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METABOLIC INDICATORS OF FIBRE RECRUITMENT IN MAMMALIAN MUSCLES DURING LOCOMOTION

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SUMMARY

Fast-twitch-oxidative-glycolytic (FOG), fast-twitch-glycolytic (FG) and slow-twitch-oxidative (SO) fibres are distributed within and among physiological extensor muscles in mammals in predictable patterns. Deep muscles and the deep portions of extensor muscles are primarily composed of SO and FOG fibres, and the more peripheral portions of the muscles have higher concentrations of FG fibres. During terrestrial locomotion, the fibres are recruited in this same general order from postural standing through high speed running to jumping (i.e. during standing deep SO fibres are active and during locomotion there is a progressive peripheral recruitment of fibres from SO to FOG to FG). Several metabolic indicators may be used to map these fibre recruitment patterns, including glycogen loss in fibres, metabolic enzyme changes during training at different speeds, and distribution of blood flow within and among the muscles. Concerning the latter, during standing in rats blood flows in the hindlimb muscles are directly proportional to the SO fibre populations in the muscles. However, during locomotion the elevations in blood flow over pre-exercise are a function of the populations of FOG fibres in the muscles. Blood flows in the peripheral white portions (FG fibres) of extensor muscles are not significantly elevated until the rats run at high speeds, when the FG fibres presumably are recruited. During swimming, when flexor muscles are relatively more active than extensor muscles (as compared with terrestrial locomotion), blood flows in the flexors are correspondingly higher. Thus, there exists a clear 'biological economy' in the matching of blood flow to the specific fibres that are active within and among muscles during exercise.

INTRODUCTION

The purpose of this paper is to discuss spatial patterns of skeletal muscle fibre activity during locomotory exercise, and to relate these to several metabolic correlates. The data emphasize the presence of metabolic heterogeneity both within and among skeletal muscles with a dependence of metabolic patterns on the fibre activity patterns.

Key words: Exercise, circulation, fibre types.

SKELETAL MUSCLE FIBRE TYPES IN MAMMALS

That mammalian skeletal muscles are composed of fibre types with different physiological and metabolic properties is well known. Although there have been a variety of systems suggested for classifying the fibres, most investigators agree they can be divided into three general types (see reviews by Close, 1972; Burke & Edgerton, 1975; Burke, 1981; Saltin & Gollnick, 1983). The nomenclature proposed by Peter *et al.* (1972), in which the fibres are referred to as fast-twitch-oxidative-glycolytic (FOG), fast-twitch-glycolytic (FG) and slow-twitch-oxidative (SO), will be used in this paper, although recognizing there are some problems in reliably differentiating between FOG and FG fibres using histochemical analysis for mitochondrial oxidative enzymes (Nemeth, Hoffer & Pette, 1979; Gollnick, Parsons & Oakley, 1983). This method (Peter *et al.* 1972) has the advantage of incorporating both the contractile and metabolic characteristics in the system of nomenclature.

FIBRE TYPE DISTRIBUTION IN MUSCLES

Recognizable patterns of fibre type distribution exist within and among mammalian locomotory muscles (Baldwin *et al.* 1972; Ariano, Armstrong & Edgerton, 1973;

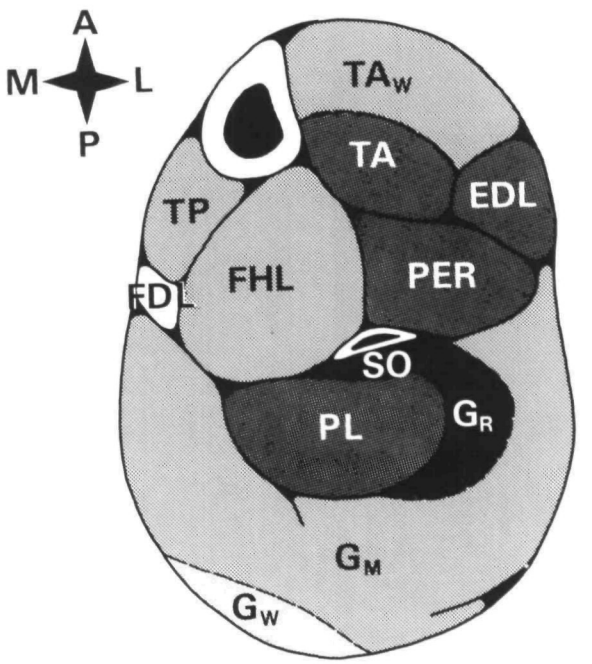

Fig. 1. Cross-section of rat leg with shading intensity proportional to the sum of SO plus FOG populations in the muscles. Muscles are: tibialis anterior red (TA_R) and white (TA_W); tibialis posterior (TP); flexor hallicus longus (FHL); flexor digitorum longus (FDL); extensor digitorum longus (EDL); peroneals (PER); soleus (SO); plantaris (PL); and red (G_R), white (G_W) and middle (G_M) gastrocnemius. Compass directions are anterior (A), posterior (P), lateral (L) and medial (M). Reproduced from Armstrong & Phelps (1984).

