Motor Unit Recruitment and Firing Rates Interaction in the Control of Human Muscles

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Muscle contractions are modulated by the number of motor units recruited and their respective firing rates. The work described in this report documents an interplay between recruitment and firing rates of motor units. The recruitment of a new motor unit appears to have a disfacilitatory influence on the firing rates of previously activated motor units. It is speculated that this effect is likely to be mediated, at least partially, via the stretch reflex loop and possibly by the recurrent inhibition of the Renshaw circuit. Such a mechanism would be functionally useful in providing smooth control of muscle output via peripheral circuitry (consisting of proprioceptive reflexes and recurrent inhibition), thus lessening the amount of detailed supervision of the α-motoneuron pool required by the central nervous system.

INTRODUCTION

Recruitment of motor units and modulation of firing rates of active motor units are the two mechanisms available to the nervous system for regulation of muscle force. It is generally accepted that the recruitment of motor units occurs in an orderly manner, obeying the 'size principle' which was convincingly demonstrated by Henneman et al.[14]. It is known that different strategies are used in contractions requiring slow and fast (ballistic) rates of force production. In ballistic contractions motor units often fire only a few times with relatively short interpulse intervals, approaching and at times even exceeding instantaneous firing rates of 100 pulses/s[1,11]. Whereas during attempted isometric contractions, De Luca et al.[9] have shown that specific muscles differ in their use of recruitment and firing rate for modulating force output. It is also widely reported that the firing rates of active motor units generally increase monotonically with force output (refs. 9, 15 and others). Using crosscorrelation analysis on the firing rates of concurrently active motor units and on the muscle-force output, De Luca et al.[10] showed that small, possibly compensatory 1–2 Hz fluctuations are simultaneously present in all the observed muscle-force output and firing rates of the active motor units. This fact indicates that all active motoneurons in a single muscle are subject to a 'common drive'.

It has been customary to consider the properties of recruitment and firing rate as independent variables. However, reports that have appeared during the past decade have begun to describe the existence of functional coupling between the discharges of single motoneurons and the output of muscle spindles, Golgi tendon organs and Renshaw cells. These receptors and cells all provide feedback, which either individually or in conjunction have the potential of altering the total amount of excitation to the motoneuron pool. The coupling between single motor units and muscle spindle afferents has been studied by stimulating the former and recording spike trains from the latter[2,4,8,21]. These reports concur in revealing that both spindle group Ia- and II-afferent activities are

strongly coupled with contractions of some motor units closely located to the spindle, and are more or less indifferent to contractions of remotely located motor units. These results support the proposition that muscle receptors generate a 'sensory partitioning' of their homonymous muscle. Further support for this concept has been provided by Brink et al.[6], Botterman et al.[5] and Lucas and Binder[18], working on the splenius, medial gastrocnemius and the biceps femoris of the cat respectively. The 3 studies all indicated that the Ia-afferent input to the homonymous muscle exert greater synaptic effects in motoneurons that project to the same 'compartment' than in other homonymous motoneurons.

The functional coupling between single motor unit twitches and Golgi tendon organ activity has been reported by Binder et al.[3]. In an analogous study to that involving the muscle spindles, they observed that the tendon organs are also highly sensitive to single motor unit twitches. Individual motoneurons are also coupled to other motoneurons via the Renshaw recurrent inhibitory pathway. In this regard, it has been shown that Renshaw cells can be activated by the discharge of a single motoneuron[23] and that Renshaw cells are more strongly excited by collaterals of large motoneurons than small ones[22,24].

Because of these functional couplings among motor units within a muscle, it is possible that the recruitment of a new motor unit may have an effect on the motor units which are already active. The present investigation was undertaken to document any possible interaction between recruitment and firing-rate coding of motor units in *humans during voluntary contractions*.

