Intrinsic Activation of Human Motoneurons: Reduction of Motor Unit Recruitment Thresholds by Repeated Contractions

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Gorassini, Monica, Jaynie F. Yang, Merek Siu, and David J. Bennett. Intrinsic activation of human motoneurons: reduction of motor unit recruitment thresholds by repeated contractions. J Neurophysiol 87: 1859–1866, 2002; 10.1152/jn.00025.2001. The main purpose of this study was to examine whether facilitation of human motor unit recruitment by repeated voluntary contractions is mediated, in part, by time and activity-dependent increases in the intrinsic excitability of the parent motoneuron. To do this, pairs of tibialis anterior or soleus motor units were recorded during slowly increasing and then decreasing voluntary contractions. The firing rate of the lower-threshold motor unit of the pair (control unit) was used as a measure of effective synaptic excitation (i.e., drive) to the motoneurons. This rate was used to estimate the recruitment threshold of the higher-threshold unit of the pair (test unit). The test unit was repeatedly recruited and de-recruited in a series of contractions, and the interval between the de-recruitment and re-recruitment of the test unit (interaction interval) was systematically varied between 0.6 and 60 s. An increase in intrinsic excitability of a unit was considered to have occurred if the level of estimated synaptic input (as measured by the firing rate of the control motor unit) needed to recruit a unit was reduced. At short interaction intervals (1–2 s), the control unit firing frequency was significantly lower when the test unit was recruited on the second contraction, compared with the first (by 3.9 Hz or a 64% reduction). This suggested that the intrinsic excitability of the test motor unit had increased during the second contraction because it could be recruited at a much lower level of estimated synaptic drive. Longer interaction intervals (2–6 s) produced less recruitment facilitation. At even longer interaction intervals (>6 s) there was no significant facilitation (time constant of effect was 4.8 s). In some motor units, the effect of this short-term facilitation appeared to be so pronounced that it resulted in reversing the order of de-recruitment with the other initially lower-threshold motor units. Such reversals were occasionally observed for orderly re-recruitment. The time course and behavior of the observed short-term facilitation of motor unit discharge was qualitatively similar to the warm-up phenomenon of plateau potentials seen in motoneurons of reduced preparations (e.g., 4–6 s). The possibility of warm-up contributing to the time and activity-dependent facilitation of human motor unit recruitment is discussed.

INTRODUCTION

The threshold for activation of a motor unit is not always constant, rather recruitment thresholds have been shown to be dependent on the history of activation of a unit. For example, the torque recruitment threshold of a unit progressively reduces during repetitive, isometric contractions that follow one another closely in time (at <10-s intervals) (Denier van der Gon et al. 1985; Romaique et al. 1993; Suzuki et al. 1990). Possible mechanisms responsible for this phenomenon have been proposed to be mediated by increases in contraction-related synaptic inputs to the motor units under study. For example, postcontraction increases in muscle spindle discharge and/or progressive focusing of excitation to muscles in line with the direction of pull have been postulated to contribute to the time-dependent reductions in recruitment thresholds (Suzuki et al. 1990). In addition, hysteretic properties of the muscle fibers themselves may also contribute to the lowered torque threshold with repeated muscle contractions (Binder-Macleod and Clamann 1989).

Alternatively, time-dependent changes in the intrinsic excitability of the parent motoneurons may also explain the reduction in recruitment thresholds of motor units during repetitive contractions. For example, stimuli that repeatedly depolarize dorsal horn neurons in rats and turtles can increase the excitability of these cells with each repetition (referred to as warm-up). This phenomenon is considered to be related to the central sensitization of pain (reviewed in Herrero et al. 2000; Morisset and Nagy 1996; Russo and Hounsgaard 1994, 1996). A similar warm-up phenomenon has also been shown to occur in motoneurons (turtle, Svirakis and Hounsgaard 1995, 1997; decerebrate cat, Bennett et al. 1999b). Warm-up has been attributed to the facilitation of a voltage-dependent persistent inward current (IPIC) intrinsic to the neurons, since this facilitation can occur with intracellular current injection alone. This results in a short-term facilitation of plateau potentials and self-sustained firing associated with these currents (Bennett et al. 1998b; Russo and Hounsgaard 1994; Svirakis and Hounsgaard 1995, 1997).