Collatos, Edgerton, Smith & Botterman, 1977; Armstrong, 1980; Armstrong, Saubert, Seeherman & Taylor, 1982; Armstrong & Phelps, 1984). Fig. 1 shows the distribution of high-oxidative fibres in the leg muscles of rat. Deep physiological extensor muscles are predominantly or totally composed of SO fibres (e.g. soleus muscle). More peripheral extensor muscles generally contain more fast-twitch fibres (e.g. gastrocnemius muscle), with the SO and FOG fibres primarily situated in the deeper portions of the muscles. FG fibres generally predominate in the most superficial portions of the muscles. This stratification of the fibres is most apparent in the extensor muscle groups of quadrupeds (Ariano *et al.* 1973; Collatos *et al.* 1977; Armstrong, 1980), but the pattern can also be perceived in human muscles (Johnson, Polgar, Weightman & Appleton, 1973; Edgerton, Smith & Simpson, 1975; Lexell, Henriksson-Larsen & Sjostrom, 1983).

FIBRE TYPE RECRUITMENT PATTERNS

Not only are the muscle fibre types *distributed* in regular patterns in the muscles, they also appear to be *recruited* in reasonably predictable spatial patterns during locomotory exercise. The most direct evidence indicating the general patterns of recruitment of the fibres in conscious animals during locomotion comes from

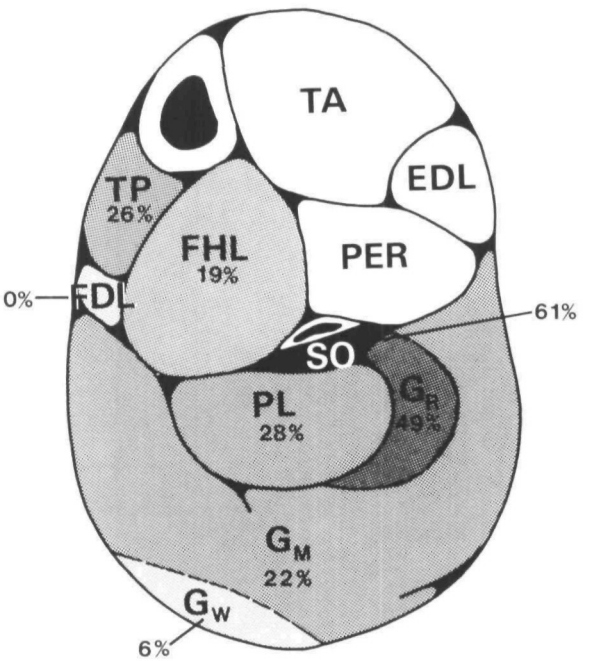

Fig. 2. Cross-section of rat leg showing percentage of glycogen lost in foot extensor muscles after 5 min of treadmill exercise at 15 m min^{-1}. Muscle abbreviations are explained in the legend for Fig. 1 (unpublished data from R. B. Armstrong, C. D. Ianuzzo & M. H. Laughlin).

electromyographic (EMG) measurement. These recordings indicate the deep SO extensor muscles, such as soleus, are maximally active during quiet postural standing (Smith, Edgerton, Betts & Collatos, 1977; Walmsley, Hodgson & Burke, 1978), as well as during locomotion and jumping (Smith *et al.* 1977; Walmsley *et al.* 1978; Gardiner, Gardiner & Edgerton, 1982). On the other hand, more peripheral fast-twitch synergists (i.e. gastrocnemius and plantaris muscles) are progressively activated from walking through running and jumping (Smith *et al.* 1977; Walmsley *et al.* 1978; Gardiner *et al.* 1982). Thus, in extensor muscle groups there is a progressive activation of motor units from deep slow muscles to more peripheral fast ones with increasing locomotory speed.

There are also several less direct metabolic indicators of fibre type recruitment patterns during locomotion. One that has commonly been used to infer the patterns of muscle fibre use is to determine glycogen loss in the fibres during a bout of exercise. The assumption is made that if a fibre loses glycogen, it has been active at some time during the exercise (Gollnick *et al.* 1973; Costill *et al.* 1973; Armstrong *et al.* 1974, 1977; Sullivan & Armstrong, 1978). Findings from glycogen loss experiments indicate that during walking, deep SO and FOG fibres are primarily recruited in extensor muscle groups (Fig. 2), and with increasing locomotory speed there is

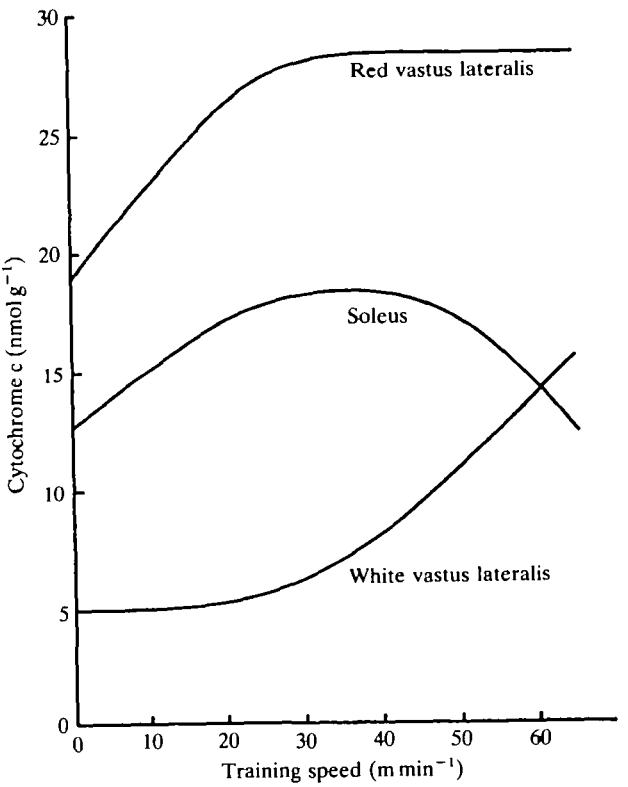

Fig. 3. Cytochrome c concentrations in rat muscles as a function of prolonged training at various treadmill speeds. Figure modified from Dudley, Abraham & Terjung (1982).

progressive recruitment of more peripheral fibres with lower oxidative capacities (FG fibres) (Armstrong *et al.* 1974, 1977; Sullivan & Armstrong, 1978). During high speed galloping, FG fibres in the most superficial portions of the muscles are active (Sullivan & Armstrong, 1978).

