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SUSTAINED FORCE DEVELOPMENT: SPECIALIZATIONS AND VARIATION AMONG THE VERTEBRATES

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SUMMARY

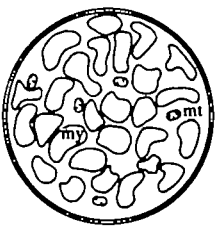
The kinds of muscle fibre that are recruited for sustained force production by different vertebrates are described. Although aerobic metabolism always accounts for a significant proportion of their ATP turnover, no single characteristic such as colour, number and form of motor endplates, membrane properties, myosin isotype or contraction speed is diagnostic of such muscles. As mechanical power output increases, there is a tendency for a decrease in fatigue resistance with repetitive usage and an increase in both aerobic capacity and the fraction of energy requirements derived from glycolysis.

INTRODUCTION

The ability of a muscle to function in sustained force generation is dependent on the types and proportion of fibres present and on their pattern of recruitment during activity. Within the vertebrates there is great variety in the design of muscle fibres involved in sustained force generation (Fig. 1). No *single* characteristic, for example, colour, mitochondrial volume density, innervation pattern, or crossbridge cycling time is diagnostic of such muscles. Furthermore, not all of these kinds of muscle are found in any one class of vertebrate. The development of histochemical techniques has led to numerous attempts to classify these broad groupings of characteristics into different 'fibre types'. Attempts to translate classifications of fibre types derived for one vertebrate group to others is fraught with difficulties and has given rise to a certain amount of confusion in the literature. For example, whilst all very slow muscles are multiply innervated so are some of the fastest (e.g. in fishes). Similarly, whilst most muscles involved in sustained force generation are red, some of the most fatigue resistant fibres are pale. This is because they have slow contraction speeds (Fig. 2), and low mechanical power outputs and hence do not require high concentrations of myoglobin or high capillary or mitochondrial volume densities to maintain a constant ATP supply. With the exception of mammals and fish, little is known about the patterns of recruitment of muscle fibres during locomotion. Techniques available for studying recruitment patterns include electromyography, glycogen depletion by

Key words: Skeletal muscle, vertebrates, fibre type.

JP (amphibia)
JP/AP (birds)

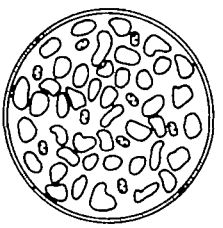


SLOW TYPE MYOSIN

PALE TONIC FIBRES
Characteristics

M-line:	absent
Z-disc:	thick-jagged
$Vv_{(mt,f)}$:	low, $\leq 5\%$
SR:	sparse
Glycolytic capacity:	low
Occurence:	most vertebrate classes

JP and/or AP

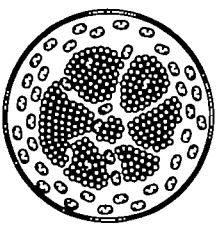


SLOW TYPE MYOSIN

PALE/PINK FIBRES
Characteristics

M-line:	present
Z-disc:	thick-jagged
$Vv_{(mt,f)}$:	intermediate, $\leq 10\%$
SR:	moderately developed
Glycolytic capacity:	?
Occurrence:	amphibia, reptiles, birds

JP

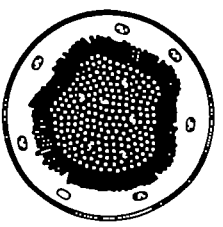


FAST OR SLOW TYPE MYOSIN

RED FIBRES
Characteristics

M-line:	present
Z-disc:	straight
$Vv_{(mt,f)}$:	usually high 15–50 %
SR:	moderately well developed
Glycolytic capacity:	low to high
Occurrence:	agnathans (lamprey, hagfish) fish

AP and/or JP (?)



FAST TYPE MYOSIN

PALE/PINK FIBRES
Characteristics

M-line:	present
Z-disc:	straight
$Vv_{(mt,f)}$:	low-intermediate 2–9 %
SR:	very well developed
Glycolytic capacity:	high
Occurrence:	advanced teleost fish

fibres and force recordings using strain gauges attached to tendons (see Armstrong, 1981).

