Comparative histochemical composition of muscle fibres in a pre- and a postvertebral muscle of the cervical spine

L. C. BOYD-CLARK[1], C. A. BRIGGS[1] AND M. P. GALEA[2]

[1] *Department of Anatomy and Cell Biology, and* [2] *Laboratory for Sensorimotor Research, School of Physiotherapy, University of Melbourne, Australia*

(*Accepted 28 August 2001*)

ABSTRACT

References to histochemistry are extensive for human limb muscles but occur less frequently in relation to vertebral muscle. Most vertebral muscle literature has been concerned with muscle fibre characteristics in the lumbar and thoracic spine, due in large part to the incidence of low back pain and idiopathic scoliosis. However few studies have investigated the histochemical composition of neck muscles in humans: and, to our knowledge, no previous study has examined the antagonistic longus colli and multifidus muscle pair. In addition, while age-related segmental degeneration is most prominent between C5 and C7, it is not known whether these osteoligamentous changes are paralleled by changes in muscle fibre ratio. Tissue blocks comprising muscle and bone from C5–C7 segments were harvested at autopsy from 16 subjects with ages ranging from 4 to 77 years. The prevertebral longus colli and postvertebral multifidus muscle pairs were randomly selected from one or other side in each subject. The tissue was frozen, sectioned and histochemically stained for myofibrillar adenosine triphosphatase. Analysis of muscle fibre types was performed by light microscopy. Wilcoxon paired *t*-tests were used to ascertain whether intramuscular and intermuscular differences in fibre composition were significant. In addition, correlation and regression analyses were used to determine whether fibre type proportions changed in either muscle with increasing age. The present study has revealed histochemical differences between longus colli and multifidus at the level of the C5–C7 vertebral segments. Multifidus comprises a significantly greater proportion of type I than type II fibres. Longus colli comprises a significantly greater proportion of type II fibres than multifidus. Further there were no changes in fibre type proportion in either muscle with increasing age. These observations suggest that longus colli responds equally to postural and phasic demands, whereas multifidus is predominantly postural. Also it would appear that age-related structural alterations in lower cervical segments are not paralleled by changes in muscle fibre ratio.

Key words: Longus colli; multifidus; antagonist; type I; type II.

INTRODUCTION

Axial muscles may be classified as segmental stabilisers or prime movers on the basis of their moment-generating capacity (Vasavada et al. 1998). Fibre characteristics contribute to contractile force and moment-generating capacity (Lexell et al. 1983; Richmond et al. 1999), although these properties are subject to alteration following high intensity endurance training (Andersen & Henriksson, 1977; Rose & Rothstein, 1982; Abernethy et al. 1990), denervation (Dhoot & Pearce, 1984), or immobilisation (Rose & Rothstein, 1982; Lieber et al. 1988). Loss of cervical lordosis with increasing age is accompanied by osteoligamentous changes that briefly restore motion segment stability, prior to further degeneration and postural perturbation (Macnab, 1975; Klara & Foley, 1993; Joosab et al. 1994). Reactive processes of this kind are predominantly evident in the lower cervical spine (Bayley et al. 1995). Although neck muscles functionally adapt to these structural changes, little is known about their muscle fibre histochemistry. Previous studies have confirmed greater type I fibre size and composition in

Correspondence to Professor M. P. Galea, Laboratory for Sensorimotor Research, School of Physiotherapy, University of Melbourne, Parkville 3010, Victoria, Australia. Tel.: +61 3 8344 4118; fax: +61 3 9347 4188; e-mail: m.galea@unimelb.edu.au

various back muscles (Johnson et al. 1973; Lexell et al. 1983; Ng et al. 1998), although few studies have described the histochemistry of human neck muscles, whether in health or disease. Uhlig et al. (1995) examined fibre compositions in several ventral and dorsal neck muscles from patients suffering various forms of cervical dysfunction. Three further studies have examined fibre distributions in sternocleidomastoid and trapezius in control autopsy tissue (Johnson et al. 1973; Lindman et al. 1990, 1991).