Similar general conclusions about the spatial patterns of recruitment during locomotion may be drawn from studies of mitochondrial changes in the muscles with training (Dudley, Abraham & Terjung, 1982). As shown in Fig. 3, when rats are trained to run on the treadmill at slow speeds the mitochondrial (cytochrome c concentration) adaptations primarily occur in the deep red muscles and muscle parts (soleus and red vastus lateralis). However, with increasing training speeds, the more peripheral portions (white vastus lateralis) of the extensor muscle groups progressively demonstrate the training effect. Thus, these results can be interpreted as indicating a progressive peripheral recruitment of fibres as the training speed was increased.

We have recently observed that blood flow distribution within and among the muscles in rats appears to be related to the recruitment patterns during postural maintenance and locomotory exercise (Laughlin & Armstrong, 1982, 1983; Armstrong & Laughlin, 1983*a*, 1984). Thus, when rats are standing on the treadmill, blood flows in the extensor muscles are a function of the SO fibre populations (Laughlin & Armstrong, 1982). When the proportion of a muscle composed of SO

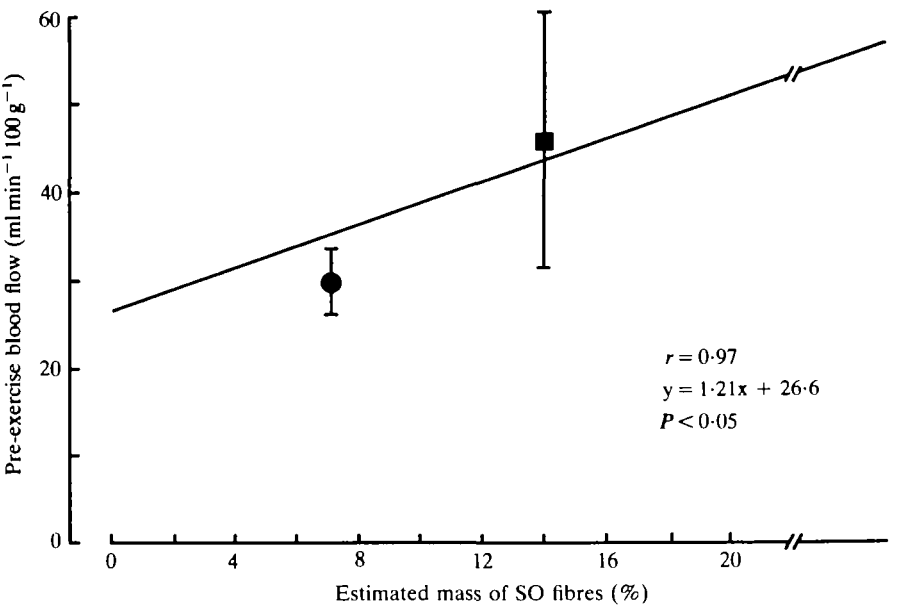

Fig. 4. Regression line for pre-exercise ('resting') blood flows in nine rat extensor muscles as a function of the proportion of the muscles composed of SO fibres. Included on the plot are average values for normal plantaris muscles (●) and plantaris muscles induced to enlarge by removal of synergistic gastrocnemius muscle (■). Normal muscle SO fibre mass data are from Armstrong & Phelps (1984), normal muscle blood flows from Laughlin & Armstrong (1982), hypertrophied plantaris SO mass data from Ianuzzo, Gollnick & Armstrong (1976) and hypertrophied plantaris blood flow data from R. B. Armstrong, C. D. Ianuzzo & M. H. Laughlin (unpublished observations).

fibres is experimentally increased, as in overload hypertrophy (Ianuzzo, Gollnick & Armstrong, 1976), the blood flow to the muscle during postural standing is increased proportionately (Fig. 4). Thus, in a standing rat there is a close relationship between the population of SO fibres, which presumably are recruited during postural maintenance (Smith *et al.* 1977; Walmsley *et al.* 1978), and the blood flow to the muscles. However, when the animal begins to move, the increases in blood flow in the muscles over pre-exercise are in direct proportion to the populations of FOG fibres in them (Laughlin & Armstrong, 1982). This is true in rats for speeds from 15 m min^{-1} (fast walk) to 105 m min^{-1} (fast gallop) (Fig. 5). Thus, even at running speeds (i.e. $\geq$75 m min^{-1}) at which most of the peripheral FG units are recruited in the muscles (Sullivan & Armstrong, 1978), the blood flows are primarily directed to the FOG fibres. In fact, extrapolation of regression curves relating blood flows to fibre type populations suggests blood flow in a hypothetical pure FOG muscle would exceed 600 ml min^{-1} 100 g^{-1} (Armstrong & Laughlin, 1983*a*). Similar calculations yield values of 250 and 110 ml min^{-1} 100 g^{-1} for pure SO and FG muscles, respectively (Armstrong & Laughlin, 1983*a*). Thus, although the flows are markedly less than those in red muscles, blood flow is significantly elevated in white (FG) muscles at high running speeds ($\geq$60 m min^{-1}) (Laughlin & Armstrong, 1982; Armstrong & Laughlin, 1983*a*), speeds at which FG fibres are known to be recruited (Sullivan & Armstrong, 1978).

