COMPARISON OF THE RECRUITMENT AND DISCHARGE PROPERTIES OF MOTOR UNITS IN HUMAN BRACHIAL BICEPS AND ADDUCTOR POLLICIS DURING ISOMETRIC CONTRACTIONS

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SUMMARY

Experiments were designed to assess the relative contribution of rate coding and motor unit recruitment to force production in two muscles of different fiber composition and function. Single motor unit action potentials were recorded during steady isometric contraction in biceps brachii, a large proximal limb muscle of mixed fiber composition, and adductor pollicis, a small hand muscle comprised mainly of type I muscle fibers. Action potential spike trains were obtained over the entire force range in each muscle. The results suggest that these two muscles are controlled in different ways. In biceps brachii, recruitment was observed from 0 to 88% maximum voluntary contraction (MVC). In adductor pollicis, no motor unit was observed to be recruited at forces greater than 50% MVC, with the majority of recruitment occurring below 30% MVC. On the average, motor units in adductor pollicis discharged at higher rates, with less regularity, and with a greater frequency of occurrence of short interspike intervals (intervals ≤ 20 msec) than those in biceps brachii. Such findings suggest that rate coding plays a more prominent role in force modulation in adductor pollicis, while recruitment plays a more important role throughout the contractile force range in biceps brachii.

INTRODUCTION

It has long been recognized that increases in force production during voluntary muscular contraction are due to the interaction of two basic mechanisms, recruitment of motor units and increases in the discharge rates of units already active\cite{1,2}. The relative roles of recruitment and rate coding in the grading of muscle force have since been much discussed. Some investigators have attributed the greatest changes in force

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output to rate coding, with recruitment occurring over a limited force range. Other workers have assessed a more prominent role for recruitment.

That different muscles may be controlled in different ways was suggested by the first reports of Adrian and Bronk. They showed that rate coding was the dominant mechanism for grading force in the diaphragm while recruitment played a much greater role in the control of certain hindlimb muscles. This suggests that the degree to which either mechanism is used in force modulation may depend on the size and the function of the muscle, its degree of use, or the muscle fiber composition (which in turn may be related to muscle function).

The ratio of fiber types varies greatly among different skeletal muscles, probably reflecting the type of use the muscles serve in daily activities. Muscle fiber types are here referred to as type I or type II. Type I fibers are considered to belong to slow twitch oxidative motor units, while type II fibers include both the fast twitch glycolytic and fast twitch oxidative-glycolytic motor unit.

Muscles which exhibit a great deal of electrical activity and are frequently used, such as those active in posture, have a large proportion of type I fibers, whereas those which display less activity and are less frequently used have fewer type I fibers. Motor units are recruited in order of increasing force output and thus presumably in order of the sizes of their neurons. The motor pools of homogeneous muscles are therefore likely to be more uniform in size than are the pools of heterogeneous muscles. This has been directly demonstrated in cat soleus (homogeneous) and medial gastrocnemius (heterogeneous) motoneuron pools. Since recruitment order depends in part on cell size, it is possible that such different motor pools will exhibit different recruitment patterns.

The present experiments were designed to determine whether rate coding and recruitment play different roles in two muscles differing in fiber composition and function. Motor unit recruitment and discharge patterns were studied throughout the range of isometric contraction forces in two human muscles, the adductor pollicis and brachial biceps. Adductor pollicis is composed predominantly of type I (72–91%) muscle fibers, lies distal in the arm, and is involved in fine control of thumb movements; brachial biceps is a mixed (34–61% type I fibers), proximal muscle of much greater power and generally involved in gross movements. The experiments suggest that these two muscles are controlled in different ways. Rate coding plays a predominant role in force modulation in adductor pollicis while recruitment is more prominent in biceps brachii. On the average motor units in adductor pollicis discharge at higher rates, with less regularity, and with a greater frequency of short interspike intervals (ISIs) (<20 msec). A preliminary report of some of these results has been presented in abstract form.

MATERIALS AND METHODS

Single motor units were recorded in the right adductor pollicis and biceps brachii muscles of 7 subjects ranging in age from 23 to 38 years. A total of 78 motor units were studied, of which 49 were from biceps brachii and 29 from adductor pollicis.
Subsequent experiments, in which 50 more units have been investigated, support the findings presented here, but due to differences in experimental protocol, are not included in the analysis. Intramuscular recordings of single motor units were obtained using fine wire electrodes as described by Clamann\textsuperscript{7,8} using a method modified from Basmajian and Stecko\textsuperscript{3}.

Determination of individual motor unit firing rates was critically dependent upon the isolation of the single unit spike. To aid in detection of single motor units, the amplified action potentials were differentiated electronically\textsuperscript{10}. Identification of a single unit potential was based upon amplitude discrimination, consistency in the shape of the waveforms, and a more or less statistically predictable discharge rate of the spike train.