The bulk of available vertebral literature has concentrated on the lumbar (Fidler et al. 1975; Jowett et al. 1975; Sirca & Kostevc, 1985; Thorstensson & Carlson, 1987; Rantanen et al. 1993; Rantanen et al. 1994; Mannion et al. 1997; Ng et al. 1998; Zhao et al. 2000), and thoracic spines (Zetterberg et al. 1983; Ford et al. 1984; Sirca & Kostevc 1985; Mannion et al. 1997; Meier et al. 1997), due in part to the incidence of low back pain and idiopathic scoliosis. Studies of lumbar longissimus and multifidus in healthy subjects has confirmed that both muscles contain greater proportions of type I than type II fibres, despite their different anatomical position (Sirca & Kostevc, 1985; Thorstensson & Carlson, 1987). Also, studies of multifidus in cases of lumbar spinal derangement and lumbar disc herniation have consistently noted that type I: type II ratios remain unchanged from normal values (Fidler et al. 1975; Jowett et al. 1975; Rantanen et al. 1993; Zhao et al. 2000). However type II fibre transformations may occur, notably an increase in the type IIB: type IIA ratio in instances of low pack pain and immobilisation (Rose & Rothstein, 1982; Lieber et al. 1988; Rantanen et al. 1993; Mannion et al. 1997; Ng et al. 1998; Zhao et al. 2000), and a decrease following high intensity endurance training (Andersen & Henriksson, 1977; Abernethy et al. 1990). By contrast, studies of thoracic erector spinae muscle in cases of idiopathic scoliosis have revealed more type I fibres on the convex side of the curved spine, whether at the level of the apex or bilaterally adjacent to it. Type I predominance is paralleled by diminished type II fibre population on the convex side, the fibres of which shift from type IIB to IIA, bearing more oxidative-glycolytic properties. Interestingly, fibre compositions on the concave side of the apex reflect ratios seen in healthy subjects (Zetterberg et al. 1983; Ford et al. 1984; Meier et al. 1997).

Multifidus and longus colli are functionally regarded as segmental stabilisers (Mayoux-Benhamou et al. 1994; Conley et al. 1995). We therefore hypothesised that both may exhibit a predominance of slow twitch muscle fibres, the proportion of which may decrease with increasing age, consistent with disuse and denervation. Here we describe for the first time muscle fibre characteristics for intrinsic longus colli and multifidus muscles spanning C5–C7 in autopsy material, and consider these properties in the context of age-related degenerative changes known to occur in this region.

MATERIALS AND METHODS

Study design

Tissue was gathered from 16 subjects at autopsy, for which ethical approval had been received. The 16 subjects (10 male, 6 female) ranged in age from 4 to 77 (mean 42 ± 20) y. All autopsies were performed within 24 h of death and medical histories were not available for review. Blocks including bone were harvested via an anterior approach from C5–C7 and immediately transferred to ice for transportation and subsequent processing. The longus colli and multifidus muscle pairs on both sides were used. As tissue became available, C5–C7 blocks were in turn allocated a random number. For odd-numbered blocks, the right longus colli and multifidus pair was used. In even numbered blocks, the left muscle pair was used. Using this random design equal numbers of left and right muscle pairs were assigned for muscle fibre analysis, without bias and independent of age and gender characteristics.

Muscle histochemistry

Longus colli and multifidus muscles were carefully resected from the vertebral bodies and laminae respectively. Muscle biopsies ($3 \times 3 \times 5$ mm) were cut using a scalpel from the resected C5–C7 muscle segments, such that samples were obtained from C5–C7 for both longus colli and multifidus in each subject. Therefore a total of 96 muscle biopsies were harvested and prepared in this manner. In each case sampling occurred in the muscle belly since C5–C7 motion segments represent mid portions in each of these muscles. In addition, biopsies were taken at variable depths in each muscle sample to control for the possibility of non-uniform fibre type distributions (Richmond et al. 1999). Biopsies were oriented in plastic moulds ($5 \times 5 \times 5$ mm) and embedded in TissueTek OCT Compound (Sakura Finetek, USA) for transverse muscle fibre sectioning. Samples were then frozen in precooled isopentane using liquid nitrogen. Frozen muscle samples were immediately transferred to a -30 °C freezer and stored for