Although the purpose of this paper is to discuss the distribution of flow specifically in muscles, the reader is reminded that the distribution of total cardiac output also

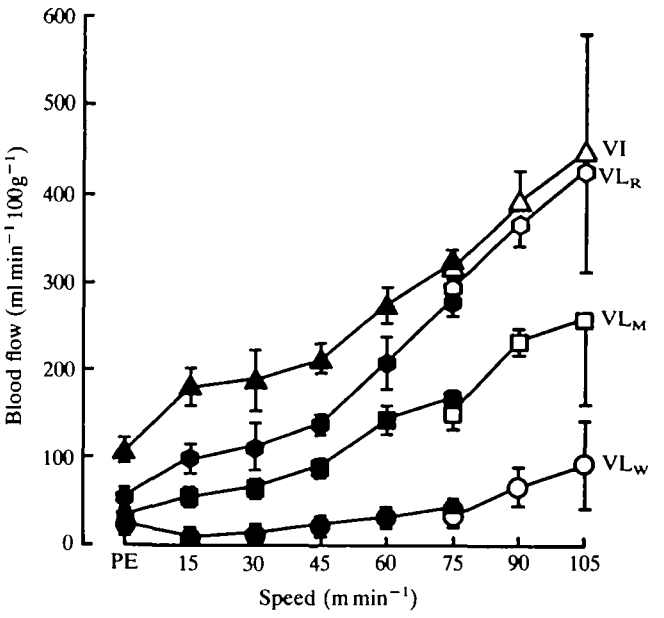

Fig. 5. Muscle blood flows at the end of the first minute of treadmill running as a function of speed. Data represented by solid symbols are from Laughlin & Armstrong (1982). Open symbols are unpublished values (M. H. Laughlin & R. B. Armstrong). VI, vastus intermedius; VL_R, vastus lateralis, red; VL_M, vastus lateralis, middle; VL_W, vastus lateralis, white.

changes quite dramatically with increasing exercise intensity (Rowell, 1974). This redistribution in rats is illustrated in Fig. 6. It is apparent that a nearly complete cessation of blood flow to visceral organs may occur under heavy treadmill exercise conditions, which further facilitates delivery of blood flow to the active muscle fibres.

The precision of the matching of blood flow to muscle fibre activity is illustrated by the relative differences in flows in extensor and flexor muscles during quadrupedal locomotion *versus* swimming in rats (Fig. 7). During pre-exercise and during walking and galloping, flows in ankle extensor muscles are higher than in the antagonistic flexor muscles, but during swimming the flows are higher in the flexor muscles (Laughlin, Mohrman & Armstrong, 1984). In fact, soleus muscle, which always has near maximal blood flow whenever the rat is supporting its body mass in the upright quadrupedal position (Laughlin & Armstrong, 1982), has a significant decrease in flow when the animal begins to swim (Laughlin *et al.* 1984) (Fig. 8). Also, during the first 5 min of swimming the soleus muscle loses no glycogen, unlike the synergistic plantaris and red gastrocnemius muscles (Armstrong & Laughlin, 1983*b*). These data suggest that soleus muscle is recruited less during the first 5 min of swimming than

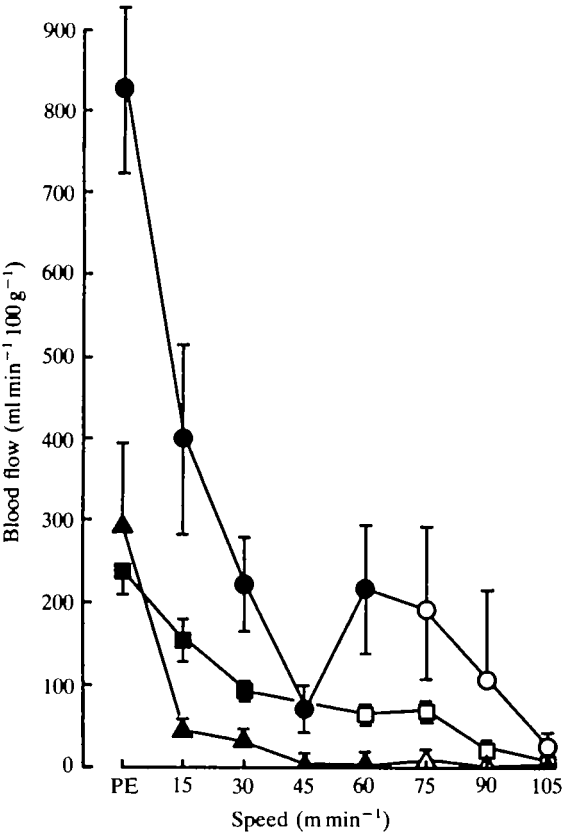

Fig. 6. Visceral blood flows (kidney, ◐; duodenum, ◧; spleen, ◭) at the end of the first minute of treadmill running as a function of speed. Data for pre-exercise (PE) to 75 m min^{-1} (black symbols) are from Laughlin & Armstrong (1982). Data for 90 and 105 m min^{-1} (open symbols) are unpublished (M. H. Laughlin & R. B. Armstrong).

during postural maintenance or terrestrial locomotion. Flexor muscles are relatively more active during swimming (Gruner & Altman, 1980), so that differences in blood flows in the antagonistic muscle groups during treadmill locomotion and swimming could be predicted.