MULTIPLY-INNERVATED FIBRES

Pale/pink (tonic) muscles

In general, muscle fibres with the greatest capacity for sustained force generation are those involved in postural support for skeleton and/or soft tissue. These are often referred to as tonic or 'true slow fibres' and occur in all land vertebrates, being particularly common in amphibians and reptiles, where they may have a role in

stabilizing joints (Fig. 1). Tonic fibres are invariably multiply innervated and are amongst the slowest contracting muscles (Fig. 2). They give slow graded contractions dependent on the extent of membrane depolarization by junction potentials (Kuffler & Vaughan-Williams, 1953). In many cases, junction potentials can be graded into a number of individual components by varying the strength of stimulation to the motor nerve, providing evidence for polyneuronal innervation (Hess & Pilar, 1963; Elizalde, Huerta & Stefani, 1983). Tonic fibres produce prolonged contractions following the application of acetylcholine or after immersion in solutions containing high KCl concentrations ($\geqslant 30\,\text{mmol}\,l^{-1}$) (Kuffler & Vaughan-Williams, 1953; Ginsborg, 1960; Hess & Pilar, 1963). Structurally, such fibres are characterized by the absence of M-lines, by thick jagged Z-lines in longitudinal section and by the presence of large, irregular shaped ($3–5\,\mu m^2$) myofibrils in cross-section (Smith & Ovalle, 1973; Ovalle, 1982). This arrangement of myofibrils is sometimes termed 'Felderstruktur' (Hess, 1970). Volume densities of mitochondria are generally low and their internal cristae structure is usually simple (Page, 1965). Amphibian tonic fibres stain weakly for both mitochondrial and glycolytic enzyme activities (Spurway, 1984). The sarcoplasmic

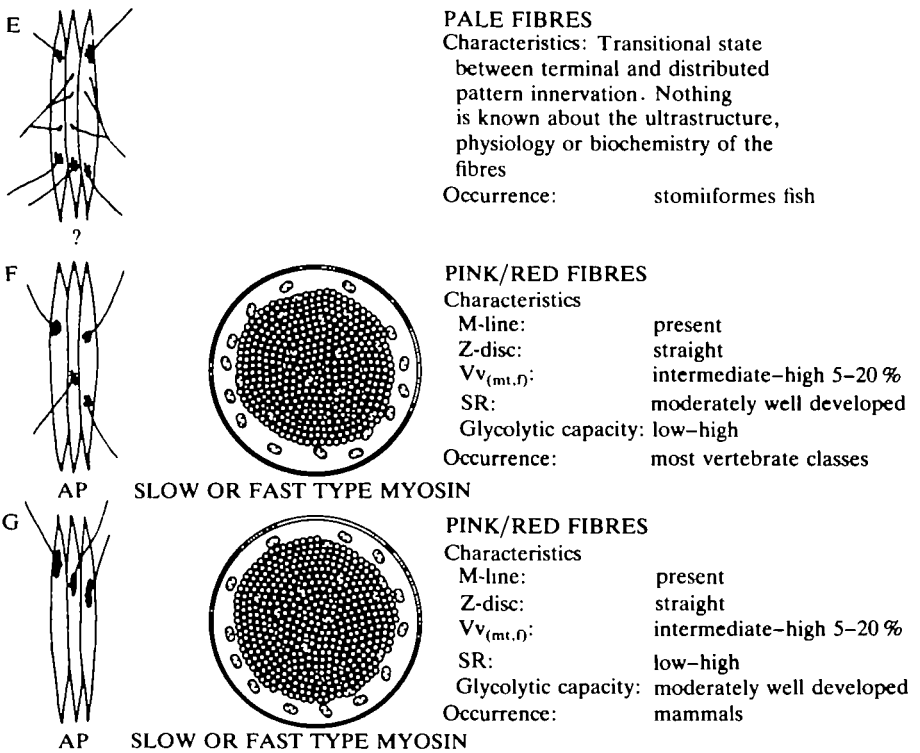


Fig. 1. (*A*)–(*G*). Diversity of muscle fibres involved in sustained force generation among vertebrates. These diagrams are not intended to represent specific 'fibre types', rather broad groupings of structural and physiological characteristics. Abbreviations: $Vv_{(mt,f)}$, mitochondrial volume density; SR, sarcoplasmic reticulum; my, myofibrils; mt, mitochondria; JP, junction potentials; AP, action potentials.

reticulum is generally sparse and diadic and triadic coupling between sarcoplasmic reticulum (SR) and T-tubes is fairly infrequent (Page, 1965; Flitney, 1971; Ovalle, 1982). For example, the sarcotubular system in tonic fibres of the chicken anterior latissimus dorsi (ALD) muscle (which functions to hold the wings back against the body) only constitutes 0·7 % of fibre volume (Ovalle, 1982).