METHODS

The experiments of this study were performed on the tibialis anterior and the first dorsal interosseus muscles. Three adult male subjects (30, 37 and 39 years of age) without known history of disorder of the neuromuscular system participated in the study. Subjects were seated comfortably. And the appropriate limb was placed in a specially constructed device which housed a force transducer, having high stiffness (3×10^6 N/m). The limb was secured firmly to the transducer to ensure that all contractions were as isometric as possible. The design of the device and the arrangement of the limb was such that the torque output of the monitored joint was mechanically directly related to the force output of the muscle being studied. The output of the force transducer was displayed on one channel of a dual trace oscilloscope. A newly developed needle electrode* containing 4 detection surfaces providing selective and stable recordings of single motor unit activities was inserted into the muscle under study. The needle electrode was manipulated until a recording site fulfilling the following two criteria was located. First, at least one motor unit (preferably more than one) recruited at a relatively low force level was present. Second, while the previously activated motor unit(s) continued to discharge, another motor unit was recruited and discharged continuously as the force level increased. The subject then made 2–3 practice runs to identify the force level at which the new motor unit was recruited. The action potential of this newly recruited motor unit had to be clearly visible in the detected signal and had to have an amplitude sufficiently large to provide immediate evidence of its presence in the visual and auditory feedback provided to the subject. The force level of recruitment was displayed as a target line on the second channel of the oscilloscope. Next, the subject was instructed to initiate a contraction and to approach the recruitment level by slowly increasing the force, in the order of a few % of the maximal voluntary contraction (MVC) per second. Once the new motor unit was recruited, the subject was required to maintain a steady force output or to increase the force output slightly. Special precautions were taken to insure that the force output did not decrease. The subject was also directed to main-

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* The needle electrode used in this study consists of 25-gauge stainless-steel tubing having an opening in the wall of the shaft approximately 2 mm from the edge of the tip. In this opening are exposed the cross-sectional areas of four 75 μm-diameter insulated wires (90% platinum–10% iridium), located at the corners of a square and spaced approximately 200 μm apart. This geometrical arrangement was chosen so that the activity from 4 or 5 motor units would be consistently detected in most muscles. The 5 different detection surfaces (4 wires and shaft) may be connected to form a variety of differential detecting arrangements, each providing a channel of myoelectric signal. Three independent derivations of the myoelectric signal were recorded for subsequent decomposition into motor unit action potential trains. For additional details refer to Mambrito and De Luca[19,20].

tain the newly recruited motor unit continuously active.

The myoelectric signals and the force transducer output were recorded on an FM tape recorder and subsequently transferred to mass-storage on a digital computer. The myoelectric signals were decomposed into their constituent motor unit action potential trains, using interactive computer algorithms**. Plots of the timing of the motor-unit discharges, as well as the interpulse intervals and the mean firing rates of individual motor units were produced. The mean firing rates of a motor unit at a particular instant of time were estimated by calculating the weighted (Hanning) average number of firings within a 800-ms time window centered at the instant of time where the mean firing rate was to be estimated. This seemingly long time window was chosen as it enhances recognition of the presence of slow trends in the firing rates.

RESULTS

Figs. 1 and 5 contain examples of all the observations noted in the analyzed data.

In Fig. 1, the mean firing rates (broken lines) of 4 concurrently active motor units of the tibialis anterior muscle are plotted as a function of the time of the contraction. The force (solid line) is presented as % of the MVC (right scale). Note that motor unit No. 4 is recruited at 3 different times. At its first recruitment, occurring approximately at time 8 s, an abrupt decrease in the firing rates of motor units Nos. 1–3 occurs. The trains of these same 4 motor units are represented in Fig. 2, which present the data from 7–9 s in Fig. 1. At the time of its first recruitment, motor unit No. 4 is activated with a 'doublet' (two consecutive discharges having an interpulse interval
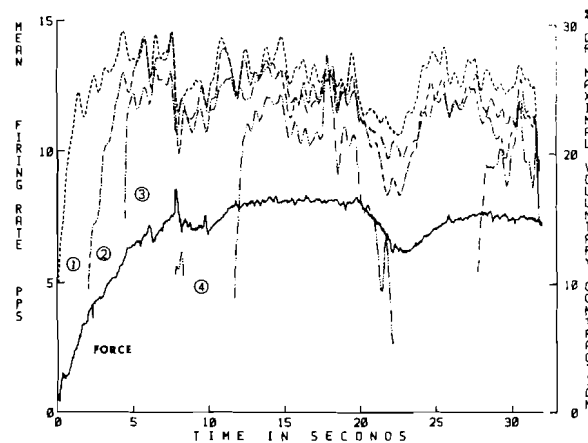