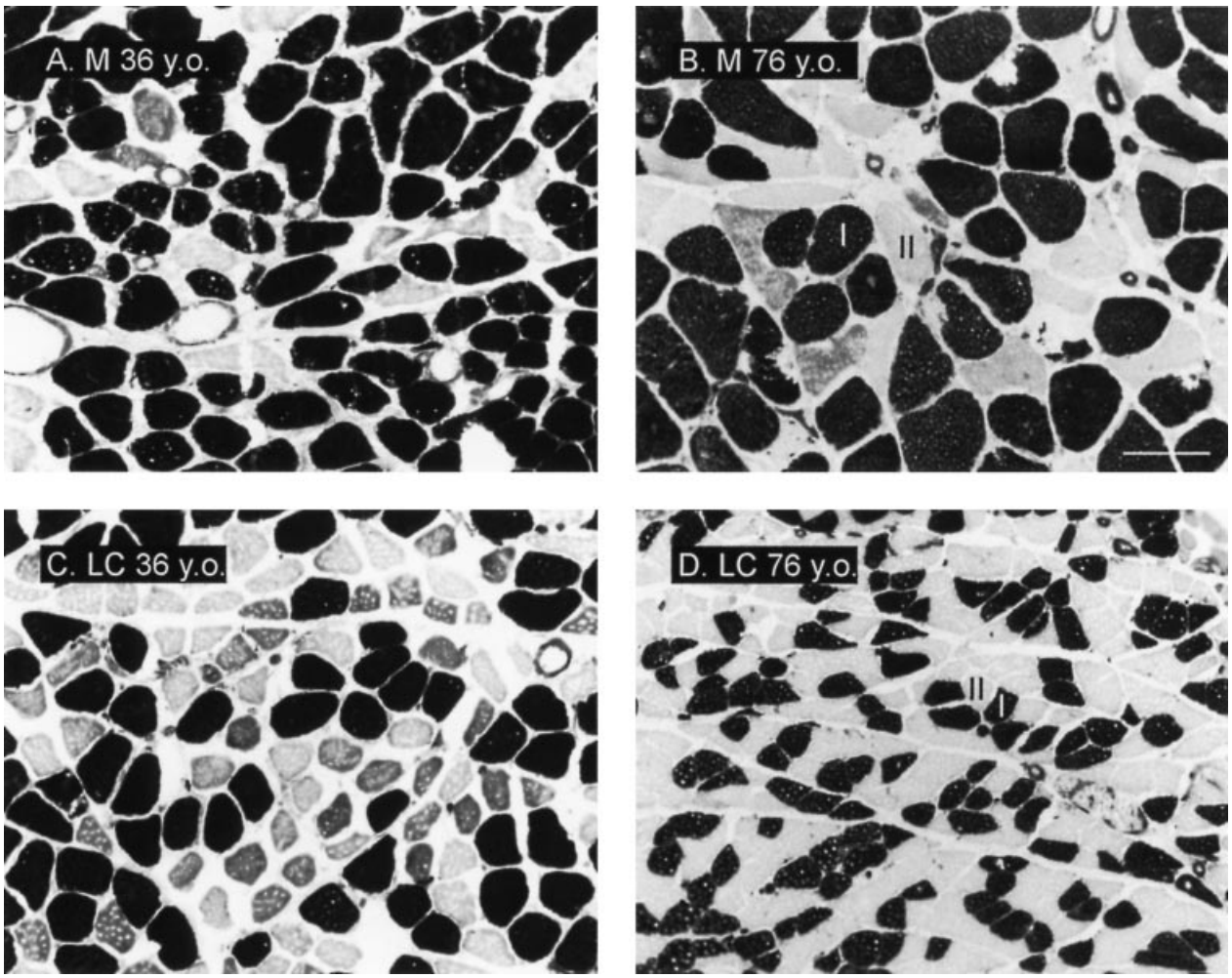

Fig. 1. Muscle fibre composition at C6 in subjects aged 36 and 76 y. The top panels indicate multifidus (*a*, *b*), the bottom panels longus colli (*c*, *d*). Sections stained for myofibrillar adenosine triphosphatase (ATPase) following preincubation at pH = 9.4 and 4.3. Type I and type II muscle fibres are labeled in multifidus (*b*) and longus colli (*d*). Objective magnification, ×20; bar, 100 μm; M, multifidus; LC, longus colli.

subsequent sectioning. Five serial 8 μm sections were cut from each of the tissue blocks on a Leica cryostat, in which cryostat object and chamber temperatures were pre-set to −20 °C. As for biopsy sampling, the sequence of serial sections in each case were collected following a random start such that on average, sections used in analysis were representative of full biopsy depth. Paired longus colli and multifidus transverse muscle sections corresponding to the same vertebral levels were mounted on non-adhesive glass slides and air-dried prior to staining. Sections were then stained with adenosine triphosphatase (ATPase) at pH = 9.4 and 4.3.

Method for determining muscle fibre composition

We did not attempt to differentiate between type IIC (transitional), type IIA (fast-oxidative) and type IIB (fast-glycolytic) fibres in light of postmortem delay in preparing the biopsies (Elder et al. 1982). Rather, observations were restricted to distinguish slow-oxidative (type I) fibres from fast-glycolytic (type II) fibres, for which ATPase staining at pH = 9.4 and 4.3 is routinely used. Under light microscopy type I fibres appeared dark and type II fibres light, in accordance with a modified staining protocol (Hamalainen & Pette, 1993). All slides with stained sections were coded so that subject characteristics were not known to the observer. Using a ×20 objective and a projectoscope fitted with automatic x,y coordinate stage advance, 4 tissue fields were randomly selected and counts of fibre number made. An average of 550 muscle fibres from C5–C7 in each subject were counted using this protocol. The sum of all type I and type II fibre counts made in each biopsy were used to estimate overall muscle fibre composition for the respective muscles in each subject.

