Talking of muscles and motion

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Design and Performance of Muscular Systems. Edited by C.R. Taylor, E. Weibel and L. Bolis. *The Company of Biologists Limited: 1985. Pp.412. £25, $60. Available from the Biochemical Society Book Depot, PO Box 32, Commerce Way, Colchester CO2 2HP, UK.*

One of the main themes of this book, which is based on papers presented at the Seventh International Conference on Comparative Physiology in June 1984, concerns problems of gait during locomotion, such as why animals adopt narrow ranges of speed for particular gaits and why they change from one gait to another (Cavagna, Hedlund, McMahon and Taylor). Some of the illustrations are drawn from unusual human gaits such as hopping, Groucho running (that is, with very bent knees like Groucho Marx) and running on very compliant surfaces.

One idea, now 10 years old, is that an animal can be considered during locomotion as a multi-jointed mass-spring system with a characteristic resonant frequency, and thus a preferred stride rate. As speed increases, say in walking, the ride becomes uncomfortable and less economical because of the stiffness of the spring arrangement and running is more comfortable as the ride is softer and it is less costly in energy consumption. Maximum speed might be determined by maximum stress and this varies with body size much as expected (Alexander). Under the mass-spring model, unusual gaits extend the range of observations.

In locomotion on a flat surface the net external work done is small, but groups of muscles alternately shorten and are stretched thus performing positive and negative work respectively. The tuned-spring model implies that energy imparted to muscles by stretch is recovered when they shorten; indeed, this was first demonstrated in Margaria's laboratory 20 years ago. The positive work phase can thus appear surprisingly efficient, up to 70% in large animals, though much lower in smaller animals for reasons that are not entirely clear. More details of the process of energy storage come from experiments on isolated muscles (by Cavagna and his colleagues), showing increased energy output when an actively contracting muscle is first stretched before being allowed to shorten, some of the power coming from elastic energy stored in the tendons and some apparently stored in the cross-bridges.

Another theme in the book concerns the properties and determinants of the two main muscle fibre types in mammals, the fast-twitch fibres whose mechanical properties are fast and whose metabolism is mainly glycolytic, and the slow-twitch fibres which are slower and are mainly oxidative. The current state of knowledge about structural protein isoforms is given by Perry and Whalen, but most of the new findings about the proteins in mammalian muscle are concerned with mitochondrial enzymes: in separate studies Pette and Edgerton agree that the heterogeneity found in a given fibre type implies a different mode of specification than for the structural proteins, but disagree about whether fibres innervated by branches of the same nerve show heterogeneity. Kushmerick presents his now completed study of the energetics of isometric contractions in two muscles from the mouse, one predominantly slow and the other fast.

A third theme concerns the malleability of the system. Muscles predominantly of one fibre type can be converted into the other by cross-innervation or by changing the pattern of muscle activation artificially: continuous low-frequency stimulation yields slow-twitch charateristics, whereas occasional bursts of stimulation make for fast-twitch fibres. The major determinant of muscle speed is the myosin isoform, while the duration and rapidity of response to a stimulus is probably determined by the membrane systems.

From painstaking stereological measurements it appears that the membrane systems change before the structural proteins (Eisenberg): this can induce an abnormally high mitochondrial content in a fast to slow transformation, the muscle's response to the energetic demands caused by more frequent stimulation and longer response times while fast-cycling myosin is still present. A similar type of mismatch arises during early post-natal development in the rat if a nerve is crushed and then allowed to re-innervate a muscle (Vrobova). The pattern of motorneurone activity is changing during this period, so that by the time re-innervation is complete the immature muscle encounters a mature rate of stimulation and partial atrophy results. In the adult, complete recovery results, the reverse of what might be expected intuitively of variation in plasticity with age.

The sequence of appearance of myosin isoforms during development now seems well established (Whalen). Development from embryonic through neonatal to fast myosin occurs whether or not the muscle is innervated, but induction of slow myosin is nerve-driven. However, thyroid hormone is needed for the transition from neonatal to adult fast myosin. A recent report (discussed here both by Howald and Goldspink) describes changes in myosin isoform from slow to fast as a consequence of training in the rat, but changes in man seem to be less pronounced. Successful athletes in endurance events, such as long-distance runners, have a preponderance of slow twitch fibres and sprinters have more fast twitch fibres. Training in man can induce selective fibre type hypertrophy and an increase in mitochondrial content (Gollnick, Hoppeler), but it is still not clear whether an athlete's fibre typology selects the best event for him or the athlete selects the typology for his chosen event by training.

Other aspects of muscle performance such as whole body response and the control of movement are also covered by appropriate experts. There are in all 34 articles, mostly by different authors, and although the introductory chapters (by H. Huxley, Peachey and Wilkie as well as those by Perry and Whalen already mentioned) are good, I think the novice might find it hard to follow the threads of some of the arguments. For the professional and others with some background in the fundamental properties of muscle, however, this book offers some valuable insights into the design and performance of muscular systems. □

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Running out of time: Deinonychus, *a medium-sized carnivorous dinosaur from the Early Cretaceous Cloverly Formation of Montana, reconstructed by Robert T. Bakker.*

The illustration is reproduced from Bones for Barnum Brown: Adventures of a Dinosaur Hunter *by Roland T. Bird, edited by V. Theodore Schreiber. Publisher is Texas Christian University Press (and distributor Texas A & M University Press), price is hbk $29.95, pbk $14.95.*