

MUSCLE FIBRE COMPOSITION OF THE BOVINE TAIL: A PILOT STUDY

O.A. Young and Paula M. Kenrick, Meat Industry Research Institute of New Zealand (Inc.), P.O. Box 617, Hamilton, New Zealand

SUMMARY

A bovine tail was cross-sectioned at four vertebrae, to expose its muscles - dorsal extensors, ventral flexors, and the lateral flexors that pass between the transverse processes. Muscle cross-sectional areas were measured at these faces and muscle sections were stained to distinguish slow and fast fibre types. From muscle and fibre area data and fibre type occurrences, preliminary conclusions are drawn about the roles of different muscles. The tail as a model for muscle studies is discussed.

INTRODUCTION

From many limb muscle studies, a model of muscle structure and function has emerged that explains posture and movement in terms of muscle fibre recruitment. Slow-twitch fibres, and therefore muscles dominated by this type, are responsible for posture. Fast-twitch fibres, and thus faster muscles, are recruited as locomotion begins and speed increases (Armstrong, 1981).

Limb muscle systems, however, are complex, arising from asymmetry, the presence of one- and two-jointed muscles, and from meeting variable needs of stance and gait. In contrast, axial muscles are symmetric about the body axis, are segmentally arranged, and are probably more restricted in their action than those of limbs. As the caudal extension of the backbone, the bovine tail's dominant action is rhythmic lateral strokes, with a less-frequent action being tail raising before waste elimination. Since the speed and frequency of these movements differ, the characteristics of the muscles that perform them might also differ. Moreover, the characteristics might vary between vertebral levels. This pilot study explores these possibilities and outlines how the study of tail muscles might further understanding of muscle action.

Although the coccygeus, the major extrinsic muscle of the tail, aids lateral flexion (Nickel et al. 1986), the intrinsic muscles, which are continuations of the long spinal muscles, are largely responsible for the tail's great mobility. On each side of the tail there are two dorsal extensors, sacrocaudalis dorsalis medialis and lateralis (the latter being the caudal continuation of the longissimus), two ventral flexors, sacrocaudalis ventralis medialis and lateralis, and the lateral flexor, the intertransversarii caudae (Fig.1). The extensors insert dorsolaterally, the flexors insert ventrolaterally, and the lateral flexor links the transverse processes.

To relate muscle structure and function, sections of intrinsic muscles were stained for myofibrillar adenosine triphosphatase (ATPase) activity, which distinguishes slow fibres from fast (Brooke and Kaiser 1970).

MATERIALS AND METHODS

The tail was cut from the carcass of a normal Friesian steer aged 18 months. When in rigor the tail was cut transversely at the cranial surfaces of the second, fourth, sixth and seventh caudal vertebrae, and the cut surfaces were photographed for muscle area measurements. Muscle blocks for cryosectioning were cut from the centre of all intrinsic muscles (left and right) at the cranial surfaces. Precise sampling was considered important to minimize the effect of any possible intramuscular variation in fibre occurrences. Blocks were frozen and stored in liquid nitrogen. Cross-sections (8 m) were cut from muscle blocks at -20°C, stained for ATPase at pH 9.4 (Guth and Samaha 1969) and representative fields were conventionally photographed through a 10X microscope objective. Micrographs were analysed by a transect technique. Fibres struck by a random line were counted to yield percent fibre type occurrence. Because larger fibres tend to be struck more often, the occurrences are weighted towards relative cross-sectional area contributed by each type. Fibre areas (90 per block) were measured by a computer-assisted method. Muscle areas were similarly measured from photographs. Left and right sides of each muscle yielded similar data, so values were averaged.

RESULTS

The cross-sectional areas of all muscles decreased distally (Fig. 2). By the fourth vertebra the ventralis medialis had disappeared, and by the seventh all muscles were becoming tendinous to the point that there was insufficient dorsalis medialis to obtain a useful sample.

At the second vertebra the dorsal and ventral lateral muscles had the largest cross-sectional areas; at the other three sites the dorsalis lateralis was the largest (Fig.2). The intertransversarii were small compared to adjacent muscles at the second vertebra, but distally their area remained fairly constant, whereas the areas of the other muscles markedly decreased.

Table 1. Muscle fibre areas in a bovine tail. Areas are averages, expressed in μm^2 .

Muscle	Fibre type	Vertebral level			
		2	4	6	7
Sacrocaudalis	slow	3330	2640	3680	-
dorsalis medialis	fast	2780	2020	-	-
Sacrocaudalis	slow	2180	1730	2050	2800
dorsalis lateralis	fast	1780	1620	2220	2650
Intertransversarii	slow	2310	2500	2610	2820
caudae	fast	1940	1910	2530	2470
Sacrocaudalis	slow	3430	2540	4290	3370
ventralis lateralis	fast	2300	2000	3650	-
Sacrocaudalis	slow	3640	-	-	-
ventralis medialis	fast	2470	-	-	-

- means none present or no muscle tissue.