RESULTS

Muscle histochemistry

Longus colli contained type I and type II fibres in approximately even ratios, while multifidus comprised predominantly type I fibres. These fibre differences are evident in micrographs of longus colli (Fig. 1 *c*, *d*) and multifidus (Fig. 1 *a*, *b*). On average longus colli comprised 53% type I fibres and 47% type II fibres, while on average multifidus comprised 77% type I fibres and 23% type II fibres (Fig. 2). Wilcoxon paired *t*-tests revealed significant fibre type differences in multifidus ($P < 0.01$) and type II fibre differences between longus colli and multifidus ($P < 0.01$) at C5–C7 (Fig. 2).

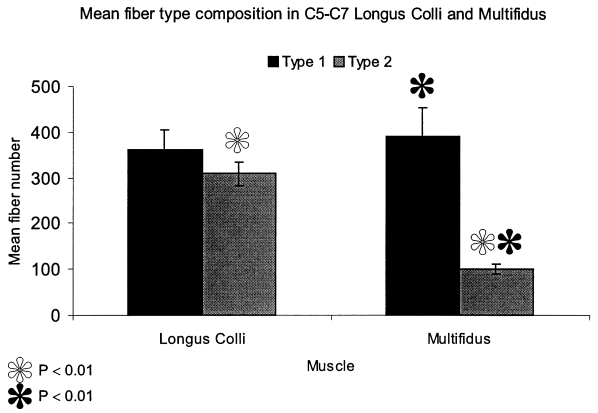

Fig. 2. Wilcoxon paired *t*-tests revealed significant intramuscular fibre type differences for multifidus and intermuscular type II fibre differences at C5–C7. Error bars represent standard error of the mean (S.E.M.; n = 16 subjects).

Age differences

Figure 1 illustrates the muscle fibre composition of multifidus and longus colli at the level of C6 in two subjects aged 36 (left) and 76 (right) years respectively. The histochemical profile of multifidus is indicated in the top panels (*a*, *b*) and that of longus colli on the bottom (*c*, *d*). Figure 1 reveals that fibre proportions remained largely unchanged in either muscle from age 36 (*a*, *c*) to 76 (*b*, *d*). Correlation and regression analysis of all subjects in the present study confirmed that fibre counts did not change in longus colli (type I, $c = -0.08$, $P = 0.78$ and type II, $c = 0.23$, $P = 0.40$) or multifidus (type I, $c = -0.48$, $P = 0.06$ and type II, $c = 0.14$, $P = 0.62$) with increasing age (Fig. 3).

Sex differences

The subject group was further examined by gender to determine whether differences in fibre composition

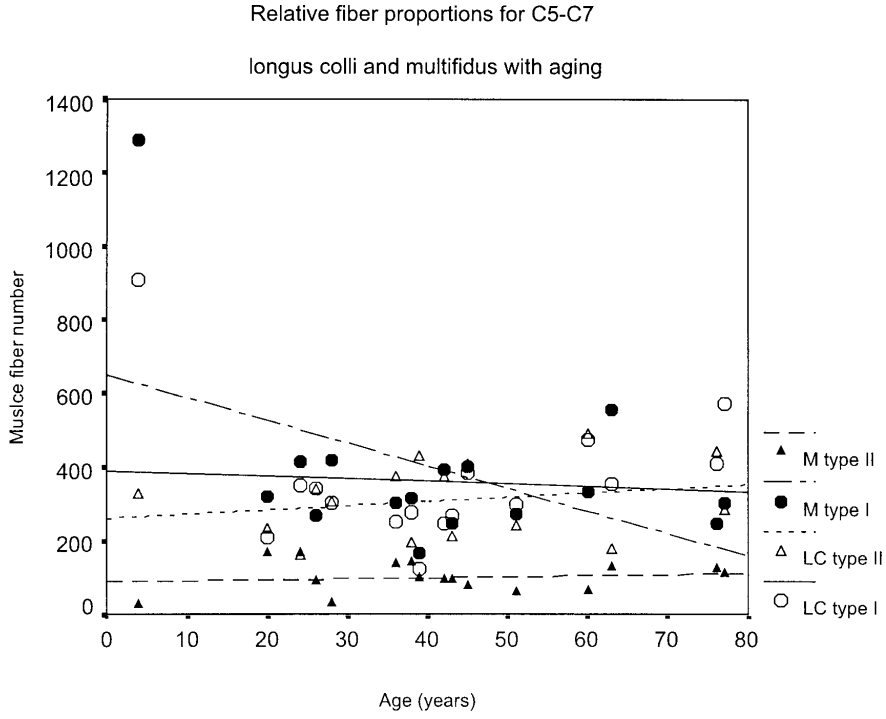

Fig. 3. Correlation and regression analysis of type I and type II fibre counts in longus colli and multifidus as a function of age. Fibre counts did not change in longus colli (type I, $c = -0.08$, $P = 0.78$ and type II, $c = 0.23$, $P = 0.40$) or multifidus (type I, $c = -0.48$, $P = 0.06$ and type II, $c = 0.14$, $P = 0.62$) with increasing age.

