – other] for (a) Scaled muscle mass (b) Scaled PCSA (physiological cross sectional area) (c) Scaled fascicle length and (d) Architectural Index. Bars represent mean + standard error.

Figure 4. Functional regionalisation of Staffordshire bull terrier muscle architecture by region of the vertebral column [cervical - dark, thoracic - pale and lumbar - mid] and by muscle functional group [red- longissimus; blue – transversospinalis; green – iliocostalis; orange – other] for (a) Scaled muscle mass (b) Scaled PCSA (physiological cross sectional area) (c) Scaled fascicle length and (d) Architectural Index. Bars represent mean + standard error.

Figure 5. (a) Scaled mean fascicle length against scaled physiological cross sectional area (PCSA) for epaxial muscles of greyhounds (circular symbols) and Staffordshire bull terriers (triangular symbols). Bars represent SEM. Muscles towards the bottom right of the plot are suited to performing work over a wide range of motion; muscles to the top right are suited to work and power production; muscles to the top left of the plot have ability to generate high amounts of force. (b) Re-scaled plot, with the longissimus dorsi muscles removed to show, with improved clarity, the functional regionalisation of other back muscles. Point colours represent muscle group (red- longissimus; blue – transversospinalis; green – iliocostalis; orange – other). Muscle abbreviations are given in Table 1.