Fig. 1. Firing rates (broken lines) of 4 concurrently active motor units of the tibialis anterior muscle recorded during a 32-s isometric contraction. The force (solid line) is measured in % MVC. Note that motor unit No. 4 is recruited at 3 instances, the first time with a doublet. The firing rates of motor units Nos. 1–3 behave differently each time motor unit No. 4 is recruited at time 8 s, a step-wise decrease is observed; between times 12 s and 15 s, the firing rates are essentially constant, possibly due to the fact that the force output increased too rapidly, thus masking any decrease that might otherwise be present between times 28 s and 30 s, decreases in the firing rates occur to varying degrees. The common decrease in the firing rates at time 15 s could be caused by a recruitment of a motor unit not detected by the electrode.

in the order of 10 ms). The occurrence of the doublet precedes a marked and sharp deflection in the force record by 95 ms, strongly suggesting a causal relationship.

In Fig. 2, it can also be seen that the discharges of the 3 previously activated motor units are inhibited after the occurrence of the doublet. This effect is better seen in Fig. 3 which presents the instances of firing of motor units Nos. 1–3 with respect to the doublet of motor unit No. 4. Note the lack of discharges between 10 and 60 ms. When motor unit No. 4 is recruited the second time, at approximately 12 s into

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** The decomposition algorithms use motor unit firing statistics (estimated on-line during the decomposition operation) and the shapes of motor unit action potential waveforms (in a 3-dimensional representation obtained from 3 channels of myoelectric signal) to extract action potentials from the myoelectric signal. The algorithms consist of logic based on a modified form of matched filtering extractions. The statistical parameters of the discharge times are recursively estimated and the templates in each channel are updated at each motor unit action potential detection. Special algorithms designed to resolve superpositions, such as those that may occur during synchronous discharges, are included. This latter set of algorithms attempts to identify a complex waveform (in 3 dimensions) by creating the waveform by superimposing the templates of all identified motor action potentials in 3 dimensions. The technique has been tested for accuracy by decomposing the simultaneously recorded activities from two needle electrodes inserted into a muscle. Whenever a motor unit was present in the records from both needle electrodes, a 100% agreement between the firings was obtained. Only those motor unit action potential trains that could be decomposed with absolute confidence (100% accuracy) have been presented in the Results section. For further information the reader is referred to LeFever and De Luca[16,17] and Mambrito and De Luca[19,20].
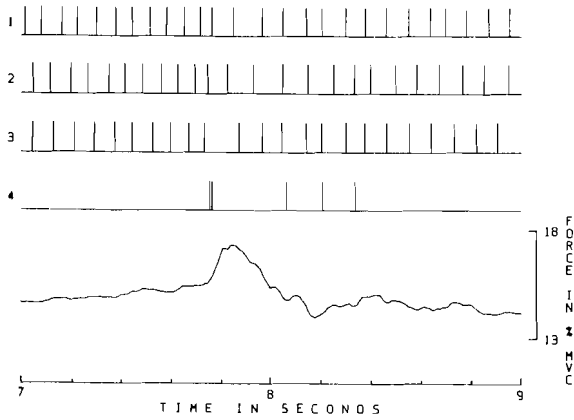
Fig. 2. Firing times of the same 4 motor units of Fig. 1 are shown on an expanded time scale at the time of the first recruitment of motor unit No. 4. Note that motor unit No. 4 is recruited with a doublet, which precedes a sharp transient increase in the force output of the muscle. Also note that motor units Nos. 1 and 3 fire synchronously during discharges 2–9 after the doublet.

Fig. 4. The firing rates (broken lines) of the same 4 motor units of Fig. 1 are shown on an expanded time scale at the time of third recruitment of motor unit No. 4.

the contraction (see Fig. 1), there is no apparent decrease in the firing rates of motor units Nos. 1–3, and there is no associated sharp disturbance in the force output. At the third recruitment (in the time interval 25–30 s) the firing rates of motor units No. 2 (dash-dot-dash) and No. 3 (dash-dot-dot-dash) clearly decrease, while the firing rate of motor unit No. 1 (dash-dash) remains essentially unaffected. The firing rates of motor units Nos. 1–4 are also represented in Fig. 4 with an expanded time scale at the time of the third recruitment.

