Discharge Properties of Motor Units in Man

Single motor units can be identified by the characteristic shape of their potentials in electromyographic recordings. Owing to interference activity from many motor units and displacement of the electrode upon strong contraction of the muscle, the electromyographic recording technique previously used limited the studies in non-paretic subjects to about 25% of the maximum tonic muscle strength.

With such a recording technique TOKIZANE et al.[1] attempted to distinguish between slow and fast twitch motor units through their tendency to discharge at regular intervals. By plotting the standard deviation from the mean value against the mean value of the discharge intervals of motor units active in a tonic voluntary contraction, 2 distinct groups of motor units, 'tonic' motor units and 'kinetic' motor units, were found in almost all muscles tested.

However, by fixing a selective electrode in the muscle, it is now found possible to observe the discharge of a single motor unit from weak to maximum tonic contraction. In this study the TOKIZANE approach was used. About 100 motor units in the anterior tibial muscle were investigated in two healthy male subjects. The results can be summarized as follows:

Optimal frequency. When a motor unit is activated at its lowest discharge frequency, it discharges at irregular intervals. The intervals become more regular the more the frequency is increased up to a certain level. At high frequencies there may again be an increasing irregularity of the intervals. The regularity of the discharge is never total. It is, for instance, influenced by breathing. The lowest possible discharge frequency with a standard deviation of less than 10 msec counted from at least 50 successive intervals is defined as optimal. Different motor units in the anterior tibial muscle are found to have different optimal frequencies, varying from about 7/sec to about 35/sec.

Maximum frequency. Some motor units are difficult to keep activated at maximum frequency for a whole second. The maximum frequency is therefore calculated from the maximum frequency attained in a period of only 250 msec. Different motor units in the anterior tibial muscle are found to have different maximum frequencies, varying from about 25/sec to about 65/sec. Generally, motor units with a low optimal frequency have a low maximum frequency and the higher the optimal frequency, the higher is the maximum frequency of the motor unit.

Recruitment order in tonic voluntary contraction. Motor units are recruited in a stable order in tonic voluntary contraction[2]. The first activated motor units have a low optimal and maximum frequency. Generally, the higher the threshold of the motor unit in tonic voluntary contraction, the higher is the optimal and maximum frequency of the motor unit.

Recruitment order in phasic voluntary contraction. Motor units are recruited in a different order in phasic and in tonic voluntary contraction[2]. The recruitment order in a series of phasic contractions is not stable[3]. The first activated motor units in phasic voluntary contraction may have a higher optimal and maximum frequency than the motor units first activated in tonic voluntary contraction.

No distinct groups of motor units are found; instead, there is a continuous range from low- to high-frequency motor units. All motor units first recruited in phasic voluntary contraction are also found in tonic voluntary contraction. This does not preclude the existence of motor units which may only be active synchronized with other motor units in strong phasic activity, thus escaping identification. However, such motor units should be in a minority as it is likely that most motor units are active at maximum tonic voluntary contraction.

[1] T. TOKIZANE and H. SHIMAZU, *Functional Differentiation of Human Skeletal Muscle* (University of Tokyo Press 1964).

[2] L. GRIMBY and J. HANNERZ, J. Neurol. Neurosurg. Psychiat. *31*, 565 (1968).

[3] J. HANNERZ and L. GRIMBY, J. Neurol. Neurosurg. Phychiat., in press.

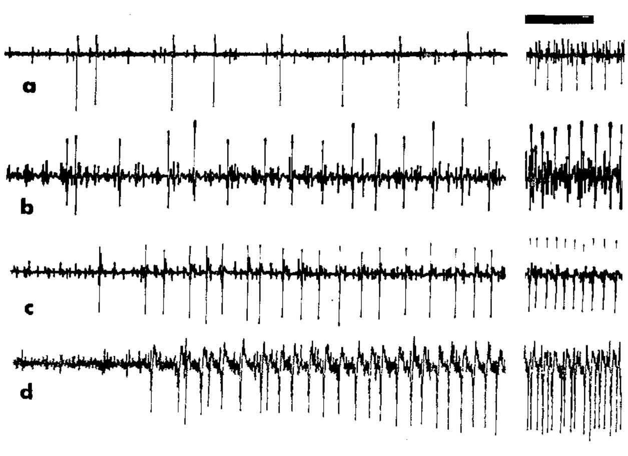

Fig. 1. Initiation and frequency at maximum tonic strength of 4 motor units activated at a) 10%, b) 40%, c) 60% and d) 90% of the maximum tonic strength of the anterior tibial muscle. The higher the threshold of the motor unit in tonic contration, the higher is the frequency when the motor unit attains a discharge at regular intervals and the higher is the frequency at maximum tonic strength. Time bar: 100 msec.

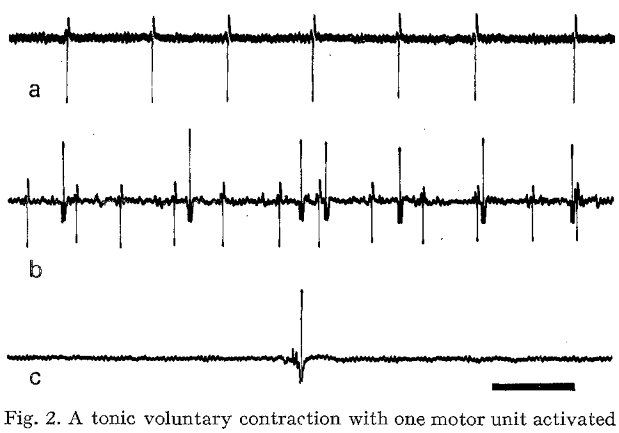

Fig. 2. A tonic voluntary contraction with one motor unit activated at about 18% of the maximum tonic strength of the anterior tibial muscle (a) and another motor unit activated at about 40% of the maximum tonic strength of the same muscle (b). At a frequency of 9 per sec 'the 40% motor unit' discharges at more irregular intervals (b) than 'the 18% motor unit' does (a). c) shows 'the 40% motor unit' activated alone in a phasic voluntary contraction. Time bar: 100 msec.