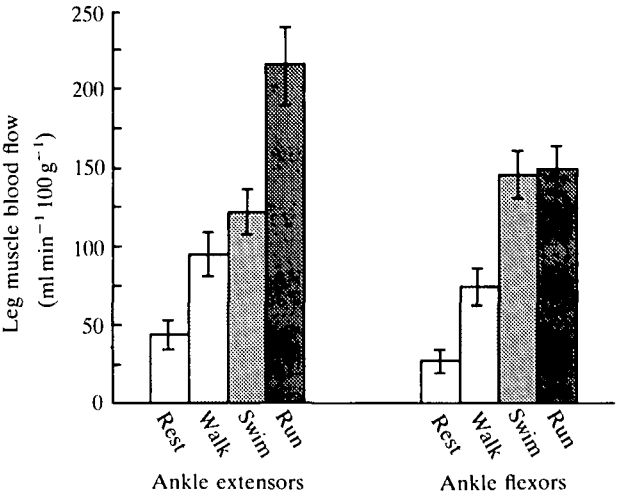

Fig. 7. Blood flows in ankle extensor and ankle flexor muscles under different conditions: resting (Laughlin & Armstrong, 1983), walking (Laughlin & Armstrong, 1983), swimming (Laughlin, Mohrman & Armstrong, 1984) and running (Armstrong & Laughlin, 1983*a*). Values are means ± S.E.M.

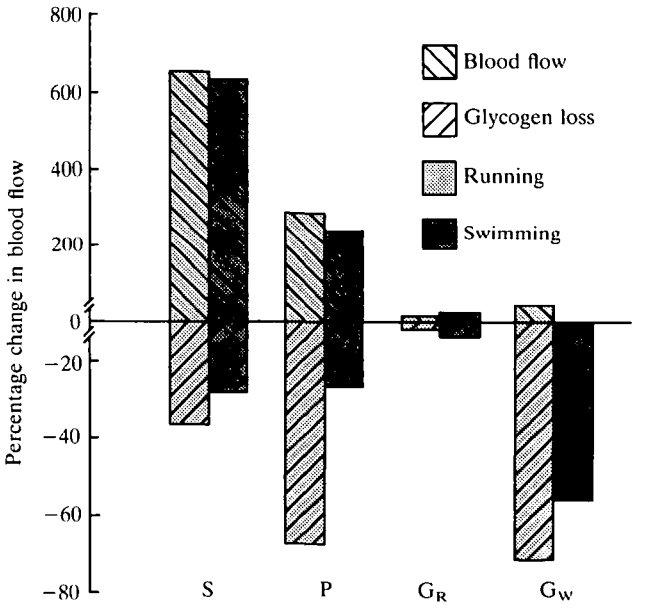

Fig. 8. Percentage changes in muscle blood flows [(pre-exercise—post-exercise) × 100/pre-exercise values] and glycogen concentrations from pre-exercise values with swimming and treadmill running at 30 m min^{-1} (Armstrong & Laughlin, 1983*b*). Muscles are soleus (S), plantaris (P) and red (G_R) and white (G_W) gastrocnemius.

The close matching between blood flow and muscle fibre activity is often considered to result from the release of vasodilatory substances from the active fibres (for reviews see Skinner, 1975; Sparks, 1980), although some have suggested a more direct link