Table 1. *Muscle fibre composition by gender*

	Longus colli			Multifidus		
	Male	Female	*P*-value	Male	Female	*P*-value
n	10	6		10	6	
Age	40.2±6.6	45.0±8.2	0.66	40.2±6.6	45.0±8.2	0.66
Type I (%)	49.3±4.6	58.3±3.4	0.14	76.5±3.4	77.2±3.8	0.90
Type II (%)	50.7±4.6	41.7±3.4	0.14	23.5±3.4	22.8±3.8	0.90

±, standard error of the mean (S.E.M.).

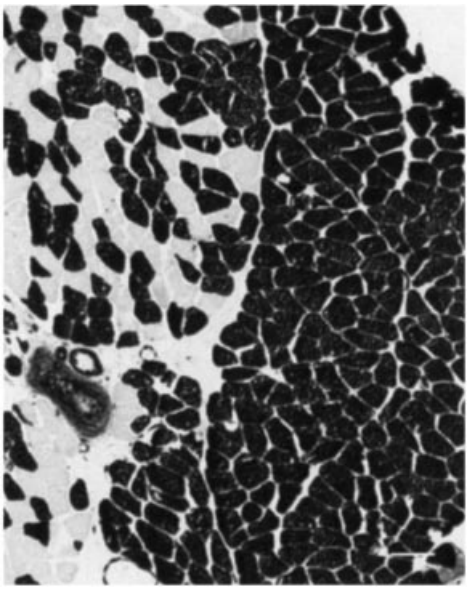

Fig. 4. Fibre distribution in longus colli at C5 for a subject aged 20 y. Section stained with adenosine triphosphatase (ATPase) following acid preincubation (pH = 9.4 and 4.3). Homogeneous type I fibres are evident to the right and mixed fibre distributions evident to the left. Objective magnification ×5; bar, 100 μm.

were apparent (Table). A 2-sample *t*-test revealed no difference ($P = 0.66$) in age range between males and females. Therefore the samples were statistically comparable, however two-sample *t*-tests of fibre composition revealed no gender differences in longus colli ($P = 0.14$) or multifidus ($P = 0.90$, Table).

Muscle fibre compartmentalisation

Figure 4 illustrates a section of longus colli muscle from a subject aged 20 y, in which a muscle fibre gradient is evident. A homogeneous type I fibre distribution is evident nearing the biopsy margin to the right, that is distinct from the mixed fibre representation to the left (Fig. 4). This was only observed in two samples of longus colli and was not observed in multifidus.

DISCUSSION

The objective of the present study was to characterise the fibre composition of 2 intrinsic and antagonistic muscles in the human neck spanning C5–C7 segments in autopsy tissue. Longus colli, a flexor muscle, comprised on average 53% type I and 47% type II fibres and in multifidus, a segmental stabiliser, the corresponding values were 77% type I and 23% type II fibres (Fig. 2). Furthermore, neither muscle sustained consistent changes in fibre composition with increasing age (Fig. 3). Results of the present study are comparable with those in the literature. Specifically, previous studies have confirmed that type I fibre proportions increase in extensors of the back from lumbar (57–65%) to thoracic (73–77%) regions (Joseph & McColl, 1961; Fidler et al. 1975; Selbie et al. 1993). The greater dependence on type I fibres with rostral muscle position is thought to be related to larger flexion moments and anterior displacement of rotational axes in the thoracic spine (Joseph & McColl, 1961). Previous studies have also failed to identify consistent changes in muscle fibre composition with increasing age (Grimby et al. 1984; Rantanen et al. 1994). The net effect of these observations implies a greater dependence on slow-twitch postural fibres in vertebral muscles, that is conserved with age and increases sequentially from lumbar to cervical levels.

The histochemical profile of neck muscles has to date received little attention in healthy or diseased subjects. Combined with this scarcity it is not known whether fibre type changes are dependent on factors such as gender (Lindman et al. 1990, 1991; Uhlig et al. 1995; Mannion et al. 1997; Ng et al. 1998), or the presence and duration of symptoms (Fidler et al. 1975; Jowett et al. 1975; Zetterberg et al. 1983; Dhoot & Pearce, 1984; Ford et al. 1984; Rantanen et al. 1993; Uhlig et al. 1995; Meier et al. 1997; Ng et al. 1998; Zhao et al. 2000), where these exist. However it is generally acknowledged that large intra- and intermuscular variability exists within and between