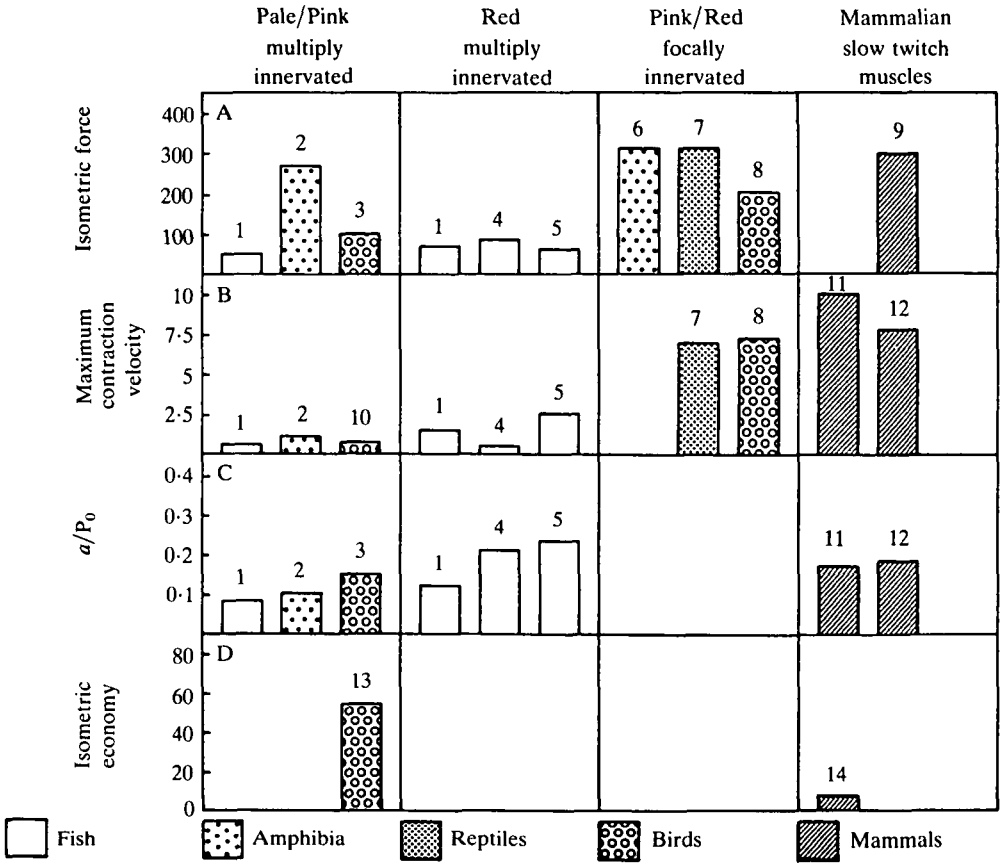


Fig. 2. Contractile properties of some of the kinds of muscle fibres involved in sustained force generation. (A) Isometric force ($kN\,m^{-2}$); (B) maximum contraction velocity (muscle length s^{-1}, $L_0\,s^{-1}$); (C) Hill's coefficient a/P_0 provides a measure of the curvature of the force-velocity (P-V) relation; (D) isometric economy of chemically poisoned whole muscles ($g\,s^{-1}\,\mu mol^{-1}$ high energy phosphate). *Source of data* 1. Dogfish (*Scyliorhinus canicula* L.) myotomes, Q. Bone, I. A. Johnston, A. Pulsford & K. P. Ryan, in preparation. 2. Aquatic toad (*Xenopus laevis*) iliofibularis muscle, Lännergren, 1978 (live fibres, 22°C). 3. Chicken, anterior latissimus dorsi muscle (ALD), Moore, Johnston & Goldspink, 1983 (skinned fibres, 35°C). 4. Cod (*Gadus morhua* L.) myotomes, Altringham & Johnston, 1982 (skinned fibres, 8°C). 5. Pacific blue marlin (*Makaira nigricans*) myotomes, Johnston & Salamonski, 1984 (skinned fibres, 25°C). 6. Aquatic toad, iliofibularis muscle Type 2 fibres, Lännergren & Smith (1966) (live fibres, 22°C). 7. Desert iguana (*Dipsosaurus dorsalis*) iliofibularis muscle, Johnston & Gleeson, 1984 (skinned fibres, 40°C). 8. Quail pectoralis major muscle, C. J. M. Nicol & I. A. Johnston, unpublished results. 9. Rat soleus muscle, Stephenson & Williams (1981) (skinned fibres, 35°C). 10. Chicken ALD muscle, Canfield, 1971, (whole muscle, 20°C). 11. Mouse soleus muscle, Luff, 1981 (whole muscle, 35°C). 12. Rat soleus muscle, Close, 1964 (whole muscle, 35°C). 13. Chicken ALD muscle, Goldspink, 1975 [1-fluoro-2,4 dinitrobenzene (FDNB) poisoned whole muscle 35°C]. 14. Hamster soleus muscle, Goldspink, 1975 (iodoacetate/N_2 poisoned whole muscle, 20°C).