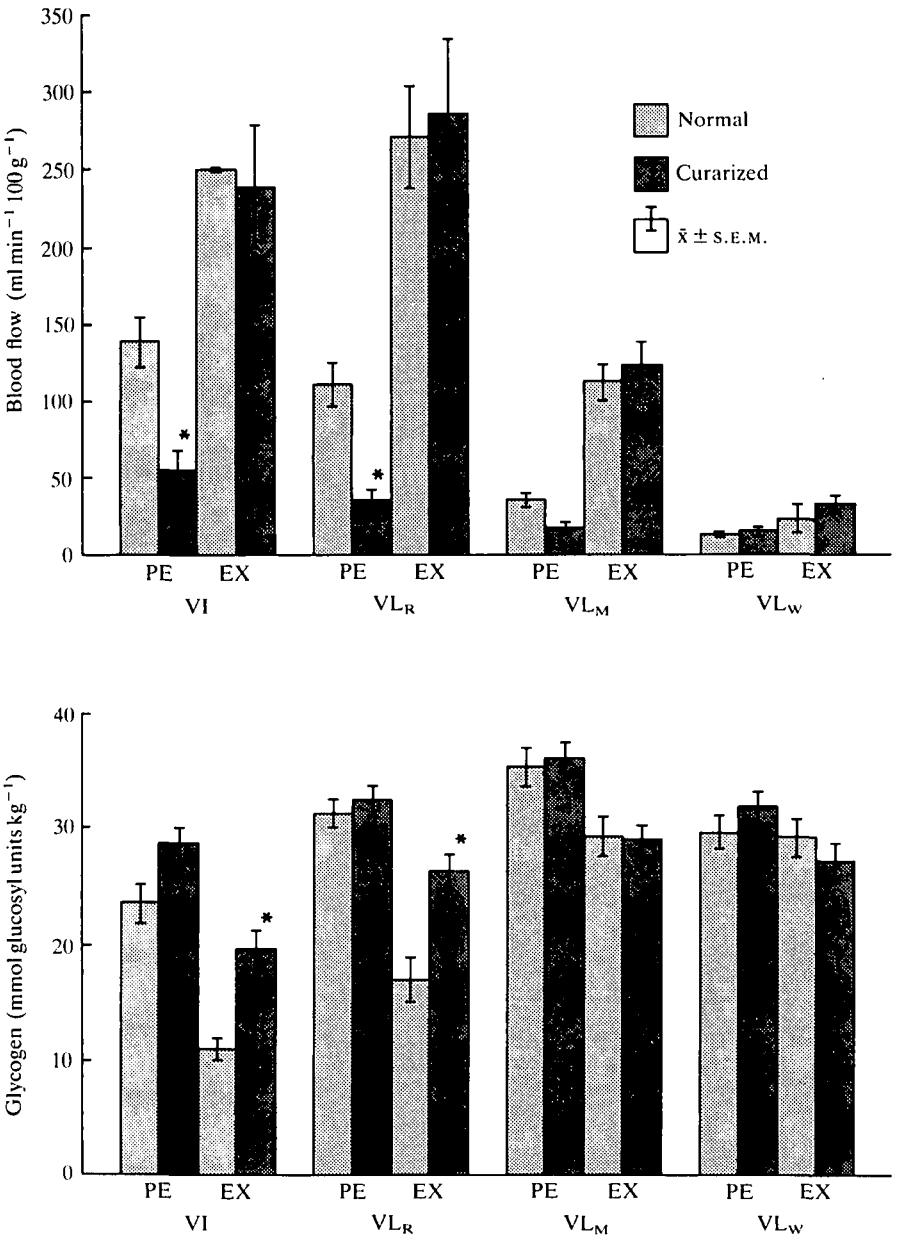

Fig. 9. Histograms showing blood flows and glycogen concentrations in normal and partially-curarized rats before exercise (PE) and at the end of 1 min of treadmill walking at 15 m min^{-1}. Asterisks (*) indicate values for curarized rats that are different from the values for normal animals ($P < 0{\cdot}05$). Data from Armstrong, Vandenakker & Laughlin (1985).

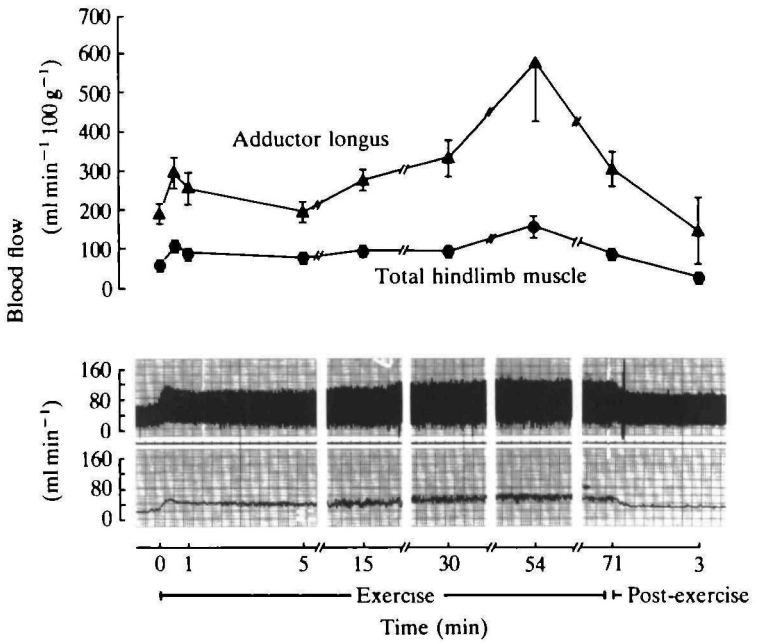

Fig. 10. Blood flows in rat muscle during prolonged low-intensity treadmill exercise (15 m min^{-1}). The upper curves for adductor longus and total hindlimb muscle were obtained with the radiolabelled microsphere technique (Laughlin & Armstrong, 1983). The polygraph tracings were obtained with an electromagnetic flow probe placed on the descending aorta just above the bifurcation of the iliac arteries (M. H. Laughlin & R. B. Armstrong, unpublished observations). The upper tracing shows raw flows, whereas the bottom tracing is the average flow through the distal aorta.

between neural activation of the skeletal muscle fibres and the elevations in blood flow through adjacent vasculature (Antal, 1968; Honig, 1979). The extremely rapid and dramatic elevations in blood flow to muscles that occur at the initiation of exercise (Van Citters & Franklin, 1969; Donald, Rowlands & Ferguson, 1970; Armstrong & Laughlin, 1983*a*) certainly make it intuitively attractive to suggest such a linkage.

We have recently completed experiments in which we preferentially blocked high-oxidative fibres in the muscles with low dosages of curare during slow treadmill exercise (Armstrong, Vandenakker & Laughlin, 1985). This induced more peripheral recruitment of lower oxidative fibres to maintain tread speed. However, the deep red muscles that were recruited less, and/or were less metabolically active in the curarized rats (as indicated by decreased glycogen loss) during the first minute of exercise, had the same increases in blood flows as the normal animals (Fig. 9). These data suggest that the initial exercise hyperaemia in the red muscles is not dependent upon muscle fibre metabolism. Since the alpha-motor neurones to the deep red motor units in the curarized rats presumably continued to be activated (Henneman & Mendell, 1981), the results support the concept of a direct linkage between the motor neurones and the resistance vessels in the muscles.