In the preceding paper (Gorassini et al. 2002), we presented evidence that the firing behavior of human motoneurons may be influenced by intrinsic mechanisms (e.g., IPIC and associated plateau potentials), possibly contributing to ~40% of a motoneuron’s activation. The motor units were recruited to rates higher than their minimum rate, and after recruitment, the estimated synaptic excitation (reflexive or voluntary) to the parent motoneuron could be reduced significantly without de-
recruiting the motor unit. Motoneurons in unanesthetized de-
cerebrate cats behave in a very similar manner during synaptic
activation (Bennett et al. 1998a; Hounsgaard et al. 1988; Lee
and Heckman 1998). This has been attributed to the abrupt
activation of \( I_{\text{PIC}} \) at, or just below, the threshold for action
potential generation which boosts the initial firing rate at re-
cruitment and subsequently provides a sustained current to
maintain firing. In the cat and turtle experiments when the
interval between the stimuli was reduced, there was a pro-
nounced warm-up effect, with a reduction in the synaptic
excitation required to activate the \( I_{\text{PIC}} \) (i.e., the threshold of the
\( I_{\text{PIC}} \) or plateau was reduced). The reduction of the plateau
potential’s threshold with each repeated excitation enabled the
\( I_{\text{PIC}} \) to participate earlier in the motoneuron’s recruitment
thereby lowering the synaptic excitation required to recruit the
cell (turtle, Russo and Hounsgaard 1996; cat, Bennett et al.
1998b).

The purpose of this study was to test whether a qualitatively
similar warm-up phenomenon occurs in human motor units
during voluntary contractions. We have hypothesized that
warm-up would be signified by a reduction in the amount of
synaptic drive required to recruit motor units during repeated
motoneuron activation. As in the preceding paper (Gorassini et
al. 2002), pairs of human motor units were recorded from ankle
joint muscles [tibialis anterior (TA), or soleus] during slowly
increasing, and then decreasing, isometric contractions. The
firing rate of the lowest-threshold motor unit of the pair (con-
trol unit) was used as an indicator of the effective synaptic
excitation to the motoneuron pool and, more specifically, to the
second, relatively higher-threshold motor unit of the pair (test
unit, see Discussion for rationale). We found that the firing rate
of the control unit was a better indicator of estimated synaptic
drive than joint torque since the latter can be influenced by
activity from other agonist or antagonist muscles. In this study,
the firing rate of the control unit was compared during the
sequential recruitment of the test unit at various intervals to
examine whether the level of synaptic drive needed to recruit
the test unit could be reduced in a time-dependent manner. The
time course of this facilitation was compared with the warm-up
of \( I_{\text{PCS}} \) and associated plateau potentials observed in decere-
brate cat motoneurons. Because recruitment thresholds can be
reduced as the rate of rise of the contraction increases (Freund
1983), care was taken to compare sequential contractions hav-
ing identical or slower speeds of contraction.

Parts of the present study have been presented in abstract
form (Gorassini et al. 1997).

**Methods**

Single motor unit activity was recorded in either the tibialis anterior
(TA; \( n = 13 \) unit pairs) or soleus (\( n = 2 \) unit pairs) muscle in 10 adult
subjects with no previous history of neuromuscular disease or injury.
Approval for this study was obtained from the Faculty of Rehabilita-
tion Medicine Ethics Committee at the University of Alberta, and
informed consent was obtained from each participant.

Detailed methods are described in Gorassini et al. (2002). Briefly,
intramuscular wire electrodes (50 \( \mu \)m diam, stainless steel) were
inserted into the muscle with a 24-gauge needle to record the com-
 pound action potentials of single motor units (MUAPs). Subjects were
seated with their left foot strapped to a foot rest that was coupled to
 a force transducer. They were asked to make isometric contractions,
with visual feedback of the torque to match a desired profile. In
preliminary trials, the signal from the intramuscular wire was played
on a speaker while locating motor units. However, during the main
trials, only the torque signal was displayed. Subjects were asked to
make moderately sized increasing, and then decreasing, contractions
to recruit at least two clearly distinguishable motor units. The higher
threshold unit (by \( \pm 2-5\% \) MVC) was considered to be the test unit,
and its recruitment and de-recruitment were observed. The lower-
threshold (control) unit fired during the recruitment and de-recruit-
ment of the test unit. The control unit’s firing rate was used as a
monitor of the effective synaptic input to the motoneuron pool, and
more specifically, to the test motor unit under study (see introduc-
tion) (also see Gorassini et al. 2002).