Fig. 5 displays the mean firing rates and the force record of another contraction. Note the gradual decrease of the firing rates of the top two tracings (while the force is increasing) as the third motor unit is re-
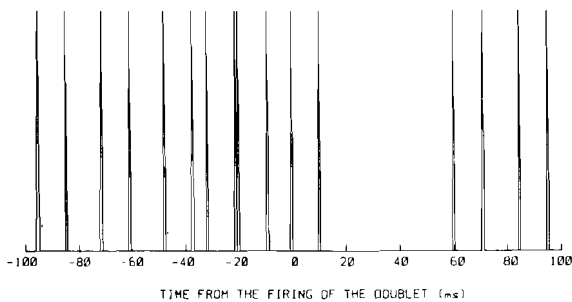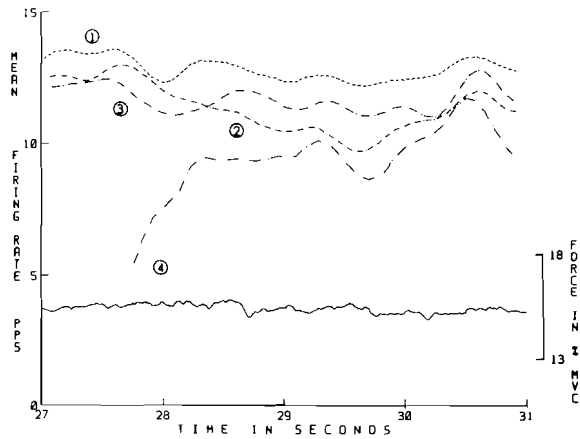
cruited. This same phenomenon is not visible in motor unit No. 1 when motor unit No. 2 is recruited. However, note that at this time the force record shows a higher rate of increase.

Using the described paradigm of attempted slow increase in force output of the muscle, we have observed decreases in the firing rates of some or all previously activated motor units upon recruitment of a new motor unit in both the tibialis anterior and the first dorsal interosseous muscles. Despite the fact that for both muscles the protocol was designed to investigate recruitment–firing rate interaction irre-

Fig. 3. Instances of firing of motor units Nos. 1–3 with respect to the doublet of motor unit No. 4 in Fig. 2. The time segment between 7.5 and 8.0 s was analyzed. Note the suppression of the previously activated motor units when the new unit is recruited.
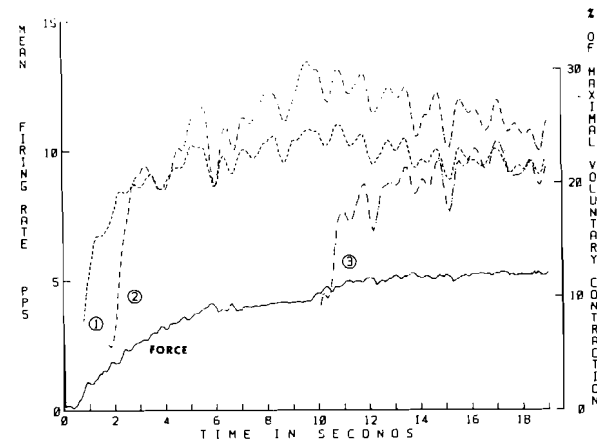

Fig. 5. Firing rates (broken lines) of 3 concurrently active motor units of the tibialis anterior muscle recorded during an isometric contraction. The force (solid line) is presented as % MVC (right scale). Note the gradual decrease of the firing rates of the top two tracings while the firing rate of the third motor unit increases.

TABLE I

Details of the effect of the recruited motor unit on previously activated units. Each asterisk indicates a previously activated motor unit (MU) whose firing rate decreases when a new motor unit (indicated by the bottom asterisk in each column) is recruited.

