Biochemical efficiency and intrinsic shortening speed in selected vertebrate fast and slow muscles

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Summary. The biochemical efficiency was measured in iodoacetate N_2 and NaCN-treated muscles by dividing the work done by the amount of phosphoryl creatine hydrolysed when contracting at their optimum velocity. An inverse relationship was found between the intrinsic speed of shortening (V_{max}) of the muscles and their mechanochemical efficiency.

In recent years it has become very apparent that there is considerable diversity in the structure, physiology and biochemistry of muscle fibres. It is known that some muscle fibres are fast contracting whilst others are slow contracting. Most vertebrate muscles are in fact mixed in that they have 2 or more populations of fibres within the same anatomical muscle. The reason for having different kinds of muscle fibres is not obvious, particularly the need for slow contracting fibres. It has been shown that slow contracting muscles are able to develop and maintain isometric tension with less energy expenditure than fast contracting muscle[2,3]. In this work we studied the efficiency of fast and slow muscles to do work whilst they are contracting at their optimum velocity.

A direct relationship between intrinsic shortening speed (V_{max}) and specific activity of actin-activated myosin ATPase has been established for the wide variety of vertebrate and invertebrate muscles[4]. Several workers have measured mechanochemical efficiency in different living frog muscles[5-9], but these have not been related to intrinsic speeds of contraction. In a comparison between tortoise and frog muscles Woledge[10] noted that the maximum efficiency of tortoise muscle was 77% compared with 45% for the faster contracting frog muscle[7].

An attempt has now been made to investigate the relationship between intrinsic shortening speed and biochemical efficiency in living preparations of some vertebrate muscles which were known to vary widely in their shortening speeds.

Material and methods. The following muscles were selected for this study; m. soleus (mouse), m. soleus (hamster), m. biceps brachii (mouse), m. biceps brachii (hamster), m. rectus femaris *(testudo gracca)*, m. sartorius *(rana temporaria)* and m. posterior latissimus dorsi (chicken). The maximum velocity of shortening (intrinsic rate of shortening) was determined for each muscle by establishing a force-velocity curve. Several muscles of each type were first subjected to the incubation procedure described below, and then stimulated to contract against different loads. The intrinsic rate (V_{max}) was then obtained by expressing the velocity at zero load as muscle fibre lengths per sec. For the energetic measurements the muscles were used in pairs; the muscle from one side was stimulated whilst the contralateral muscle acted as the control. Both were fully metabolically inhibited with iodoacetate and sodium cyanide before the start of the experiment. This consisted of incubating the muscle at 2 °C for 30 min in 1 mM iodoacetate Ringer with O_2 followed by 4 min in 2 mM NaCN/1 mN iodoacetate Ringer with N_2. Similar procedures have been shown to be suitable for inhibiting glycolysis and oxidative phosphorylation in mammalian muscles[11] as well as for muscles of cold-blooded vertebrates[12]. No rigor contractions occurred in any of the muscles. Also preliminary investigations had shown that ATP levels were not significantly depleted unless the contractions were of very long duration. Hence in these muscles the energy turnover can be followed by measuring the change in phosphoryl creatine levels.

Work done was obtained from the stimulated member of each pair which was optimally loaded and stimulated to perform a series of after-loaded contraction-relaxation cycles. Optimum loading was determined from preliminary experiments in which work was measured at various loads for large groups of muscles that had been subjected to the incubating procedure. The optimum load was taken as the one which permitted the maximum amount of work. The pulse train durations were carefully chosen to effect full shortening during each cycle without involving any isometric components. The stimulated muscles were allowed to do several contractions and were then rapidly frozen at the end of relaxation from the last contraction-relaxation cycle. Rapid-freezing was achieved by immersion in cooled freon (about -160 °C). These procedures were carried out on a stimulation and quick freeze assembly which was similar to that described by Cain and Davies[13]. Shortening was measured by means of a ferrite rod and coil type isotonic transducer and recorded on a Physiograph (E. & M. Instrument Co., Texas). The stimulated and control muscles were maintained at 30 °C throughout the stimulation period. The stimulated and control muscles were stored in liquid nitrogen until chemical analyses were carried out. The analytical procedure for measuring the change in phosphoryl creatine was essentially that of Ennor and Rosenberg[14] with a correction for the amount of creatine converted to creatinine[15].

Results and discussion. As can be seen from the table the range of values of V_{max} for the muscles studied is from 1.0 length sec^{-1} (optimum muscle length sec^{-1}) for the tortoise rectus femoris to 17.5 lengths sec^{-1} for the fast posterior latissimus dorsi of chick. Frog and mammalian muscles occupy intermediate positions between these extremes. In the 2 mammals studied, where two different muscles from each animal were investigated, the soleus muscle in each case had a lower V_{max} than the biceps brachii. This is in agreement with their muscle fibre composition as determined by histochemical staining for myosin ATPase[16].