The optimal and maximum frequency of a motor unit can be assumed to be related to the fusion frequency and the contraction time of the motor unit. Consequently, the motor unit first recruited in tonic activity should have a long contraction time and the later the motor units are recruited in tonic activity, the shorter should be the contraction time of the motor units. On the other hand, the motor units first recruited in phasic activity should have a shorter contraction time than that of the motor units first recruited in tonic activity. It should thus be possible to recruit slow and fast twitch motor units in a different order in different types of activity.

Zusammenfassung. Bei willkürlichen tonischen Muskelkontraktionen werden motorische Einheiten mit niedriger Maximalfrequenz zuerst rekrutiert. Dagegen können bei willkürlichen phasischen Muskelkontraktionen motorische Einheiten mit hoher Maximalfrequenz zuerst rekrutiert werden.

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The Effect of Temperature and of Relative Acidity on the Concentration of Lactate in Cardiac Muscle

The physiological importance assigned to pH values obtained in biological material such as plasma at various temperatures, has to account for the effect of temperature on the ionic product of water or the ratio OH^-/H^+ as suggested by WINTERSTEIN[1]. Actually the arterial pH in poikilothermic animals increases, thereby keeping the ratio OH^-/H^+ constant when the animals are acclimatized to a lowered temperature (RAHN[2]). Instead of using this ratio, RAHN introduced the term 'relative alkalinity' which he defined as the ratio H_N^+/H^+, where H_N^+ is the hydrogen ion concentration of pure water and H^+ the hydrogen ion concentration of e.g. plasma, both at the same temperature. Mathematically H_N^+/H^+ is the square root of the ratio OH^-/H^+. A line chart for the evaluation of both terms as a function of pH and temperature was given by ALBERS[3]. As pointed out by REEVES[4], the constancy of the OH^-/H^+ ratio implies also a constancy of the fractional dissociation of imidazole which in turn provides for optimal enzyme activities and protein conformation. However, though RAHN's experiments clearly demonstrated that in lower vertebrates the relative alkalinity or the fractional dissociation of imidazole appears as a regulated variable, up to now no physiological reaction has been found which is correlated to the relative alkalinity rather than to the hydrogen ion concentration itself. In what follows the well-known increase of the lactate concentration caused by hyperventilation is shown to be possibly such a reaction. The concentrations of lactate and pyruvate in blood and cardiac muscle of rats were determined enzymatically (TFELT-HANSEN and SIGGAARD-ANDERSEN[5]) at a body temperature of 37.9°C (group I) and after cooling the rats to 22.3°C (group II) and 21.2°C (group III). The ventilation in the hypothermic rats in group II was adjusted to give the same OH^-/H^+ ratio of about 15 as was obtained at 37.9°C. In group III the ventilation was increased to give an OH^-/H^+ ratio 3 times as large. As shown in the Table, no change in the OH^-/H^+ ratio is observed if the arterial pCO_2 in the hypothermic rats is lowered to 17 torr and the arterial pH increased to 7.63 (group II) which corresponds to a reduction in the hydrogen ion concentration to 58% of the control value. There is no difference in the blood and tissue lactate between the rats under these conditions and the rats at 37.9°C. If, however, the ventilation in the hypothermic rats is increased, thereby lowering the arterial pCO_2 to 7.9 torr and increasing the pH to 7.90 (group III), the OH^-/H^+ ratio is increased to about 47, the blood lactate is doubled and the lactate in cardiac muscle is increased by more than 300%. The pyruvate concentration in blood and muscle does not change during hypothermia at both levels of ventilation. If at a normal body temperature the arterial pCO_2 is lowered and the arterial pH is increased to values compar-

[1] H. WINTERSTEIN, Arch. exp. Path. Pharmak. *223*, 1 (1954).
[2] H. RAHN, in *Development of the Lung* (Eds. A.V.S. DE RENCK and R. PORTER; Churchill London, 1967), p. 3.
[3] C. ALBERS, in *Fish Physiology* (Eds. W. S. HOAR and D. J. RANDALL; Academic Press, New York, London 1970), vol. 4, p. 173.
[4] R. B. REEVES, Resp. Physiol. *14*, 219 (1972).
[5] P. TFELT-HANSEN and O. SIGGAARD-ANDERSEN, Scand. clin. Lab. Invest. *27*, 15 (1971).

Blood gases and concentration of lactate and pyruvate in blood and cardiac muscle of artificially ventilated rats at normal and hypothermic body temperatures

	Group I	Group II	Group III	S.D.
Rectal temperature	37.9	22.3	21.2	± 0.8
pCO_2 (torr)	38.7	17.3	7.9	± 1.6
pH	7.398	7.632	7.895	± 0.051
$[H^+] \times 10^8$	4.00	2.34	1.29	± 0.23
$[OH^-]/[H^+]$	15.1	14.9	47.2	± 7.8
Lactate (blood) meq/l	1.26	1.05	2.36	± 0.33
Pyruvate (blood) meq/l	0.042	0.043	0.058	± 0.013
Lactate (muscle) meq/kg	1.30	1.68	4.38	± 1.00
Pyruvate (muscle) meq/kg	0.062	0.068	0.067	± 0.016

Each value is the mean of 5 animals. S.D. = standard deviation obtained by analysis of variance.