Amongst reptiles, tonic fibres are particularly common in the trunk muscles of snakes and slowworms where they may constitute 30–40 % of the total muscle (see Guthe, 1981 for a review). Multiply innervated fibres are uncommon in mammals, principally occurring in certain extraocular muscles (Hess & Pilar, 1963; Hess, 1970).

The density, distribution and morphology of nerve terminals on tonic fibres varies considerably between muscles and species. For example, nerve terminals occur every 10–30 μm on fibres from the superior rectus muscle of the cat, but are 750–1000 μm apart on fibres from the ALD of the adult chicken (Hess, 1970). Postjunctional sarcolemmal infoldings are usually absent from the endplates of tonic fibres.

Maximum forces (P_0) produced by tonic fibres are 50–100 kN m^{-2} for chicken ALD muscle (Rall & Schottelius, 1973; Moore, Johnston & Goldspink, 1983), 294 kN m^{-2} for garter snake costocutaneous muscle (Ridge, 1971) and 300 kN m^{-2} for toad iliofibularis muscle (Lännergren, 1978). The higher range of forces produced by amphibian and reptilian tonic fibres are comparable to those for twitch fibres (Fig. 2).

Unloaded contraction speeds for tonic fibres are generally 1·0 muscle length s^{-1} or less, and are amongst the lowest for the kinds of muscle illustrated in Fig. 1. Lännergren (1978) has investigated the force-velocity (P-V) characteristics of 'tonic' fibres isolated from the iliofibularis muscle of the aquatic toad, *Xenopus laevis*. Calculations showed that crossbridge turnover rates were about 15 times lower than for twitch fibres. The shape of the P-V curve can be described by a variety of empirical equations. Hill's (1938) equation for muscle shortening [$a(P+V) = b(P_0-P)$], where P is muscle load, V is the velocity of contraction and a and b are constants, provides a good fit for most muscles for loads less than 0·6 P_0. The constant a/P_0 provides a measure of the curvature of the P-V relation and is characteristic of a particular muscle. Values for a/P_0 for toad tonic fibres (0·10) are lower than for twitch fibres (0·38) indicating a more curved P-V relation (Lännergren, 1978). Tortoise rectus femoris muscle has an a/P_0 value of 0·07 at 0 °C (Woledge, 1968), compared with 0·26 for frog sartorius muscle (fast twitch) at the same temperature (Hill, 1938). On the basis of heat measurements during recovery from isotonic shortening, Woledge (1968) argued that tortoise slow muscle is around 70 % more efficient in converting free energy into work than frog twitch fibres at 0 °C. However, a/P_0 values for chicken ALD fibres (0·15) are similar to that obtained for the twitch fibres of the posterior latissimus dorsi muscle and do not fit into this pattern (Canfield, 1971). The chicken PLD muscle reaches maximum tetanic tension 10 times faster and relaxes 8 times faster than the ALD but begins to fatigue after a few seconds' continuous stimulation at 50 Hz, compared to over 2 min for the ALD (Canfield, 1971). Goldspink (1975) measured the isometric economy of these two muscles by measuring ATP utilization following poisoning of the creatine kinase reaction with 1-fluoro-2,4 dinitrobenzene (FDNB). The cost of maintaining isometric tension was 250 times greater for the ALD than PLD (see also Fig. 2).