Although there is a close association between fibre recruitment patterns and metabolic correlates as discussed above, it is clear that metabolic events alone cannot

be used to quantify muscle fibre activity or even to measure the relative degrees of activity in different populations of fibres (Gollnick *et al.* 1973; Armstrong *et al.* 1974; Burke & Edgerton, 1975). Fig. 10 illustrates the progressive elevations in blood flow that occur in rat muscles over time during prolonged, low intensity treadmill exercise (Laughlin & Armstrong, 1983). One of the hypotheses offered to explain this gradual rise was that a progressive recruitment of new motor units occurs as the initially-recruited fibres become fatigued (Laughlin & Armstrong, 1983), as has previously been observed under other conditions (Gollnick *et al.* 1973; Armstrong *et al.* 1974). However, in subsequent experiments adductor longus muscle (which had the highest blood flow of all hind-limb muscles after about 1 h of exercise, Fig. 10) showed large decreases in glycogen content in almost all of its fibres during the first 20 min of exercise, with no further loss occurring from 20 to 80 min (Tan & Armstrong, 1984). These data suggest the elevations in blood flow were not related to changes in fibre recruitment.

In summary, several types of metabolic changes within and among muscles may be used to estimate whether the fibres in the particular regions are active during *in vivo* locomotion. Because of the widely differing oxidative and glycolytic capacities and substrate preferences of the fibres, it is not possible to quantitate their activities, but the use of metabolic indicators does provide insight into the spatial relationships of fibre recruitment patterns in the muscles.

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REFERENCES

ANTAL, J. (1968). Changes in blood flow during exercise in unanesthetized animals. *Circulation in Skeletal Muscle*, (ed. O. Hudlicka), pp. 181–187. New York: Pergamon Press.

ARIANO, M. W., ARMSTRONG, R. B. & EDGERTON, V. R. (1973). Hind limb muscle fiber populations of five mammals. *J. Histochem. Cytochem.* **21**, 51–55.

ARMSTRONG, R. B. (1980). Properties and distributions of the fiber types in the locomotory muscles of mammals. In *Comparative Physiology: Primitive Mammals*, (eds K. Schmidt-Neilsen & C. R. Taylor), pp. 243–254. Cambridge: Cambridge University Press.

ARMSTRONG, R. B. & LAUGHLIN, M. H. (1983*a*). Blood flows within and among rat muscles as a function of time during high speed treadmill exercise. *J. Physiol., Lond.* **344**, 189–208.

ARMSTRONG, R. B. & LAUGHLIN, M. H. (1983*b*). Is rat soleus muscle recruited during swimming? *Brain Res.* **258**, 173–176.

ARMSTRONG, R. B. & LAUGHLIN, M. H. (1984). Exercise blood flow patterns within and among rat muscles after training. *Am. J. Physiol.* **246**, H59–H68.

ARMSTRONG, R. B., MARUM, P., SAUBERT, C. W., IV, SEEHERMAN, H. J. & TAYLOR, C. R. (1977). Muscle fiber activity as a function of speed and gait. *J. appl. Physiol.* **43**, 672–677.

ARMSTRONG, R. B. & PHELPS, R. O. (1984). Muscle fiber type composition of the rat hind limb. *Am. J. Anat.* **171**, 259–272.

ARMSTRONG, R. B., SAUBERT, C. W., IV, SEEHERMAN, H. J. & TAYLOR, C. R. (1982). Fiber type distribution in locomotory muscles of dogs. *Am. J. Anat.* **163**, 87–98.

ARMSTRONG, R. B., SAUBERT, C. W., SEMBROWICH, W. L., SHEPHERD, R. D. & GOLLNICK, P. D. (1974). Glycogen depletion in rat skeletal muscle fibers at different intensities and durations of exercise. *Pflügers Arch. ges. Physiol.* **352**, 243–256.

ARMSTRONG, R. B., VANDENAKKER, C. B. & LAUGHLIN, M. H. (1985). Distribution of muscle blood flow during exercise in partially-curarized rats. *Am. J. Appl. Physiol.* **58**, (in press).

BALDWIN, K. M., KLINKERFUSS, G. H., TERJUNG, R. L., MOLE, P. A. & HOLLOSZY, J. O. (1972). Respiratory capacity of white, red, and intermediate muscle: Adaptative response to exercise. *Am. J. Physiol.* **222**, 373–378.

BURKE, R. E. (1981). Motor units: anatomy, physiology, and functional organization. In *Handbook of Physiology. The Nervous System.* Bethesda, MD: Am. Physiol. Soc., Sect. 1, Chapter 10, pp. 345–422.

BURKE, R. E. & EDGERTON, V. R. (1975). Motor unit properties and selective involvement in movement. *Exercise Sport Sci. Rev.* **3**, 31–81.

CLOSE, R. I. (1972). Dynamic properties of mammalian skeletal muscles. *Physiol. Rev.* **52**, 129–197.

COLLATOS, T. C., EDGERTON, V. R., SMITH, J. L. & BOTTERMAN, B. R. (1977). Contractile properties and fiber type compositions of flexors and extensors of elbow joint in cat: implications for motor control. *J. Neurophysiol.* **40**, 1292–1300.

COSTILL, D. L., GOLLNICK, P. D., JANSSON, E. D., SALTIN, B. & STEIN, E. M. (1973). Glycogen depletion pattern in human muscle fibres during distance running. *Acta physiol. scand.* **89**, 374–385.

DONALD, D. E., ROWLANDS, D. J. & FERGUSON, D. A. (1970). Similarity of blood flow in the normal and the sympathectomized dog hind limb during graded exercise. *Circulation Res.* **26**, 185–199.

DUDLEY, G. A., ABRAHAM, W. M. & TERJUNG, R. L. (1982). Influence of exercise intensity and duration on biochemical adaptations in skeletal muscle. *J. appl. Physiol.* **53**, 844–850.