First dorsal interosseous			Tibialis anterior		
Subject	Recruitment (% MVC)	MU in contraction	Subject	Recruitment (% MVC)	MU in contraction
HB	2	1**	HB	3	1*
	3	2**		4	2*
	3	3**		8	3*
	4	4**			
	4	5 *	HB	1	1*
	5	6 *		10	2*
	5	7 *			
			HB	4	1*
HB	1	1*		19	2*
	2	2*		20	3*
	2	3*			
	2	4*	HB	2	1 *
	3	5*		3	2**
				6	3**
HB	2	1		18	4**
	3	2**		19	5 *
	4	3**			
	5	4 *	BM	5	1
				7	2*
CD	2	1*		7	3*
	8	2*			
			BM	1	1***
CD	2	1*		9	2***
	16	2*		13	3 **
	27	3*		15	4 *
	28	4 *			
	28	5 *	BM	2	1*
				10	2*
CD	2	1**		13	3*
	22	2**		21	4*
	27	3 *			
	27	4	BM	4	1*
	27	5		9	2*
				9	3*
CD	1	1*		19	4*
	27	2*			
	27	3	BM	1	1*
	27	4		2	2*
			BM	1	1*
				2	2*
			BM	1	1*
				2	2*
				6	3
			CD	2	1*
				2	2*
				50	3*
				51	4

spective of the force level, after numerous trials and random electrode insertions, the described effect was observed among motor units whose recruitment threshold ranged from 1 to 50% of MVC. The typical contraction lasted 20 s. Details of the data are presented in Table I.

In 3 records from the tibialis anterior muscle, recruitment with a doublet was observed. In each of these cases, all the observed previously activated motor units decreased their firing rates.

Visual inspection of the firing rates displayed in Figs. 1 and 5 reveals an in-phase fluctuation of approximately 1–2 Hz in all the concurrently active motor units. This behavior has been termed 'the common drive'. This phenomenon will not be addressed in this paper; the interested reader is referred to De Luca et al.[9,10].

Scrutiny of our data from other investigations[9,10] has shown one instance of decreased firing rate with recruitment of a new motor unit during an isometric, attempted constant-force contraction of the deltoid muscle. Also, decreased firing rates have been observed in two cases of voluntarily initiated and sustained co-contractions of the flexor and extensor pollicis longus muscles. In one of these two cases, the effect occurred simultaneously in the flexor and extensor muscles, presumably as the subject increased the contraction levels of both muscles, to increase the stiffness of the interphalangeal joint.

DISCUSSION

To our knowledge, this work provides the first documentation of an inhibitory effect on the firing rates of motor units, which are already active, upon recruitment of new motor units. The effect provides an apparently simple strategy for the smooth control of muscle output. Upon recruitment of a new motor unit it may be desirable to produce an increase in muscle force which is less than the minimal incremental contribution of the new motor unit. One way to achieve this goal is to decrease the firing rates of the motor units which are already active, so as to diminish their contribution to the total force output when the new motor unit is recruited. Thus, compensatory decreases of the firing rates of previously activated motor units will enable the muscle to produce a more smooth force output during recruitment. This effect

becomes more important if the newly recruited motor unit provides a strong twitch contribution to the total force. Because larger motor units are recruited at higher contraction levels[14], it would be expected that later recruited motor units should have a stronger effect on the firing rates of previously activated motor units. The hierarchy of the effect may be seen in Fig. 1 where the recruitment of motor unit No. 4 is associated with the decrease in the firing rates of motor units Nos. 1–3. Many other examples are presented in Table I.

The mechanisms responsible for the observed inhibitory effect of a newly recruited motor unit on the firing rates of those already active may well differ in the case of rapid (Fig. 1 at the first recruitment of motor unit No. 4) vs slow (Fig. 5 and Fig. 1 at the third recruitment of motor unit No. 4) changes in firing rates.