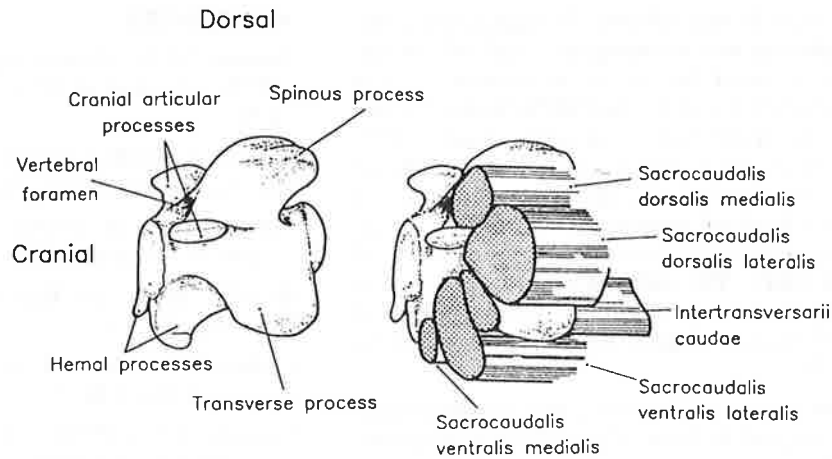


Figure 1. Second caudal vertebra, and left muscles schematically superimposed.

Slow fibres dominated all the intrinsic muscles, the lowest occurrence being 50%. The occurrence of these fibres increased distally in all muscles (Fig. 3). Where it could be sampled the dorsalis medialis always contained a higher proportion of slow fibres than the other muscles, reaching 100% at the sixth vertebra.

At each of the vertebral levels and for both fibre types, dorsalis lateralis fibres had the smallest cross-sectional area (Table 1).

DISCUSSION

Macroscopic and microscopic anatomy

The muscles became smaller (Fig. 2) and increasingly tendinous distally. The force they generate is transmitted by tendons to distal tail vertebrae, similar to the situation in limbs, where force developed by the muscle bulk, located proximally, is transmitted by tendons to distal bones (Davies 1981).

Muscle force is proportional to cross-sectional area (Maughan and Nimmo 1984). Although the dorsalis lateralis was not the largest muscle at the second vertebral

level, it dominated elsewhere (Fig. 2) and is probably the intrinsic muscle most responsible for the tail's frequent side-to-side movement. Fibres in this muscle had the smallest diameters (Table 1) presumably allowing rapid metabolite diffusion and thus high metabolic activity (Gauthier and Padykula 1966; Armstrong et al. 1977).

Compared to other muscles the intertransversarii showed the least distal decrease in size, so their relative contribution to potential force increases distally.

The dorsalis medialis, always a small muscle, was the first to become fully tendinous, which suggests that fine extension movements near the tip are difficult. Indeed, when an ox raises its tail, the tip droops, suggesting a diminished elevator ability at distal vertebrae.

Slow fibres dominate deep "antigravity" muscles like soleus and vastus intermedius of five quadrupeds and man (Ariano et al. 1973; Johnson et al. 1973), as well as anconeus and certain heads of triceps brachii of the cat (Collatos and Smith 1976). In these muscles, the slow fibres maintain posture (Henneman and Olson 1965; Armstrong 1981). The increased occurrence of slow