Relatively little is known about the patterns of fibre recruitment in tonic muscles and this would be a fruitful area for future study. The opercularis muscle of the frog *Rana catesbeiana* contains a mixture of twitch and tonic fibres. It is thought to have a role in detecting sounds and vibrations when the frog is submerged with the tip of its

snout exposed to the air. From electromyographical recordings Hethrington & Lombard (1983) have reported that the erratic low-amplitude signals obtained from the muscle during submergence give way to rhythmic low amplitude activity on emergence. Muscle e.m.g.s can be resolved into components with characteristic frequencies of 30 Hz and 200–250 Hz which have been attributed to the firing of tonic and twitch fibres respectively.

Fish have less of a need for muscles dedicated to postural support than land vertebrates, and such fibres are uncommon. However, fibres with very similar structural, electrophysiological and contractile properties to tonic fibres have been described from the myotomal muscle of dogfish (*Scyliorhinus canicula* L.) (Q. Bone, I. A. Johnston, A. Pulsford & K. P. Ryan, in preparation). These large diameter pale fibres constitute less than 0·5 % of the muscle in any segment and may have a role in maintaining body tone and/or attitude when the dogfish is resting on the seabed. Skinned fibres from dogfish superficial muscle (12°C) have low maximum Ca^{2+}-activated forces ($49\,kN\,m^{-2}$) and unloaded contraction velocities ($0{\cdot}58\,L_0\,s^{-1}$) and produce only 16 % and 2·5 % of the maximum power output of red and white myotomal muscle fibres, respectively (Q. Bone, I. A. Johnston, A. Pulsford & K. P. Ryan, in preparation). Fibres with similar ultrastructural characteristics have also been described for a teleost fish, the stickleback, (*Gasterosteus aculeatus* L.) (Kilarski & Kozlowska, 1983) but have not so far reported for agnathans.

In some muscles, tonic fibres may be sub-divided into two or more types. For example, in the anterior latissimus dorsi muscle of the chicken, Type I and Type II tonic fibres have been distinguished (Ovalle, 1982). Type II fibres represent 16 % of the total population and differ from the more numerous Type I fibres in having M-lines, higher mitochondrial volume densities and a more abundant sarcotubular system (Fig. 1). These results suggest that they probably have faster contraction speeds than the Type I fibres. Ginsborg (1960) found that 7 out of 71 multiply innervated fibres of the chicken biventer cervicis muscle produced action potentials following maximal nerve stimulation. It is possible that these action potential generating fibres correspond to the Type II fibres described by Ovalle (1982).

Lännergren (1979) has described an 'intermediate' twitch fibre from the iliofibularis muscle of the aquatic toad (*Xenopus laevis*) which has similar structural characteristics to those of true slow or tonic fibres in the same species. These fibres are multiply innervated by 5–6 discrete but diffuse endplates, they have wide (~80 nm), slightly wavy Z-lines, a sparse sarcoplasmic reticulum, relatively few small mitochondria and large irregular ($1{\cdot}7\,\mu m^2$) myofibrils in cross-section (Lännergren, 1979). Intermediate fibres give long-lasting K^+ contractures, respond to low doses of acetylcholine and give all or none twitches. Maximum tetanic tensions were produced at a stimulation frequency of 40–60 Hz and the twitch/tetanic ratio was 0·21.

Extrapolated values for V_{max} from the P-V relationship of these fibres was $2{\cdot}2\,L_0\,s^{-1}$ or around twice that of tonic fibres at 20°C (Lännergren, 1978, 1979). Structurally, the 'intermediate' or type 4 fibres described for the toad by Lännergren (1979) are similar to the Type II fibres described for the chicken ALD by Ovalle (1982) and for certain external eye muscles of the rat by Mayr (1971) (Fig. 1B).

Red muscles

The parietal muscles of hagfish (*Myxine glutinosa*) (Agnatha) contain both multiply innervated slow and fast twitch fibres (Andersen, Jansen & Loying, 1963). Slow fibres differ from those of amphibia in that they receive only one motor neurone from each myoseptal end and do not produce quantized junction potentials on nerve stimulation (Andersen *et al.* 1963). In contrast, fish red fibres are polyneuronally innervated (Bone, 1964).