(1) Concerning the observed rapid changes in firing rates of previously activated motor units, results of this study as well as information present in the literature strongly suggest a local reflex mode of action. As reported in the introduction of this paper, spindle and Golgi tendon organs are coupled to individual motor-unit contractions. Furthermore, it has been shown that activation of a motor unit with a doublet with less than 10 ms interpulse interval may result in a peak tension as high as 5 × the peak twitch tension[7] and that doublet activation of motor units may cause long pauses in Ia-afferent firings[29]. The discharge relationship analysis (of the motor-unit action potential trains of Fig. 2) which is presented in Fig. 3 shows that the interpulse intervals of the motor unit already active at the time of recruitment of motor unit No. 4 are affected up to 60 ms after the second pulse of the doublet, suggesting that the disfacilitation (reduction in excitation) is caused by a local reflex loop. The observed time delay in the discharges of the previously activated motor units is consistent with the time required to build up force (change the internal length) of the recruited motor unit, affect the receptor, transfer the afferent information from the receptor to the α-motoneuron pool and for the result to manifest itself in the myoelectric signal. The other 2 records from the tibialis anterior muscle which also contained doublets at recruitment demonstrated similar disfacilitation (inhibition). In fact, the occurrence of a discharge within 10 ms after the doublet

supports the notion that the afferent feedback is involved with the inhibitory mechanism because the discharge occurred too soon for the reflex action to have an effect. The involvement of the local reflex loop is also suggested by the presence of the relatively long interpulse interval of 287 ms following the doublet of motor unit No. 4 in Fig. 2.

On the basis of the results of this study it is not possible to distinguish between a muscle spindle effect and a Golgi tendon organ effect. In fact, a muscle spindle may be slackened if a nearby motor unit contracts, thus producing a decrease in the Ia excitation to the homonymous motoneuron pool. Alternatively, a tendon organ may be stressed if an attached motor unit contracts[3], thus producing an increase of the Ib inhibitory effect on the homonymous motoneuron pool. In both cases the effect on the pool will be disfacilitatory, that is, it will provide a reduction in excitation.

It would be expected that the described effect of the recruitment of a new motor unit on the firing rates of previously activated ones would be most obvious when the resulting muscle output would be substantially increased by the new motor unit.

(2). The slow decrease of the firing rates of previously activated motor units and the simultaneous increase or constancy of the firing rate of the newly recruited one implies a non-uniform shift in the drive to the α-motoneurons within the pool, or a non-uniform shift in their excitability that takes place after the recruitment. It is unlikely that the possible shift in drive within the pool would be mediated purely by higher centers, as this would imply that the central nervous system controls α-motoneurons individually, a concept that is inconsistent with current understanding of the principles of orderly recruitment[14] and the common drive[10].

It also seems difficult to base the slow decrease of previously activated motor units coupled with the simultaneous increase in the mean firing rate of the newly recruited motor unit solely upon stretch reflexes. Therefore, an additional mechanism, complementing the stretch reflex feedback is required. A possible candidate is Renshaw circuit-mediated recurrent inhibition. In fact, it has been shown that Renshaw cells can be activated by the discharge of a single motoneuron[23,27] and that Renshaw cells are more strongly excited by collaterals of large moto-

neurons than small ones[12,13,22,24]. Consequently, if the Renshaw cell inhibitory action on the α-motoneuron pool is achieved in a size-related fashion (small-diameter motoneurons being affected more than large-diameter ones); then this complementary mechanism could have the desired selective property of preferentially slowing down the relatively smaller motor units which are already active. The following scenario is envisioned:

(a) In response to the need to increase the force output of a muscle, the centrally mediated excitation to the motoneuron pool increases — and a motor unit is recruited.

(b) The discharge of the recruited motor unit causes a disfacilitation (diminution of excitation) of the motoneuron pool via the stretch reflex and recurrent inhibition. But the recurrent inhibition disfacilitates the smaller, earlier recruited motoneurons more than the larger, later recruited motoneurons.

(c) In order to maintain or increase the force output of the muscle, the centrally mediated excitation to the motoneuron pool increases.

(d) The net difference between the common motoneuron pool excitation and the proportional disfacilitation results in an observable increase in the excitation (firing rate) of the later recruited motor unit and a decrease in the excitation (firing rates) of the earlier recruited motor units.

(e) When the increase in the common motoneuron pool excitation exceeds the inhibition, the firing rates of all the motor units increase.

Thus, the time to reach equilibrium following such a scheme could be long, possibly in the order of several seconds.