Contractions of similar speeds were repeated with randomly varied
intervals (0.6–60 s) between the test motor unit’s de-recruitment near
the end of the first contraction, and its re-recruitment during the
second contraction. The period of time in which the motor unit was
silent between contractions is referred to as the “interaction activa-
tion interval.” MUAPs were discriminated off-line using Linux-based software,
and instantaneous frequency plots were constructed.

Since we were interested in re-recruitment at relatively short inter-
vals, a decision had to be made as to what was considered the start and
end of continuous, repetitive firing. For this, we were guided by
Matthews’ (1996) data, which provide a compilation of interspike-
interval ranges for a variety of motor units during rhythmic firing
produced during steady volitional contractions. The longest interspike
interval recorded for the slowest firing motor units (soleus) was \( \sim 300 \)
m. Thus as a safety margin, we considered unit activity at more than
twice this interval (i.e., 600 ms) to be noncontinuous discharge.
Slower firing would likely be generated by fractionated (nonsteady)
synaptic inputs to the motoneurons. Thus series of MUAPs that were
separated by \( < 600 \) ms were considered to be continuous repetitive
firing. To illustrate continuous firing with respect to time, the instan-
taneous rate points were connected by a line. Vertical lines that
extended to 0 Hz designated the start and stop of such continuous
firing (e.g., middle panel, Fig. 2).

To detect firing rate changes reliably and to eliminate spurious
values, the frequency profiles of the control units were smoothed by
fitting a fifth-order polynomial line through the data. In some trials,
the firing rate profiles of the control and test units were compared to
examine whether they were being modulated in a parallel manner. For
this, the mean firing rate (calculated in 500-ms bins) of the control unit
was plotted against the mean firing rate of the test unit, and a linear
regression was fit through the data (see also Gorassini et al. 2002).
Means \pm SD are reported. Statistics were performed with a Student’s
t-test at the 95% confidence level.

**Results**

**Effect of repeated motor unit recruitment (warm-up)**

During repeated isometric contractions, when the raw intramus-
cular electromyograph (EMG) was played through a
speaker or displayed on a screen, subjects reported that the
perceived effort to recruit a motor unit the first time was much
greater than the effort needed to re-recruit the unit in a second
contraction. Figure 1 shows a large-amplitude TA unit (\( \text{unit } b \)
in the intramuscular EMG record; bottom panel) was initially
recruited at a moderate torque of 23% MVC (at large arrow on
1st horizontal line). It subsequently stopped firing for 2 s when
the contraction effort was reduced to \( \sim 4\% \) MVC (at small
arrow) and subsequently was re-recruited with only a slight
increase in effort as verbalized by the subject (at large arrow on
2nd horizontal line) (see also Suzuki et al. 1990). Thus \( \text{unit } b \)
was re-recruited even though the torque and rate of rise of the
contraction was substantially lower in comparison to the first
contraction. Note that the recruitment threshold of unit b on the second contraction was reduced to that of unit a, which initially had a lower recruitment threshold with respect to unit b during the first contraction.

Our goal was to determine whether the relative ease with which motor units could be recruited the second time might be due to changes in the intrinsic excitability of the parent motoneurons (see INTRODUCTION). Thus we needed some measure of the effective synaptic drive to the motor units under study. Since the torque at the ankle can be an unreliable indicator of the synaptic drive to the motoneurons (Gorassini et al. 2002), we focused on examining the firing rate of the lower-threshold unit (control unit) in the unit pair recordings. Presumably, the firing rate of the control unit should reflect the common synaptic drive to the pair of motoneurons during the repeated recruitment of the slightly higher-threshold (test) motor unit (see following paragraph and DISCUSSION). An example of this is shown in Fig. 2 for two units from the soleus muscle. The lower-threshold unit (control unit, bottom panel) fired throughout the initial recruitment, de-recruitment and subsequent re-recruitment of the higher-threshold test motor unit (middle panel). Initially, the test unit was recruited when the control unit’s firing frequency was 9.4 Hz on the first contraction and then re-recruited when the control unit frequency only reached 6.2 Hz on the second contraction, a difference of 3.2 Hz. Thus the estimated synaptic drive at the time of recruitment of the test unit during the second contraction was 34% lower when compared with the first contraction (i.e., 6.2–9.4 Hz/9.4 Hz × 100). This suggested an increase in the intrinsic excitability of the parent motoneuron.