individuals. To this end, many authors have highlighted the need for adopting best practice sampling techniques to ensure that results are non-biased and better represent the true histochemical profile of the muscle(s) concerned (Goldspink et al. 1973; Heffron & Hegarty, 1974; Elder et al. 1982; Lexell et al. 1983; Richmond & Armstrong, 1988; Richmond et al. 1999). To our knowledge, only 3 previous studies have examined fibre distributions in neck muscle obtained from control autopsy tissue. None of these have examined intrinsic muscles of the neck. Rather, these studies have described fibre composition in sternocleidomastoid and trapezius, both large and superficial muscles. Uhlig et al. (1995) conducted a thorough examination of type I, IIC, IIA and IIB fibre composition and transformations in various dorsal (rectus capitis posterior major, obliquus capitis inferior, splenius capitis and trapezius) and ventral (sternocleidomastoid, omohyoid and longus colli) neck muscles, obtained from patients suffering cervical dysfunction. With respect to longus colli in patients suffering post-traumatic instability, Uhlig et al. (1995) reported a mean of 49.7% type I and 50.3% overall type II fibres in males, compared with 49.3% and 50.7% for corresponding muscle fibres in males of our study (Table). Similarly, Uhlig et al. (1995) reported a mean of 69.1% type I and 30.9% overall type II fibres in females, compared with 58.3% and 41.7% for corresponding muscle fibres in females of the present study (Table). We found no gender differences in fibre composition for either longus colli ($P = 0.14$) or multifidus ($P = 0.90$). Aside from gender these comparisons of longus colli reflect test and autopsy studies and their close approximation lends tentative support to the notion that muscle fibre ratios remain constant, independent of the presence or absence of disease. Low back pain promotes fibre transformation affecting the balance of type II fibres, although type I: type II ratios resemble normal values (Fidler et al. 1975; Jowett et al. 1975; Rantanen et al. 1993; Mannion et al. 1997; Zhao et al. 2000). A notable exception concerns patients with idiopathic scoliosis, in which elevated type I fibre proportions are routinely observed at the apex of the spinal convexity (Ford et al. 1984; Meier et al. 1997).

The metabolic requirements of an extrafusal muscle fibre define its histochemistry and functional properties (Fidler et al. 1975; Ng et al. 1998). Longus colli comprises an even type I:type II fibre ratio and can therefore respond equally to postural and phasic demands, whereas multifidus is predominantly type I in character (4:1) reflecting its postural function in resisting cervical flexion.

Muscle fibre compartmentalisation

The mosaic pattern of fibre distribution typical of mammalian muscle occurs as a function of differential alpha motor unit distribution within muscle fascicles (Richmond et al. 1999). However recent studies of splenius and biventer cervicis muscles in the neck of the cat (Richmond et al. 1985; Richmond & Armstrong, 1988), obliquus capitis inferior in the primate (Richmond et al. 1999) and cervical spinal accessory muscles in the rat (Brichta et al. 1987) have confirmed that a motor unit's fibre type complement may be restricted to specific zones or muscle compartments. Where fibre gradients are evident type I fibres occupy deep and type II fibres more superficial regions, the former recruited for maintenance of posture, the latter for phasic movements (Richmond & Armstrong, 1988; Selbie et al. 1993; Richmond et al. 1999). Fibre compartmentalisation was observed in two longus colli biopsies in the present study, one of which is depicted in Figure 4. By contrast no fibre gradients were observed in biopsies of multifidus, a finding consistent with observations made in deep dorsal cervical muscles of the rat (Callister et al. 1987). The lack of observed fibre gradient may be anticipated, since compartmentalisation is usually evident in muscles of complex architecture that contain an abundance of intramuscular tendinous inscriptions.

Sampling considerations

This is the first study of its kind that has examined longus colli and multifidus in autopsy tissue. Whilst the feasibility of histochemical staining on autopsy muscle has previously been demonstrated following lengthy delays (Eriksson et al. 1980), muscle fibre analysis in this study has been made conservatively since biopsies were not harvested from living subjects (Ng et al. 1998). Accordingly we sampled from three segmental levels, differentiated only slow type I from fast type II fibres and made no assessment of fibre dimensions in light of tissue shrinkage (Goldspink et al. 1973; Heffron & Hegarty, 1974; Elder et al. 1982; Lexell et al. 1983). Best practice sampling procedures of this sort provide reliable estimates of muscle fibre type, although to be regarded as rigorous and truly unbiased, these factors should be considered in concert with the theory of muscle compartmentalisation.

The present study has characterised muscle fibres for two intrinsic neck muscles in man, for which

normative data was previously unavailable. Distinct from our hypotheses, there are significant histochemical differences between prevertebral longus colli and postvertebral multifidus. Furthermore no changes in fibre type proportion are evident in either muscle with increasing age. In contrast to the effects of scoliosis, age-related loss of cervical lordosis with osteoligamentous change has little effect on muscle fibre composition. Therefore it appears that conditions resulting in spinal malalignment may act as the primary stimulus for muscle fibre transformation. This study provides a greater understanding of the functional capacity for two intrinsic muscles in the human neck. Further work incorporating a larger cross-sectional sample of ages is necessary to establish the functional characteristics of other segmental and global neck muscles.