Force output during isometric contractions was measured with a custom-built force transducer, linear over the force ranges studied (0-35 kg). All forces were recorded as a percentage of maximum to allow comparison of data from subject to subject. Force, intramuscular EMG, and a 100/sec time marker were stored onto magnetic tape for later data analysis.

Two methods were used to determine the distribution of interspike intervals. In the first, raw data, stored on magnetic tape, was differentiated, fed into a window discriminator, and the response of which was used to trigger a PDP 8/E computer. The times between pulses were determined and displayed in an interspike interval histogram. In cases where accurate triggering of the window discriminator was not possible, data were photographed onto film strip, and intervals determined by measuring the distance between spikes. Accuracy was within ± 0.5 mm (± 2 msec). A computer program determined the statistics for the distributions of intervals and constructed the ISI histograms.

RESULTS

Motor unit recruitment

The extent of motor unit recruitment with increasing force differed markedly in the two muscles. As the subject increased biceps force output, EMG activity increased considerably in amplitude. Single unit action potentials in biceps, visible at low force levels, were masked as increasingly taller spikes of newly recruited units appeared (Fig. 1A). The situation was quite different in adductor pollicis. The spikes of a single unit which were clearly visible at low force levels usually remained visible at much higher force levels. The overall amplitude of the EMG changed little with force.

The conclusion that the recruitment pattern differed markedly in these two muscles is borne out by Fig. 1B. In biceps, recruitment was observed up to 88\% MVC, with 10 of 49 units recruited above 50\% MVC. In contrast, recruitment was never observed in adductor pollicis above 50\% MVC. The majority of observed motor units (25 of 29) were recruited at force levels below 30\% MVC.

Motor unit discharge rates

Mean discharge rates for individual motor unit spike trains in biceps brachii and
Fig. 1. A: electrical activity recorded in biceps brachii (left) and adductor pollicis (right) with fine wire bipolar electrodes. Numbers to the left of each record show the isometric force (as per cent MVC) produced by the muscle during the EMG recordings. Calibration bars: vertical = 50 μV, horizontal = 100 msec for all traces. Note: the gain for the 91% MVC record in biceps brachii is half that of all other traces. B: histograms showing the number of motor units recruited in each 10% force increment from 0 to 100% MVC. Pooled data for 13 biceps brachii experiments (49 units) and for 18 adductor pollicis experiments (29 units).
Fig. 2. Firing rates of motor units pooled from biceps brachii and adductor pollicis. For biceps brachii, 57 spike trains were analyzed, while in adductor pollicis, 75 spike trains were analyzed. Filled circles designate firing rates for units discharging at their recruitment force. Open circles represent firing rates for units recruited at lower forces.
adductor pollicis were obtained at various steady-state isometric forces. Fig. 2 depicts the mean discharge rates for all spike trains recorded as a function of the percentage of the muscle's MVC. In adductor pollicis, motor units displayed firing rates ranging from 6 to 32/sec, while in biceps, a slightly smaller range, from 7 to 28/sec was observed.

Straight lines were fitted to the data of Fig. 2 by linear regression analysis. For adductor pollicis, the slope of the line was 1.9 impulses/sec for a 10% change in force output. The correlation coefficient was 0.77. For biceps, the slope was 1.1 impulses/sec for a 10% force change, with a correlation coefficient of 0.55. The difference in these two slopes was significant (Student's t-test, $P < 0.01$).

In adductor pollicis, it was possible to identify the action potential trains of 4 motor units discharging over a wide range of forces. Their discharge rates as a function of muscle force are shown in Fig. 3. Two of these units (units marked $+$ and 0) showed a nearly linear relationship between discharge rate and force. For the two others, there was an initially steep rise in discharge rate followed by a plateau at higher force levels.

Analysis of instantaneous firing rates allowed examination of motor unit discharge patterns which might be masked by the averaging of ISIs. One such pattern
Fig. 4. Distributions of brief ISIs observed in biceps brachii and adductor pollicis. For biceps brachii, brief ISIs were observed in 13 spike trains. The length of the spike trains ranged from 78 to 241 ISIs with a mean of 139 ISIs/spike train. For adductor pollicis, brief ISIs were observed in 18 spike trains. The length of the spike trains ranged from 61 to 400 ISIs with a mean of 124 ISIs/train.

was the occurrence of brief ISIs (ISI ≤ 20 msec). They were found only when the force exceeded 44% MVC in either muscle, and occurred more often in adductor pollicis spike trains than in those of biceps. Fig. 4 displays the data for spike trains which contained at least one brief ISI per spike train. The greater incidence of brief ISIs in the adductor muscle is clearly seen. For larger intervals (20–30 msec), the number of occurrences in both muscles begin to approximate each other.