Stanfield (1972) found that 8 out of 27 red fibres examined from the myotomal muscle of the elasmobranch *Scyliorhinus canicula* produced a significantly large inward current on depolarization to suggest they might be capable of generating action potentials, although one was never observed. It seems probable that fish red fibres are normally activated by junction potentials. The structure and metabolism of agnathan and fish multiply innervated fibres differ from that described above for 'higher' vertebrates (see Bone, 1978; Johnston, 1981, 1983 for reviews). These differences largely reflect their role in recruitment during slow swimming. Myofibrils in fish red fibres are small ($\sim 1\ \mu m^2$) and regular in cross section occupying around 50–65 % of fibre volume (Bone, 1978; Johnston, 1981). The sarcotubular system is relatively well developed, volume densities of SR are 6 % for eel (*Anguilla anguilla*) (Egginton & Johnston, 1982), 2·7 % for anchovy (*Engraulis encrasicolus* L.) (Johnston, 1982) and 5·1 % for trout (*Salmo gairdneri*) (Nag, 1972). Mitochondrial volume densities ($Vv_{(mt,f)}$) for fish red fibres are in the range 15–46 % (see Johnston, 1983). In anchovy, red muscle fibres are flattened in cross section, and on average each fibre is surrounded by 13 capillaries ($6000\ mm^{-2}$). More than 95 % of myofibrils in these fibres are adjacent to mitochondria which have a dense and tubular cristae structure (Johnston, 1982). The most important lipid fuels are fatty acids in teleosts and ketone bodies in elasmobranchs (Zamitt & Newsholme, 1979). Fish red muscle fibres vary considerably in their capacity for anaerobic glycogenolysis depending on the mode of swimming and life style of each species (Johnston, 1983).

Maximum force-production by fish red fibres is in the range $50–100\ kN\ m^{-2}$ (Fig. 2). The low force values are explained in part by their high volume densities of mitochondria which reduce the cross sectional area available for myofibrils. Extrapolated values for V_{max} for red myotomal muscle fibres are around 30–50 % of that of white twitch fibres and are in the range $0·6–3·0\ L_0\ s^{-1}$ (Altringham & Johnston, 1982; Johnston & Brill, 1984).

White fibres

White muscles from hagfish, lamprey, elasmobranchs, dipnoans, chondrosteans and teleosts with primitive taxonomic features are innervated by a single endplate of variable form (Bone, 1964). They are not involved in sustained force generation and are only recruited at burst swimming speeds. White fibres in these animals quickly fatigue on repetitive stimulation, have very low mitrochondrial volume densities ($\leqslant 1$ %) and capillary densities ($3–110\ mm^{-2}$) and a high glycolytic capacity (see Bone, 1978; Johnston, 1981, 1983). In contrast, white fibres in most advanced teleost

groups are polyneuronally innervated in a similar manner to the red fibres (Bone, 1964). There is electromyographical evidence that in some species multiply innervated white fibres are recruited during sustained swimming activity. For example, the threshold speeds for recruitment of white fibres for carp (*Cyprinus carpio*) is 2·1 body-lengths (Johnston, Davison & Goldspink, 1977) and 1·8 body-lengths for brook trout (*Salvelinus fontinalis*) (Johnston & Moon, 1980). These are speeds that can be maintained practically indefinitely. The metabolic characteristics of carp and trout white fibres differ from those of fish with focal patterns of innervation. Many multiply innervated teleost white muscles have mitochondrial volume densities (1000–1600 mm^{-2}) that are significantly higher than fibres with focal patterns of innervation (Johnston, 1983) consistent with a somewhat higher aerobic capacity. Hudson (1969) carried out an electrophysiological study on the multiply innervated white muscle of the teleost fish, *Myoxocephalus scorpius*. He found that stimulation of spinal nerves produced either local junction potentials leading to a slow graded contraction or a propagated action potential resulting in a fast twitch (Hudson, 1969). In contrast, elasmobranch white fibres which are focally innervated, only produce over-shooting action potentials (Hagiwara & Takahashi, 1967). The relationship between the activation of teleost white fibres and their pattern of recruitment during sustained and burst swimming remains to be established. Since multiply innervated white muscles in teleosts also function in peak force generation (in some species exclusively), they also have small, regular, densely packed myofibrils, an extensive sarcoplasmic reticulum (13·7 % in rainbow trout, Nag, 1972) and a well developed glycolytic capacity (Johnston & Moon, 1981).