The firing rate of the control unit appeared to be a good indicator of synaptic drive to the test unit since the firing rates of both units were modulated in a similar manner. For example, when plotting the mean firing rate of the control and test units against one another (not shown, see METHODS), the linear regression fit through the data points gave an $r^2$ value of 0.78. This high correlation suggested that both units were receiving a common synaptic drive (De Luca and Erim 1994; Gorassini et al. 2002).

Time course of the reduction in recruitment threshold during repeated contractions

In 15 unit pairs tested (13 TA and 2 soleus), there was a large ($\approx 30\%$ or more) decrease in recruitment threshold when the interval between the time at which the test unit was de-recruited near the end of the first contraction to when it was re-recruited during the second contraction (the interactivation interval) was $< 4$ s. Recruitment thresholds remained fairly constant for interactivation intervals of 10 s or more. Figure 3 shows the relationship between the reduction in re-recruitment threshold and the interactivation interval (on a log scale) for seven of these unit pairs that were analyzed for multiple interactivation intervals. An exponential decay ($y = ae^{bx}$) fit through the data gave a good fit ($r^2 = 0.75$), with a rate constant of 4.8 s (note that a straight line fit is expected when the x-axis is plotted on a log scale). This good fit suggested an inverse exponential relationship between the reduction in re-
De-recruitment threshold and the interaction interval. The plot was divided into four bins of equal size, and the mean of the data points in each bin were tested for statistical significance from zero. The average reduction in re-recruitment threshold for each bin was as follows: bin 1 = 3.9 ± 0.63 (SD) Hz; bin 2 = 2.2 ± 0.9; bin 3 = 0.5 ± 0.6; and bin 4 = 0.4 ± 0.7 Hz.

For interactivation intervals of 0.6–1.6 s (bin 1), 3.9 Hz represents an average reduction of 64% in control unit firing rate, considering that the average firing rate of the control unit at test unit recruitment on the first contraction was 10.8 ± 2.2 Hz (3.9–10.8 Hz/10.8 Hz). Only the mean values in bins 1 and 2, i.e., during interactivation intervals of 6 s or less, were significantly above zero (P < 0.05). This relationship is quite similar to the time course of warm-up seen for plateau potentials in turtle and cat motoneurons, which occurred at an interaction interval of 4–6 s or less (Bennett et al. 1998b; Svirskis and Hounsgaard 1997).

### Return of recruitment threshold following long interactivation intervals

If a sufficiently long period passed between contractions, then the recruitment threshold of a particular unit gradually returned to its initial higher level, even if the threshold had previously been lowered by two rapidly repeated contractions. This is shown in Fig. 4, where the recruitment pattern of three TA motor units (1 test and 2 control units) is shown during four successive contractions at progressively longer interactivation intervals [i.e., at 1 s (left panels), 5 s (middle panels), and 20 s (right panels)]. The units are displayed in ascending order with respect to their torque recruitment thresholds, with the lowest-threshold unit (control unit 2) in the bottom panel. In the first contraction, the test unit was recruited when the firing rate of control unit 1 was 12.8 Hz and the rate of control unit 2 was 11.6 Hz. During the descending phase of the contraction, the contraction effort was decreased abruptly, and all units were de-recruited together. After a ≈1-s delay, the subject then produced a small, brief increase in contraction effort (see asterisk in torque profile). The test unit fired two MUAPs at this lowered level of estimated synaptic drive, i.e., when the control unit rates were 7.7 Hz (control unit 1) and 7.6 Hz (control unit 2) as indicated by the small arrows. Similarly, the level of torque was also lower at this time. A reduced recruitment threshold occurred even though the rate of rise of the contraction was slower, as reflected in the torque profile.

Following a longer interactivation interval (≈5 s, middle panel), the firing rates of both control units increased to 10.3 Hz (control unit 1) and 10.0 Hz (control unit 2) when the test unit was re-recruited. On the fourth contraction 20 s later (right panel), the recruitment threshold had returned near to the initial value on the first contraction, with recruitment of the test unit occurring when control units 1 and 2 fired at 11.4 and 11.2 Hz, respectively. Note that control unit 1 also showed similar time-dependent changes in recruitment thresholds as measured by the firing rate of control unit 2.