The mechanisms described in this report may be the cause of the relatively low firing rate increases with force observed in the deltoid muscle[9] and the brachialis muscle[15] within a force range where recruitment still occurs. In fact, any newly recruited motor unit would decrease the firing rate of the motor units which are already active and the global effect would be to prevent large firing-rate increases as long as recruitment occurs. This is consistent with the relatively high increases in firing rate observed above 70% of maximal voluntary contraction in the brachialis muscle[15] and in the first dorsal interosseous[9] when recruitment is absent or scarce.

It is of interest to note that the disfacilitatory effect of recruiting a new motor unit on the firing rates of the previously activated ones seems to be less in the first dorsal interosseus muscle than in the tibialis anterior muscle. This is consistent with some observations in the present study and previous observations[9] which indicate that the first dorsal interosseus muscle shows a higher increase in motor unit firing rates than the tibialis anterior muscle when muscle output force is increased.

Before terminating the discussion it is important to note that the described effect may not be clearly or easily observed in the following situations:

(1) When the experimental paradigm of *slow* force increase is not properly executed when a new motor unit is recruited. This may be the case at the second recruitment of motor unit No. 4 in Fig. 1. Note that the subject was not increasing the output force *slowly* when motor unit No. 4 was recruited. Presumably, the increase in excitatory drive on the motoneuron pool was high enough to mask the peripheral disfacilitatory effect, or the disfacilitatory effect is manifest in the form of a decrease in the slope of the firing rate of the active motor units occurring at recruitment of the new unit. In most cases it may be difficult to visually detect minute changes in the slopes of the firing rate curves, thus only those records where the experimental protocol was successfully executed have been considered in the present investigation. That is, the force was slowly increasing when the new unit was recruited and there was a *decrease* (not simply a change in slope) in the firing rates of the already active motor units.

(2) When the motor unit causing the disfacilitatory action is not detected by the selective electrode used in this study. For example, this may be the case in Fig. 1 (at approximatively time 15 s), where the firing rates of all 4 active motor units decrease while the force increases slightly.

(3) When the force contribution of the newly recruited motor unit is small. In this case the disfacilitatory effect on the already active motor unit may be too small to be observed.

(4) When the newly recruited motor unit may not be strategically spatially located to effect the particular muscle spindle or Golgi tendon organ which interacts with the observed motor unit.

(5) When the influence exerted by a newly recruited motor unit on the spindle discharge is diminished

by the influence of another active motor unit whose fibers are also located in the proximity of the spindle. Schwestka et al.[25] and Windhorst and Schwestka[28] have provided evidence for such interaction among two motor units and a spindle. They noted that the resulting influence was related to the relative timing of the twitches of the two motor units.

A note of caution should be made in interpreting the force measurements made in this study. In the case of the tibialis anterior muscle, because of the possible synergist muscle contributions, it is necessary to assume that the force output of the tibialis anterior muscle is monotonically related to the force monitored at the ankle joint. Such concern is removed in the case of the thumb phalangeal joint, which is controlled only by two muscles. In the case of the first dorsal interosseous muscle, it has been reported[26] that the force of the muscle is linearly related to the force output at the metacarpo-phalangeal joint. Such caution, naturally, must be complemented by other arguments. For instance, it is unlikely that the rapid changes in the force associated with recruitment of a new motor unit, such as in the case of recruitment of motor unit No. 4 in Fig. 2, are due to simultaneously occurring recruitment of other motor units in non-monitored synergist muscles. In any case, the conclusions derived in this study are based mainly on the observed interaction among motor unit firing rates.

CONCLUSION

This study has revealed that newly recruited motor units have the potential of providing an inhibitory influence on the motor units which are already active. This phenomenon has the functional significance that muscle force output can be modulated with a finer resolution than the incremental force change otherwise resulting from the mere recruitment of one motor unit at a time. There is probably more than one mechanism responsible for this effect. The most rapid changes in the firing rates of previously activated motor units are likely mediated via the Ia-, Ib- and II-α-motoneuron reflex pathway. Slower changes in the firing rate may involve the recurrent inhibition pathway via Renshaw cells.

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