EDGERTON, V. R., SMITH, J. L. & SIMPSON, D. R. (1975). Muscle fibre type populations of human leg muscles. *Histochemical J.* **7**, 259–266.

GARDINER, K. R., GARDINER, P. F. & EDGERTON, V. R. (1982). Guinea pig soleus and gastrocnemius electromyograms at varying speeds, grades, and loads. *J. appl. Physiol.* **52**, 451–457.

GOLLNICK, P. D., ARMSTRONG, R. B., SAUBERT, C. W., IV, SEMBROWICH, W. L., SHEPHERD, R. E. & SALTIN, B. (1973). Glycogen depletion patterns in human skeletal muscle fibers during prolonged work. *Pflügers Arch. ges. Physiol.* **344**, 1–12.

GOLLNICK, P. D., PARSONS, D. & OAKLEY, C. R. (1983). Differentiation of fiber types in skeletal muscle from the sequential inactivation of myofibrillar actomyosin ATPase during acid preincubation. *Histochem.* **77**, 543–555.

GRUNER, J. A. & ALTMAN, J. (1980). Swimming in the rat: analysis of locomotor performance in comparison to stepping. *Expl Brain Res.* **40**, 374–382.

HENNEMAN, E. & MENDELL, L. M. (1981). Functional organization of motoneuron pool and its inputs. In *Handbook of Physiology. The Nervous System.* Bethesda, MD: Am. Physiol. Soc., Vol. II, Chapt. 11, pp. 423–507.

HONIG, C. R. (1979). Contributions of nerves and metabolites to exercise vasodilation: a unifying hypothesis. *Am. J. Physiol.* **5**, H705–H719.

IANUZZO, C. D., GOLLNICK, P. D. & ARMSTRONG, R. B. (1976). Histochemical adaptations to a long-term power overload condition. *Life Sci.* **19**, 1517–1524.

JOHNSON, M. A., POLGAR, J., WEIGHTMAN, D. & APPLETON, D. (1973). Data on the distribution of fiber types in thirty-six human muscles and autopsy study. *J. neurol. Sci.* **18**, 111–129.

LAUGHLIN, M. H. & ARMSTRONG, R. B. (1982). Muscular blood flow distribution patterns as a function of running speed in rats. *Am. J. Physiol.* **243**, H296–H306.

LAUGHLIN, M. H. & ARMSTRONG, R. B. (1983). Rat muscle blood flows as a function of time during prolonged slow treadmill exercise. *Am. J. Physiol.* **244**, H814–H824.

LAUGHLIN, M. H., MOHRMAN, S. J. & ARMSTRONG, R. B. (1984). Muscular blood flow distribution patterns in the hind limb of swimming rats. *Am. J. Physiol.* **246**, H398–H403.

LEXELL, J., HENRIKSSON-LARSEN, K. & SJOSTROM, M. (1983). Distribution of different fibre types in human skeletal muscles. *Acta physiol. scand.* **117**, 115–122.

NEMETH, P., HOFFER, H. W. & PETTE, D. (1979). Metabolic heterogeneity of muscle fibers classified by myosin ATPase. *Histochem.* **63**, 191–201.

PETER, J. B., BARNARD, R. J., EDGERTON, V. R., GILLESPIE, C. A. & STEMPEL, K. E. (1972). Metabolic profiles of three fiber types of skeletal muscle in guinea pigs and rabbits. *Biochemistry, N.Y.* **11**, 2627–2634.

ROWELL, L. B. (1974). Human cardiovascular adjustments to exercise and thermal stress. *Physiol. Rev.* **54**, 75–159.

SALTIN, B. & GOLLNICK, P. D. (1983). Skeletal muscle adaptability: significance for metabolism and performance. In *Handbook of Physiology. Skeletal Muscle.* Bethesda, MD: Am. Physiol. Soc., Sect. 10, Chapt. 19, pp. 555–632.

SKINNER, N. S. (1975). Skeletal muscle blood flow: metabolic determinants. In *The Peripheral Circulations*, (ed. R. Zelis), pp. 57–78. New York: Grune & Stratten.

SMITH, J. L., EDGERTON, V. R., BETTS, B. & COLLATOS, T. C. (1977). EMG of slow and fast ankle extensors of cat during posture, locomotion, and jumping. *J. Neurophysiol.* **40**, 503–513.

SPARKS, H. V. (1980). Effect of local metabolic factors on vascular smooth muscle. In *Handbook of Physiology. The Cardiovascular System.* Bethesda, MD: Am. Physiol. Soc., Sect. 2, Vol. II, Chapt. 17, pp. 475–513.

SULLIVAN, T. E. & ARMSTRONG, R. B. (1978). Rat locomotory muscle fiber activity during trotting and galloping. *J. appl. Physiol.* **44**, 358–363.

TAN, D. T. L. & ARMSTRONG, R. B. (1984). Glycogen loss patterns in rat thigh adductor muscles during low intensity exercise. *Fedn Proc. Fedn Am. Socs exp. Biol.* **43**, 1014.

VAN CITTERS, R. L. & FRANKLIN, D. L. (1969). Cardiovascular performance of Alaska sled dogs during exercise. *Circulation Res.* **24**, 33–42.

WALMSLEY, B., HODGSON, J. A. & BURKE, R. E. (1978). Forces produced by medial gastrocnemius and soleus muscles during locomotion in freely moving cats. *J. Neurophysiol.* **41**, 1203–1216.