### Maintenance of recruitment thresholds following long (>30 s) contractions

There exists the possibility that the lower firing rates of the control unit during re-recruitment of test unit was not due to a lowered synaptic drive, but rather it was due to rate adaptation of the control unit itself. That is, the firing rate of the control unit may have decreased due to intrinsic mechanisms even...
though the synaptic drive remained constant or even increased (Lee and Heckman 1998; Powers et al. 1999). However, the fact that the recruitment threshold of the test unit, in terms of control unit firing rate, remained fairly constant for contractions of relatively long duration (>10 s), where rate adaptation could be expected to occur, argues against this. This is demonstrated in Fig. 5, where despite the fact that the control unit (bottom panel) was active for more than 30 s, a similar firing rate was reached when the test unit was re-recruited on the second contraction (∼14 Hz in both contractions as marked by the solid horizontal line). Whenever there were differences in recruitment thresholds for interactivation intervals of 10 s or more (i.e., outside range of warm-up), there was always a difference in the rate of rise of the contraction. Note also in Fig. 5 the lowered recruitment threshold of the test unit (i.e., control unit rate of ∼9 Hz) when the interactivation interval was shortened to 1.2 s near the 43-s mark (indicated by arrow, bottom panel).

Short-term de-recruitment and re-recruitment order reversal

As shown in Figs. 1 and 4, after a unit was activated for some time and then re-recruited immediately following a prior contraction, the threshold difference between two units could be markedly reduced. In more extreme cases, the recruitment threshold of a higher-threshold unit on a second contraction could become lower than an initially lower-threshold unit (i.e., re-recruitment order reversal). Both of these phenomena are shown in Fig. 6, where the higher-threshold test unit (top panel) was recruited at a moderately high control unit firing frequency (9.8 Hz) on the first contraction (at 1st dashed vertical line). After ∼30 s of a moderate activity, the contraction effort was decreased almost completely (at ∼35 s), as reflected in the nearly silent surface EMG activity (not shown), and both units were de-recruited together. Following ∼1.5 s, the control and test units were then re-recruited together at a much lower threshold, i.e., at a control unit rate of 5.7 Hz. The subject then continued to lower the torque, and the control unit was de-recruited about 3 s before the test unit was de-recruited (de-recruitment order reversal, 2nd dashed vertical line). The subject then increased the contraction torque, and the test unit was re-recruited without the control unit (re-recruitment order reversal).

![Image](http://jn.physiology.org/)

**FIG. 6.** De-recruitment and re-recruitment order reversals. Pair of TA units. The higher-threshold test unit (top trace) was recruited when the control unit firing frequency (bottom trace) reached 9.8 Hz on the 1st contraction (marked by 1st dashed vertical line). Following 30 s of moderate activity, the contraction torque was decreased near to zero, and both units were de-recruited at the same time. When the subject increased the contraction torque ∼1.5 s later, the control and test units were then re-recruited together with the control unit firing at a rate of 5.7 Hz. The subject then continued to lower the torque, and the control unit was de-recruited about 3 s before the test unit was de-recruited (de-recruitment order reversal, 2nd dashed vertical line). The subject then increased the contraction torque, and the test unit was re-recruited without the control unit (re-recruitment order reversal).

In the following contraction trial minutes later (not shown), the recruitment thresholds of the two units reverted back to their original order. Similar short-term (<4 s) de-recruitment order reversals were seen in 7 of 10 unit pairs examined post hoc (in ∼25% of all trials), and re-recruitment order reversals were only seen in 2 of 10 unit pairs examined (in ∼5% of all trials).

**DISCUSSION**

The results from this study demonstrate that there is a substantial facilitation of human motor unit recruitment with repeated contractions at short intervals. Both the perceived effort of the subject and the estimated synaptic input (i.e., control unit firing rate) to recruit a unit on a second voluntary contraction was much lower than to recruit the unit on the first contraction. This short-term facilitation has a time course very similar to warm-up described in motoneurons of reduced preparations, which lasts about 4–6 s. In these reduced preparations, warm-up lowers the IPSCs and associated plateau potential activation threshold, which, in turn, can facilitate recruitment (Bennett et al. 1998b; Svirstik and Hounsgaard 1997). In the present experiments, we cannot be sure that changes in motor unit recruitment were due to similar changes in the intrinsic currents of the motoneuron (e.g., neuromodulatory-dependent
However, the fact that the estimated synaptic input to recruit a motor unit was reduced suggests that these changes were intrinsic to the motoneuron. Activation-dependent increases in motor unit excitability have been reported in human motor units in response to either repetitive voluntary contractions or muscle vibrations (Denier van der Gon et al. 1985; Gorassini et al. 1998; Romaiguere et al. 1993; Suzuki et al. 1990) and may be explained by the warm-up phenomenon described here.