Efficiencies are expressed in g · cm · μmole PC^{-1} broken down. The muscle with the smallest V_{max} tortoise rectus femoris had the highest biochemical efficiency; 438.6 g · cm · μmole PC^{-1} while the fastest muscle, chick PLD, is least efficient at 124.8 g · cm · μmole PC^{-1}. The general trend (table) shows an inverse relation between the intrinsic speed of shortening and biochemical efficiency.

Intrinsic shortening speed (V_{max}) and biochemical efficiences of selected vertebrate fast and slow muscles at 30 °C

Muscle	V_{max} muscle lengths sec^{-1}	Efficiency (g · cm · μmole PC^{-1})	Muscle pairs
Tortoise rectus femoris	1.0 ± 0.2	438.6 ± 10.1	12
Hamster soleus	5.2 ± 0.3	340.0 ± 11.2	12
Mouse soleus	5.6 ± 0.5	395.6 ± 16.4	24
Frog sartorius	10.2 ± 0.8	280.0 ± 10.8	6
Hamster biceps brachii	10.5 ± 0.6	200.2 ± 5.3	12
Mouse biceps brachii	11.8 ± 0.5	225.5 ± 7.5	24
Chick posterior latissimus dorsi	17.5 ± 1.2	124.8 ± 7.5	12

Values are ± SE.

The mammalian fast and slow muscles show a slight deviation from this trend. The mouse biceps brachii with an intrinsic speed of 11.8 lengths sec^{-1} appears more efficient than the same muscle in the hamster despite the latter's slower speed (10.5 lengths sec^{-1}). The reason for the slight deviation may lie in the different proportions and disposition of non-contractile material in these muscles.

The present results suggest that a comparative study of the energetic and dynamic properties of different muscles may lead to a clearer understanding of their role in locomotion and in the maintenance of posture. It seems that it is not only advantageous to use slow fibres for maintaining posture (isometric contraction) but also for isotonic movements providing they are required to shorten slowly. The reason why slow muscles have a higher maximum efficiency for doing work is not known. However it may be that the longer engagement time of the cross-bridges and the slower movement of the actin filaments permit each cross-bridge to develop more force (over a longer period) for each molecule of ATP used.

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Summing properties of the surround response mechanism of cat retinal ganglion cells[1]

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Summary. Evidence is presented that, in the cat retina, the region in the visual field over which the surrounds of type X ganglion cells pool adaptive information corresponds to the region over which they pool signals.

As a means to account for the results of many psychophysical studies Rushton[3] proposed the existence of signal and adaptation summation pools within the retina. The signal pool was thought to integrate spatially the effects from photic stimuli that contribute to the detection of that stimulus by the observer. Similarly, the adaptation pool was thought to sum the desensitizing effects from steady light in the visual field.

The activity of the ganglion cell, the output neuron of the retina, is believed[4-6] to be controlled by 2 spatially overlapping response mechanisms, a center mechanism and surround mechanism. A response mechanism is an aggregate of photoreceptors and retinal interneurons whose activity affects the neural discharge of the ganglion cell. The results of a number of studies provide evidence that both the center response mechanism[7-13] and surround response mechanism[14] have signal and adaptation pools. In addition, in the cat's retina there is evidence that for the center mechanism, the retinal region over which signals are physiologically pooled, the signal pooling area, and the retinal region over which the desensitizing effects from steady light flux are pooled, the adaptive pooling area, are spatially coextensive[9,10,12]. The present study sought to determine if a similar spatial relationship exists for the surround's signal and adaptive pooling areas.

The action potentials of 43 optic tract fibers in adult cats were monitored by tungsten microelectrodes. The animals were anesthetized with urethane (40 mg/kg/h). Flaxedil (40 mg/h) was infused through the femoral vein in order to immobilize the eyes. The infusion mixture also contained Ringers with lactate (3.0 ml/h) and atropine sulfate (0.05 ml/h). EKG, femoral arterial blood pressure, EEG, body temperature, and Pco_2 were continuously monitored during the experiments. Pco_2 was held between 4% and 5%, and body temperature maintained at 38 °C. Corneal contact lenses (3.8-mm pupils) were fitted to prevent corneal drying. An 8.0° bipartite contrast reversal stimulus[15,16] was used to classify ganglion cells as type X or Y. The surround mechanism was isolated using the method described by Bishop and Rodieck[17].

The adaptive and signal pooling areas were assessed by comparing area-adaptation curves with area-sensitivity curves. The stimuli used were annuli whose outside diameter was constant and whose inside diameter varied. In order to determine area-sensitivity curves the luminance of each (temporally) modulated annulus was varied until a weak (20–70 spikes/sec peak firing rate) suprathreshold response of constant magnitude and time course was produced. Henceforth this response will be referred to as the criterion response. The area-sensitivity curve is defined, therefore, as the function relating inside diameter (target size) and the log of the reciprocal of the luminance required to produce the criterion response.

The modulated annuli used to determine the area-sensitivity curves served as unmodulated field adapting stimuli to determine area-adaptation curves. These adapting stimuli were presented in conjunction with a modulated test annulus.