THE EFFECT OF ADMIXTURE OF FAST AND SLOW MUSCLE IN DETERMINING THE FORM OF THE MUSCLE TWITCH*

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Abstract—There are differences amongst various reports of the speeds of contraction of cat intercostal muscles. By analogue computer modelling it is shown that the differences are largely resolved if the muscle consists of mixtures of two types of motor unit, fast and slow. The method of simulation is extended to fast and slow limb muscles of the cat to illustrate the form of the muscle twitch to be expected from such mixtures. The validity of the model and its extension to populations of motor units, are discussed.

1. INTRODUCTION

When a voluntary muscle receives a single stimulus, it responds with a brief contraction called a "twitch". Recorded isometrically (i.e. as a tension change at constant length), cat muscle twitches have rise times ranging from 7.5 msec for medial rectus of the eye to 25 msec for gastrocnemius and 70 msec for soleus of the hind limb (COOPER and ECCLES, 1930; BUGLER, ECCLES and ECCLES, 1960). Various studies have confirmed the clear differentiation of limb muscles into fast and slow, but in other regions, such as the muscles of respiration, the situation is uncertain. Recently, three separate estimates have been made of the speeds of contraction of cat intercostal muscles. Unfortunately, there are considerable differences between the reported values.

BISCOE (1962) found the time to peak in isometric contractions of internal and external intercostal muscles taken together to be 33 msec. About the same time, GLEBOVSKII (1961) reported a time of 49 msec obtained by techniques which would be difficult to reproduce. A little later ANDERSEN and SEARS (1964) used a more refined technique than that of BISCOE and were able to record from single or small numbers of motor units. They found two groups of units; fast, with mean time to peak ($T_p$) of 24.6 msec and slow, with mean $T_p$ of 47.0 msec. It seemed possible that BISCOE's results might be explained if his larger muscle segments were composed of mixtures of the relatively fast and slow units found by ANDERSEN and SEARS. The present work tests this hypothesis and extends the consideration to the fast and slow limb muscles of the cat.

2. METHODS

Fast and slow twitches, taken from the illustrations of ANDERSEN and SEARS (their Fig. 3, the originals kindly lent by the authors), were simulated on a common time scale with an analogue computer (Electronic Associates TR 48, made available by the kindness of Dr. J. Barker, Imperial College). The method of simulation was largely arbitrary, but bore some relation to theories of muscle contraction. A simple way of describing the mechanical properties of contracting muscle is shown in Fig. 1a. The part below the dotted line is the mechanism producing force, which has to be transmitted via

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the series elastic element (SE) comprising tendon and compliant materials linking the minute contractile elements. The characteristics of the force generator are such that when shortening occurs at constant tension, the velocity is inversely proportional to tension exerted. The generator may therefore be represented as a constant force device (in the sense of a constant force device) acting across a viscous element $R$. For detailed description of such models see PRINGLE (1960). Figure 1b shows an electrical analogue, in which voltage represents force, current represents displacement and capacitance represents the compliance of the SE. The force generated within the muscle as a function of time, $F(t)$, is spoken of as the active state curve (HILL, 1949). After a single stimulus, it is believed to rise rapidly to a maximum, be maintained there for a short while and then fall more gradually. If stimuli are given at a high enough frequency, the active state is held at its maximum. The tension, $P(t)$, recorded at the tendon in a single twitch is only a fraction of maximum because the time constant of the SE and $R$ elements is such that the $P(t)$ and $F(t)$ curves intersect when the active state is substantially decayed. In reality, the situation is complicated by the non-linearity of the SE and the fact that $F$ does depart from true constant force behaviour during change of length. However, it is possible to simulate single twitches effectively on the basis of the above simple scheme by suitably manipulating the form of $F(t)$ and the time constant of the SE and viscous elements.

The actual simulation was performed as shown in Fig. 2. The upper circuit generates the time sweep at $X$ and applies this to two comparators $C_1$ and $C_2$, for the fast and slow components respectively. Each comparator controls