ACKNOWLEDGEMENTS

The authors would like to thank Dr Ken Opeskin, then of the Victorian Institute of Forensic Medicine (VIFM), whose collaboration facilitated tissue harvesting for the present study. Technical assistance received from Mr Scott Cuffe in relation to muscle fibre staining was also greatly appreciated.

REFERENCES

ABERNETHY PJ, THAYER R, TAYLOR AW (1990) Acute and chronic responses of skeletal muscle to endurance and sprint exercise. A review. *Sports Medicine* **10**, 365–389.

ANDERSEN P, HENRIKSSON J (1977) Training induced changes in the subgroups of human type II skeletal muscle fibers. *Acta Physiologica Scandinavica* **99**, 123–125.

BAYLEY JC, YOO JU, KRUGER DM, SCHLEGEL J (1995) The role of distraction in improving the space available for the cord in cervical spondylosis. *Spine* **20**, 771–775.

BRICHTA AM, CALLISTER RJ, PETERSON EH (1987) Quantitative analysis of cervical musculature in rats: histochemical composition and motor pool organization. I. Muscles of the spinal accessory complex. *Journal of Comparative Neurology* **255**, 351–368.

CALLISTER RJ, BRICHTA AM, PETERSON EH (1987) Quantitative analysis of cervical musculature in rats. Histochemical composition and motor pool organization. II. Deep dorsal muscles. *Journal of Comparative Neurology* **255**, 369–385.

CONLEY MS, MEYER RA, BLOOMBERG JJ, FEEBACK DL, DUDLEY GA (1995) Noninvasive analysis of human neck muscle function. *Spine* **20**, 2505–2512.

DHOOT GK, PEARCE GW (1984) Transformation of fiber types in muscular dystrophies. *Journal of the Neurological Sciences* **65**, 17–28.

ELDER GC, BRADBURY K, ROBERTS R (1982) Variability of fiber type distributions within human muscles. *Journal of Applied Physiology* **53**, 1473–1480.

ERIKSSON PO, ERIKSSON A, RINGQVIST M, THORNELL LE (1980) The reliability of histochemical fiber typing of human necropsy muscles. *Histochemical Journal* **65**, 193–205.

FIDLER MW, JOWETT RL, TROUP JD (1975) Myosin ATPase activity in multifidus muscle from cases of lumbar spinal derangement. *Journal of Bone and Joint Surgery* **57B**, 220–227.

FORD DM, BAGNALL KM, McFADDEN KD, GREENHILL BJ, RASO VJ (1984) Paraspinal muscle imbalance in adolescent idiopathic scoliosis. *Spine* **9**, 373–376.

GOLDSPINK G, GELDER S, CLAPISON L, OVERFIELD P (1973) Pre- and post-rigor fixation of muscle. *Journal of Anatomy* **114**, 1–6.

GRIMBY G, ANIANSSON A, ZETTERBERG C, SALTIN B (1984) Is there a change in relative muscle fiber composition with age? *Clinical Physiology* **4**, 189–194.

HAMALAINEN N, PETTE D (1993) The histochemical profiles of fast fiber types IIB, IID, and IIA in skeletal muscles of mouse, rat, and rabbit. *The Journal of Histochemistry and Cytochemistry* **41**, 733–743.

HEFFRON JJ, HEGARTY PV (1974) Evidence for a relationship between ATP hydrolysis and changes in extracellular space and fiber diameter during rigor development in skeletal muscle. *Comparative Biochemistry and Physiology* **49A**, 43–56.

JOHNSON MA, POLGAR J, WEIGHTMAN D, APPLETON D (1973) Data on the distribution of fiber types in thirty-six human muscles. An autopsy study. *Journal of the Neurological Sciences* **18**, 111–129.

JOOSAB M, TORODE M, PRASADA RAO PVV (1994) Preliminary findings on the effect of load-carrying to the structural integrity of the cervical spine. *Surgical and Radiologic Anatomy* **16**, 393–398.

JOSEPH J, McCOLL I (1961) Electromyography of muscles of posture: Posterior vertebral muscles in males. *Journal of Physiology* **157**, 33–37.

JOWETT RL, FIDLER MW, TROUP JD (1975) Histochemical changes in the multifidus in mechanical derangements of the spine. *Orthopaedic Clinics of North America* **6**, 145–161.

KLARA PM, FOLEY K (1993) Surgical treatment of osteophytes and calcified discs of the cervical spine. *Neurosurgery Clinics of North America* **4**, 53–60.