Associated with the short-term facilitation of motor units firing, we have found that the order of de-recruitment, and occasionally re-recruitment, of pairs of motor units can reverse during repeated contractions. Short-term recruitment reversals have been reported before (Stephens et al. 1978; Thomas et al. 1987), although their time-dependent association with repeated contractions has not been studied previously.

**Mechanisms of warm-up**

In reduced cat preparations, motoneurons exhibit plateau potentials that are produced by a neuromodulatory-dependent intrinsic \( I_{\text{PC}} \) (Lee and Heckman 1996, 1999). During natural synaptic excitation (compared with intracellular current injection), the threshold for plateaus is lowered to near the recruitment threshold of the motoneuron to reduce the excitation needed to recruit the cell (Bennett et al. 1998b). Further, the rapid activation of plateaus at recruitment increases the firing rate at recruitment (i.e., boosts the initial rate). Repeated excitation produces warm-up of the \( I_{\text{PC}} \) (in the majority of cells tested, 87%), resulting in lowering of the plateau threshold and increasing its duration (Bennett et al. 1998b). Warm-up enables plateaus to further aid in the recruitment of motoneurons and, ultimately, can lower the recruitment threshold. Recent studies suggest that plateau potential activation in human motoneurons may also contribute to recruitment and sustained firing of motor units (Gorassini et al. 1998, 2002; Kiehn and Eken 1997). That is, as in cat motoneurons during gradual excitation, human motoneurons are often recruited at relatively high initial rates (boost in initial rate), and firing can be sustained even when the estimated synaptic input is reduced (Gorassini et al. 2002). Presuming that plateaus occur in human motoneurons and that they participate in recruitment as in cat motoneurons, the short-term facilitation of motor unit recruitment seen in the present study would indicate that warm-up also occurs in human motoneurons.

These conclusions are necessarily indirect. Other interpretations to explain the observed facilitation of recruitment could include changes in the excitability of interneurons upstream to the motoneuron, or changes in the recruitment process itself (sodium spike threshold). However, the estimated synaptic input to the test unit, as measured by the control unit firing rate, was also lowered with repeated activation, suggesting that there are significant changes intrinsic to the motoneuron.

Alternatively, time-dependent changes in synaptic excitation to the test units that were independent of changes to the control units may have produced the observed decreases in recruitment thresholds as monitored by the control unit firing rates. We feel, however, that the firing rate of the control units was probably a reasonable estimate of the effective synaptic drive to the test motor units during the low-level, repetitive isometric contractions performed in this study. This assumption is supported by the observation that the firing rates of both the control and test motor units were modulated in a parallel manner and, thus were probably responding to a common synaptic drive (see also Bennett et al. 2001; De Luca and Erim 1994; Gorassini et al. 2002). Even when the firing rates of two control motor units were monitored (as in Fig. 4), similar increases and decreases in rate at the time of test unit recruitment were observed during the short and long interactivation intervals. In addition, the firing rate of the control units during test unit re-recruitment was constant, even after 30 s of tonic activation (e.g., Fig. 5). There was no progressive decrease in the firing rate of the control unit for similar levels of perceived effort as seen for longer-duration, fatiguing contractions (Enoka et al. 1989). Thus if there were any appreciable increases in synaptic inputs to the test motor unit during the second contractions, as proposed in previous studies (see introduction), this increase most likely would have been reflected in the firing rate of the control motor unit during these relatively low-level, short-duration isometric contractions.

**Mechanism(s) for reduction in recruitment threshold: warm-up**

In cat and turtle motoneurons, warm-up during repeated plateau activation is thought to result from \( J \) a residual depolarization from earlier plateau activation (see Fig. 4) (Bennett et al. 1998b) and/or 2) direct facilitation of the L-type \( \text{Ca}^{2+} \) -mediated \( I_{\text{PC}} \) (Swirsik and Hounsgaard 1995). In the former, an extreme situation would be that the plateau is not at all deactivated after de-recruitment during the first contraction, and during the second recruitment, the usual boost in firing rate was not provided by an abrupt plateau activation (Gorassini et al. 2002). In this situation, the initial firing rate would be lower on the second contraction than on the first. We have seen units where the second contraction started at a lower frequency (e.g., Fig. 2), and other units where it did not (e.g., Fig. 4), so it is possible that both of the above mechanisms for warm-up may be present in humans. In addition to facilitation of L-type calcium channels, warm-up of motoneurons may also be produced by activity-dependent facilitation of N-methyl-D-aspartate (NMDA) and/or tachykinin receptors, as has been proposed for the generation of wind-up in dorsal horn neurons (reviewed in Herrero et al. 2000).