In the stomiiformes (teleostei) both distributed and terminal patterns of innervation are present on the same fibres and this may represent a transitional stage in the evolution of the multiply innervated white muscles found in the advanced teleosts (Bone & Ono, 1982). Nothing is known about the structure, physiology or the recruitment patterns of these fibres (Fig. 1E).

FOCALLY INNERVATED FIBRES

Pink or red fibres with one or few endplates and intermediate to high aerobic capacities are found in representatives of all vertebrate classes (Fig. 1E). The structure of endplates is very variable for agnathans, fish, amphibians, birds and reptiles and differs from that observed for mammalian twitch fibres. In many cases, endplates are composed of numerous bead-like extensions and may be similar to the '*en grappe*' type structures observed for multiply innervated muscles (Guthe, 1981). In agnathans and fish, these fibres usually have a fast type myosin isotype and in the case of segmental muscles occupy an intermediate position between the multiply innervated red and focally innervated white muscle fibres (Bone, 1978). In other vertebrates fibre types occur in which either a 'fast' or 'slow' myosin isotype is expressed. For example, Ridge (1971) found that the costocutaneous superioris muscle of the garter snake gave either slow or fast twitches when the stimulus strength to the nerve was increased. The times to peak tension, twitch tension and

twitch : tetanus ratio were significantly different for populations of slow and fast twitch fibres (respectively, 30–40 ms, 69 kN m^{-2}, 0·33 for slow fibres and 50–60 ms, 97 kN m^{-2}, 0·23 for fast fibres at 20–23 °C).

Similar results have been obtained for the iliofibularis muscle of the toad, *Xenopus laevis*, in which histochemical and light scattering properties of live fibres using dark field illumination were correlated with endplate morphology and the contractile properties of single isolated fibres (Lännergren & Smith, 1966). Three kinds of twitch fibre were identified having 1, 2 or 3 endplates of variable morphology. The largest fibres (100–150 μm diameter), which were pale and had the shortest twitch contraction times, probably correspond to fast twitch fibres, and are involved in peak force generation. The remaining two kinds of fibre showed intermediate and heavy staining for mitochondria and could be differentiated on the basis of twitch contraction times, the peak to half-decay time of the twitch and rates of fatigue following repetitive stimulation (Lännergren & Smith, 1966). These may correspond to the slow and fast oxidative glycolytic twitch fibres identified histochemically for frog (Spurway, 1984) and by structural, physiological and biochemical criteria for mammals. Structurally, these twitch fibres have a number of features in common. They are focally innervated by one or few motor axons which have larger diameter and faster contraction velocities than those supplying tonic fibres (Kuffler & Vaughan-Williams, 1953; Hess & Pilar, 1963; Ridge, 1971). Usually nerve terminals have extensive postjunctional sarcolemmal folds and muscle fibres have prominent M-lines, straight, narrow Z-lines, numerous regularly shaped, small diameter myofibrils in cross section (sometimes called 'Fibrillenstruktur') and abundant sarcoplasmic reticulum, a regular T-tubule system either at the Z-line or at the junction of A and I bands (Hess, 1970; Close, 1972; Guthe, 1981). Twitch fibres are activated by propagated overshooting action potentials and differ from tonic fibres in that they operate in functional groups composed of a single type which are innervated by axonal branches of a single motor neurone (motor units). Mammalian twitch fibres have a single more discrete '*en plaque*' type endplate showing rather less species variation than is evident for other vertebrate groups. Slow twitch and fast twitch oxidative glycolytic fibres may be differentiated by their histochemical staining reaction for myosin ATPase following alkaline (pH 10·4) preincubation (Peter *et al.* 1972) and by their myosin heavy and light chain compositions (Young, 1982; Billeter, Heizmann, Howald & Jenny, 1981). Bovine (Young, 1982) and human (Billeter *et al* 1981) fast glycolytic and fast oxidative fibres have identical light but different heavy chain compositions.