DISCUSSION

Recruitment and rate coding

The results of the present study suggest that recruitment and rate coding play different roles in muscles of different anatomical positions, functions, or fiber type composition. The large limb muscle, biceps brachii, showed recruitment of motor units through at least 90% of its contractile force range. In marked contrast, no motor unit was observed to be recruited above 50% MVC in adductor pollicis; moreover, the majority of recruitment occurred below 30% MVC. This agrees with data from another hand muscle, first dorsal interosseus\textsuperscript{28,29}, and is similar to the recruitment
pattern in cat soleus. This finding may help to resolve the controversy regarding the relative roles of recruitment and rate coding in muscle control.

Of the 49 brachial biceps units studied, 10 (20%) were recruited above 50% MVC. It is unlikely that this is a representative sample of the biceps motor unit population. Even with the electronic filtering techniques used here, single records are easier to obtain at low to moderate force levels; moreover, motor units of different force thresholds may be somewhat segregated in biceps. It is therefore likely that a substantially larger percentage of motor units than reported here is recruited at high force levels in biceps. A small number of units recruited at high force levels could produce a major portion of the contractile force of the muscle by virtue of their greater size and strength. These would presumably be units composed of fast, powerful type II muscle fibers. Such findings are consistent with those of Garnett et al. who reported that in human medial gastrocnemius, large twitch units would be recruited ‘above about 30% of the total cumulative twitch tension’.

Since no motor units were recruited above 50% MVC in adductor pollicis, higher force levels could only be achieved by increases in discharge rate. Yet the highest discharge rates seen in adductor motor units were only 32/sec in these steady-state contractions. One mechanism by which high force output could be achieved is through occasional rapid discharges of action potentials. Pairs of action potentials with an interspike interval of less than 20 msec were frequently seen in adductor pollicis spike trains. In slow motor units, such discharges could produce a prolonged increase in force. Burke et al. showed that a single stimulus interpolated in a steady stimulus train to a motor unit, could raise the force of an unfused tetanus for several seconds. This phenomenon was referred to as the ‘catch-like property’ and was most readily demonstrated in slow soleus motor units.

Another means of evaluating the discharge behavior of the motor units is to plot the variability in firing (standard deviation) versus the mean firing. The non-linearity of such plots has previously been described and was confirmed here for both muscles. Fitting of the data to power curves of the form SD = a(ISI)^n were, for biceps, SD = 0.01 (ISI)^1.78 and for adductor pollicis, SD = 0.03 (ISI)^1.54. The larger coefficient for adductor motor units, although not statistically different from that of biceps, suggests a trend for adductor units to discharge, on average, with a greater variability than biceps’ units.

Maximum discharge rates of motor units

Maximum discharge rates for motor units in the two muscles investigated were well below the 200/sec reported by Marsden et al., and were confined to the ‘primary’ range of alpha motoneuron discharge described by Kernell. There are two possibilities which could account for the lower discharge rates observed here. In the first place, motor units are known to discharge slowly in steady contractions, as used in this study; in the second place, the unit activity probably occurred in the presence of inhibitory inputs to the motoneurons, an effect which might be negated under certain experimental conditions.

The type of contraction a muscle produces is undoubtedly reflected in the
discharge patterns observed. Unusually high discharge rates have been demonstrated at the onset of a ballistic contraction and attention has been focused on the bursting pattern observed at the initiation of such movements. For the aberrant units of Marsden et al., the highest rates were observed at the onset of the contraction. During the steady isometric holding, the rates slowed to about 50/sec. Ballistic movements may therefore necessitate burst of activity with rates well within the 'secondary' range of motoneuron discharge, while steady-state contractions (such as those tested in this investigation), may require rates only within the lower 'primary' range of discharge.

In the earlier investigations, the authors were able to isolate single neurons from the remainder of the neuronal pool and its internuncial circuitry. Motoneuron recurrent collateral excitation of Renshaw cells has been shown to exert a stabilizing influence on the motoneuron pool. This influence may be absent in the case of direct current injection into individual alpha motoneurons, thus enabling neurons to achieve much greater discharge rates than usually seen. Similarly, for the human motor units studied by Marsden et al., one or two neurons supplying adductor pollicis were contained in a nerve (median nerve) not normally innervating this muscle. The cell bodies for the units supplied by the median nerve may therefore lie outside the anatomical extent of the motoneuron pool of the muscle. Isolation of these aberrant neurons might free them from the inhibitory influences of the pool's Renshaw cells.

It should be noted that the morphological and physiological evidence for the identification of Renshaw cells has been obtained almost exclusively in the lumbosacral spinal cord of cats. An elegant demonstration of Renshaw cell activity has been reported in the soleus muscle in man, but the presence of Renshaw cells in the forelimb motor pools in man has yet to be established.

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