**Short-term de-recruitment and re-recruitment order reversals**

When a pair of units were recruited in a particular order (e.g., control unit 1st, test unit 2nd), they could be de-recruited in the opposite order (de-recruitment reversal, Fig. 6). This was most evident when the units were activated for more than 5 s and the rate of relaxation was relatively slow (i.e., <5% MVC/s). If the same units were then re-recruited within 5 s (duration of warm-up) at relatively low torque, they could occasionally do so in the opposite order to the initial recruitment order (test unit 1st, control unit 2nd; short-term recruitment reversal, Fig. 6). De- and re-recruitment reversals in torque thresholds have been reported before, and there are numerous interpretations (reviewed by Calancie and Bawa 1990).

We suggest that the observed short-term de- and re-recruitment reversals can be explained by assuming that the effect of
the plateau (size of $I_{\text{PLC}}$) was larger in the initially higher-threshold unit of the pair (e.g., test unit). Thus once they were both recruited, the initially higher-threshold test unit had a larger-amplitude or longer-duration plateau to aid in maintaining firing. This larger plateau may have been sufficient to enable the test unit to continue firing even after the initially lower-threshold control unit had been de-recruited (to produce the de-recruitment reversal). Finally, if the test unit was de-recruited at a sufficiently later time and then re-recruited within a few seconds (right of Fig. 5), it would have been influenced by warm-up during a second contraction, while the control unit would not have been. Thus the test unit would likely have been re-recruited first in a second contraction (to produce the re-recruitment reversal). If a long-enough time passed between the first and second contraction (>10 s), the effects of warm-up would have disappeared and the units would have been recruited in the original order. However, re-recruitment reversals were not common and may also have required a unilateral shift in excitatory synaptic drive to the initially higher-threshold test unit to aid in the facilitation of the plateau.

From our data, there is no evidence for a consistent trend for larger effects of plateaus in the higher-threshold test motor units (Gorassini et al. 1998; see also Lee and Heckman 1996, 1999). Thus presuming that the de-recruitment and re-recruitment reversals were due to differences in plateau amplitude, it should only happen by chance to any units with close initial thresholds, and could happen to any pair of units in the narrow recruitment range that we studied ($\approx 0$–$30\%$ MVC). The reversals could potentially produce a repeated swapping of recruitment order at these low contraction levels, i.e., cycling (Eken 1998), if the contraction intervals are varied (i.e., short, long, short, etc.). Similar de-recruitment and recruitment reversals or “motor unit rotation/substitution” have been reported before (summarized in Westgaard and De Luca 1999); however, these reversals only occur after relatively long periods of tonic motor unit activation (>2 min). The de-recruitment and re-recruitment reversals observed in this study occurred on a much shorter time scale (<6 s) and may be a different phenomenon to that seen during motor unit rotation/substitution.

**Functional implications**

The pronounced short-term facilitation of motor unit recruitment (warm-up) should be extremely important in the control of voluntary contractions repeated at intervals of <6 s, including cyclic tasks such as walking. Also, since plateau activation and warm-up are seen in reflex-mediated motoneuron firing in cats (Bennett et al. 1998a,b), warm-up will likely contribute to nonvoluntary contractions in humans (Gorassini et al. 1998). With warm-up, the threshold for the recruitment of a particular motor unit is lowered, allowing the unit to be recruited while other lower-threshold units are firing at lower rates (re: control unit results) and, thus generating less force (see above). Ultimately, if warm-up operates in all motor units, they will be able to be recruited earlier in repeated contractions (compressed recruitment range, e.g., Figs. 1, 4, and 6). Interestingly, this conclusion would suggest that recruitment grades force over a wider range in the first contraction, and that rate coding participates more in grading force in subsequent contractions. Functionally, this greater use of rate coding at lower contrac-

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