LEXELL J, HENRIKSSON-LARSEN K, SJOSTROM M (1983) Distribution of different fiber types in human skeletal muscles. 2. A study of cross-sections of whole m. vastus lateralis. *Acta Physiologica Scandinavica* **117**, 115–122.

LIEBER RL, FRIDEN JO, HARGENS AR, DANZIG LA, GERSHUNI DH (1988) Differential response of the dog quadriceps muscle to external skeletal fixation of the knee. *Muscle & Nerve* **11**, 193–201.

LINDMAN R, ERIKSSON A, THORNELL LE (1990) Fiber type composition of the human male trapezius muscle: enzyme-histochemical characteristics. *American Journal of Anatomy* **189**, 236–244.

LINDMAN R, ERIKSSON A, THORNELL LE (1991) Fiber type composition of the human female trapezius muscle: enzyme-histochemical characteristics. *American Journal of Anatomy* **190**, 385–392.

MACNAB I (1975) Cervical spondylosis. *Clinical Orthopaedics and Related Research* **109**, 69–77.

MANNION AF, DUMAS GA, COOPER RG, ESPINOSA FJ, FARIS MW, STEVENSON JM (1997) Muscle fiber size and type distribution in thoracic and lumbar regions of erector spinae in healthy subjects without low back pain: normal values and sex differences. *Journal of Anatomy* **190**, 505–513.

MAYOUX-BENHAMOU MA, REVEL M, VALLEE C, ROUDIER R, BARBET JP, BARGY F (1994) Longus colli has a postural function on cervical curvature. *Surgical and Radiologic Anatomy* **16**, 367–371.

MEIER MP, KLEIN MP, KREBS D, GROB D, MUNTENER M (1997) Fiber transformations in multifidus muscle of young patients with idiopathic scoliosis. *Spine* **22**, 2357–2364.

NG JK, RICHARDSON CA, KIPPERS V, PARNIANPOUR M (1998) Relationship between muscle fiber composition and

functional capacity of back muscles in healthy subjects and patients with back pain. *Journal of Orthopaedic and Sports Physical Therapy* **27**, 389–402.

RANTANEN J, HURME M, FALCK B, ALARANTA H, NYKVIST F, LEHTO M et al. (1993) The lumbar multifidus muscle five years after surgery for a lumbar intervertebral disc herniation. *Spine* **18**, 568–574.

RANTANEN J, RISSANEN A, KALIMO H (1994) Lumbar muscle fiber size and type distribution in normal subjects. *European Spine Journal* **3**, 331–335.

RICHMOND FJ, MACGILLIS DR, SCOTT DA (1985) Muscle-fiber compartmentalization in cat splenius muscles. *Journal of Neurophysiology* **53**, 868–885.

RICHMOND FJ, ARMSTRONG JB (1988) Fiber architecture and histochemistry in the cat neck muscle, biventer cervicis. *Journal of Neurophysiology* **60**, 46–59.

RICHMOND FJ, SINGH K, CORNEIL BD (1999) Marked non-uniformity of fiber-type composition in the primate suboccipital muscle obliquus capitis inferior. *Experimental Brain Research* **125**, 14–18.

ROSE SJ, ROTHSTEIN JM (1982) Muscle mutability. Part 1. General concepts and adaptations to altered patterns of use. *Physical Therapy* **62**, 1773–1787.

SELBIE WS, THOMSON DB, RICHMOND FJ (1993) Sub-occipital muscles in the cat neck: Morphometry and histochemistry of the rectus capitis muscle complex. *Journal of Morphology* **216**, 47–63.

SIRCA A, KOSTEVC V (1985) The fiber type composition of thoracic and lumbar paravertebral muscles in man. *Journal of Anatomy* **141**, 131–137.

THORSTENSSON A, CARLSON H (1987) Fiber types in human lumbar back muscles. *Acta Physiologica Scandinavica* **131**, 195–202.

UHLIG Y, WEBER BR, GROB D, MUNTENER M (1995) Fiber composition and fiber transformations in neck muscles of patients with dysfunction of the cervical spine. *Journal of Orthopaedic Research* **13**, 240–249.

VASAVADA AN, LI S, DELP SL (1998) Influence of muscle morphometry and moment arms on the moment-generating capacity of human neck muscles. *Spine* **23**, 412–422.

ZETTERBERG C, ANIANSSON A, GRIMBY G (1983) Morphology of the paravertebral muscles in adolescent idiopathic scoliosis. *Spine* **8**, 457–462.

ZHAO WP, KAWAGUCHI Y, MATSUI H, KANAMORI M, KIMURA T (2000) Histochemistry and morphology of the multifidus muscle in lumbar disc herniation. *Spine* **25**, 2191–2199.