In some muscles there is a tendency to segregate motor units of a given type. Ariano, Armstrong & Edgerton (1973) studied the distribution of slow (SO), fast oxidative glycolytic (FOG) and glycolytic (FG) fast fibres in the muscles of the arm and thigh, in dog and wallaby. The deepest muscles in each extensor group were found to have a higher proportion of slow twitch fibres (80–100 %) than the more superficial muscles (20–50 %). The soleus muscles in cat and guinea pig are entirely composed of slow twitch fibres (Ariano *et al.* 1973). There have been a number of studies of the contractile properties of whole mammalian muscles containing

primarily fast or slow motor units (Close, 1972; Luff, 1981). Extrapolated values for V_{max} are generally around two times lower for muscles containing primarily SO compared to FG motor units. Values of a/P_0 for slow muscles (Fig. 2) are generally less than for fast muscles (e.g. $a/P_0 = 0{\cdot}25$ and $0{\cdot}37$ for the extensor digitorum longus muscle of the rat and mouse respectively) (Close, 1964; Luff, 1981). Studies of muscles chemically poisoned with either iodoacetate and N_2 (to inhibit glycolysis and aerobic metabolism) or FDNB (to inhibit the creatine kinase reaction) have shown that slow twitch muscles have higher isometric economies (force integral/high energy phosphate utilized) but lower isotonic efficiencies (work done/high energy phosphate utilized) than fast twitch muscles (Goldspink, 1975).

Muscles involved in sustained activity are likely to have higher proportions of SO and FOG motor units than phasically active muscles with very high power outputs. In most birds which engage in flapping flight the pectoralis major muscles contain a few FG motor units which may have a role in take off, and a large number of FOG fibres which produce the power for sustained flight (Kaiser & George, 1973; Talesara & Goldspink, 1978; Khan, 1979). It seems likely that it is these fibres that are recruited during gliding. Birds such as the spruce grouse (*Canachites canadensis*) and the ring necked pheasant (*Phasianus colchicus torquatus*), which engage in occasional short distance flight starting with a fast wing beat, have pectoralis major muscles composed of over 80 % FG fibres. The limited number of FOG motor units in these species is correlated with their limited abilities for sustained flight (Kaiser & George, 1973).

Since the mechanical power requirements of flight are high, red fibres have very high mitochondrial densities (e.g. 29 % for pigeon FOG fibre, James & Meek, 1979), are relatively fast contracting and have a well developed glycolytic capacity. The power requirement of gliding flight in large birds is considerably less than for flapping (Baudinette & Schmidt-Nielsen, 1974). Goldspink, Mills & Schmidt-Nielsen (1978) carried out electromyographic recordings of flapping and gliding flight of the herring gull (*Larus argentatus*) in a wind tunnel. Evidence was obtained that relatively few motor units were recorded during periods of gliding. Talesara & Goldspink (1978) found that in species such as the herring gull, which engage in gliding, the pectoralis major muscle contained a small proportion (~ 8 %) of a third fibre type corresponding to slow oxidative fibres.

Mitochondria occupy a similar fraction of muscle fibre volume in focally innervated red fibres of the desert iguana (*Dipsosaurus dipsosaurus*) iliofibularis muscle (~ 8 %) (body temperature 35–42 °C) (Gleeson, Nicol & Johnston, 1984), to that in slow twitch fibres from the guinea pig and rabbit soleus muscles (Eisenberg, Kuda & Peter, 1974; Eisenberg & Salmons, 1981). Much higher mitochondrial volume densities are found in multiply innervated fish red myotomal muscles (20–45 %) (ectotherms) and focally innervated FOG fibres from bird flight muscles (20–30 %) (homeotherms). The size of the mitochondrial compartment is therefore not related to body temperature *per se*. Instead, by increasing the diffusional surface area for transport of substrates and metabolites (e.g. ATP and carnitine) across the outer mitochondrial membrane, high values for $Vv_{(mt,f)}$ may reflect recruitment of these fibre types for prolonged continuous activity during swimming and flying.

CONCLUSIONS

In spite of the diversity of characteristics shown by different muscles, some broad design principles do emerge. Muscles engaged in sustained force generation derive a significant proportion of their energy requirements from aerobic metabolism and are generally more resistant to fatigue with repetitive use than muscles involved in peak force production. The greater their power output, the higher their aerobic capacity and the increasing likelihood that a proportion of energy requirements will be provided by anaerobic glycolysis. Studies of the central patterns of fibre recruitment are required to understand how such less fatigue resistant muscle fibres function in sustained force generation.

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