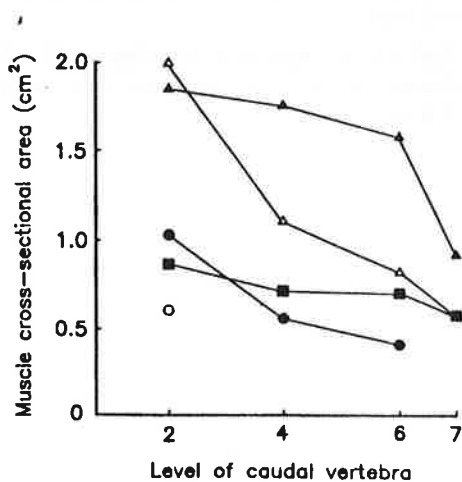


Figure 2. Mean muscle areas

S. dorsalis med./lat., ●/▲; intertransv., ■; s. ventralis lat./med., Δ/O.

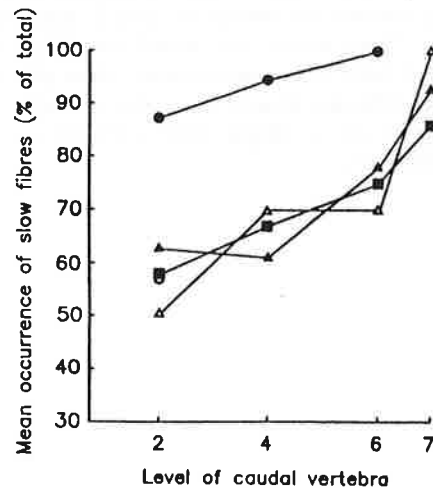


Figure 3. Occurrence of slow fibres

fibres distally in the bovine tail (Fig. 3), indicates that the muscles are playing an increasing postural role at the expense of potential for rapid movement. In a neurological study Riley and Allin (1973) found that the intertransversarii of cat comprised approximately 37% slow fibres at unspecified vertebral levels. Although not stated the authors implied that the occurrence did not vary along the tail, which contrasts with the data in Fig. 3. Also, the occurrence was lower than that encountered in the present study. The differences between cat and bovine tails presumably relate to species, and to functional differences similar to those discussed by Hickman (1979).

The dorsalis medialis was the slowest muscle and its fibre composition changed the least. These characteristics are consistent with its role in maintaining a raised tail against gravity. Although not a deep muscle, its composition is typical of a limb antigravity extensor.

The tail as a model for muscle studies

An emerging school of thought proposes that during locomotion, limb tendons and muscles alternately store and release elastic energy (Taylor et al. 1974; Taylor 1985; Horowitz et al. 1986), thus minimizing energy requirements for locomotion. For the bovine tail, it is likely that during side-to-side movement, the tendons and muscles on the extended (convex) side store elastic energy and release it on the reverse stroke. Muscles can also actively resist stretch, however. This non-elastic development of force on stretching is the braking function of muscle that permits control (Goldspink 1981), a vital concern of any muscular activity. When a lateral tail stroke is slowed before reversal, elastic and/or inelastic mechanisms will be operating in various muscles. The inelastic component could be identified by electromyography, since a muscle that is actively resisting stretch is also being neurally stimulated. On anatomical grounds, however, the lateral location of the intertransversarii between the transverse processes of adjacent vertebrae and their increasing dominance towards the tail tip, makes them appealing candidates for a braking role.

The movements of the bovine tail present opportunities to study division of labour in muscle contraction and stretch. Movements recorded on video could be correlated with electromyographic data obtained from electrodes inserted in muscles at sites along the tail. Such experiments offer a simple approach to the study of axial muscle function.

REFERENCES

- Ariano, M.A., Armstrong, R.B. and Edgerton, V.R. (1973). *Journal of Histochemistry and Cytochemistry* **21**:51.
- Armstrong, R.B., Ianuzzo, C.D. and Kunz, T.H. (1977). *Journal of Comparative Physiology* **119**:141.
- Armstrong, R.B. (1981). *Symposia of the Zoological Society of London* **48**:289.
- Brooke, M.H. and Kaiser, K.K. (1970). *Archives of Neurology* **23**:369.
- Collatos, T.C. and Smith, J.L. (1976). *Medicine and Science in Sports* **8**:69.
- Davies, A.S. (1981). *Anatomical principles of the musculoskeletal system*. A.S. Davies, Palmerston North, New Zealand. p33.
- Gauthier, G.F. and Padykula, H.A. (1966). *Journal of Cell Biology* **28**: 333.
- Goldspink, G. (1981). *Symposia of the Zoological Society of London* **48**: 219.
- Guth, L. and Samaha, F.J. (1969). *Experimental Neurology* **25**:138.
- Henneman, E. and Olson, C.B. (1965). *Journal of Neurophysiology* **28**: 581.
- Hickman, G.C. (1979). *Mammal Review* **9**:143.
- Horowitz, R., Kempner, E.S., Bisher, M.E. and Podolsky, R.J. (1986). *Nature* **323**:160.
- Johnson, M.A., Polgar, J., Weightman, D. and Appleton, D. (1973). *Journal of the Neurological Sciences* **18**:111.
- Maughan, R.J. and Nimmo, M.A. (1984). *Journal of Physiology* **351**:299.
- Nickel, R., Schummer, A., Seiferle, E., Frewein, J., Wilkens, H. and Wille, K. (1986). *The Locomotor System of the Domestic Mammals*. Berlin, Verlag Paul Parey. p320.
- Riley, D.A. and Allin, E.F. (1973). *Experimental Neurology* **40**:413.
- Taylor, C.R. (1985). *Journal of Experimental Biology* **115**:253.
- Taylor, C.R., Shkolnik, A., Dmi'el, R., Baharav, D. and Borut, A. (1974). *American Journal of Physiology* **227**:848.