Motor Unit Firing During and After Voluntary Contractions of Human Thenar Muscles Weakened by Spinal Cord Injury

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Zijdewind, Inge and Christine K. Thomas. Motor unit firing during and after voluntary contractions of human thenar muscles weakened by spinal cord injury. J Neurophysiol 89: 2065–2071, 2003. First published December 11, 2002; 10.1152/jn.00492.2002. Spinal cord injury may change both the distribution and the strength of the synaptic input within a motoneuron pool and therefore alter force gradation. Here, we have studied the relative contributions of motor unit recruitment and rate modulation to force gradation during voluntary contractions of thenar muscles performed by five individuals with chronic (>1 yr) cervical spinal cord injury. Mean ± SD thenar unit firing rates were low during both steady-level 25% (8.3 ± 2.2 Hz, n = 27 units) and 100% maximal voluntary contractions (MVCs, 9.2 ± 3.1 Hz, n = 23 units). Thus modest rate modulation, or a lack of it in some units, was seen despite an average fourfold increase in integrated surface electromyographic activity and force. During ramp contractions, units were recruited at 5.7 ± 2.5 Hz, but still only reached maximal firing rates of 12.8 ± 4.9 Hz. Motor units were recruited up to 85% of the maximal force achieved (14.6 ± 5.6 N). In contrast, unit recruitment in control hand muscles is largely complete by 30% MVC. Thus, during voluntary contractions of thenar muscles weakened by cervical spinal cord injury, motor unit rate modulation was limited and recruitment occurred over a wider than usual force range. Those motor units that were stopped voluntarily had significantly lower derecruitment versus recruitment thresholds. However, 8 units (24%) continued to fire long after the signal to end the voluntary contraction at a mean frequency of 5.9 ± 0.8 Hz. The forces generated by this prolonged unit activity ranged from 0.3 to 7.2% maximum. Subjects were unable to stop this involuntary unit activity even with the help of feedback. The mechanisms that underlie this prolonged motor unit firing need to be explored further.

INTRODUCTION

Force gradation during voluntary contractions primarily occurs by the recruitment and rate modulation of motor units. In many human muscles, motor units are recruited at 5–12 Hz (Person and Kudina 1972; Tanji and Kato 1973), but they typically fire at rates that exceed 20 Hz during maximal voluntary contractions (Enoka and Fuglevand 2001). The force range over which motor unit recruitment occurs varies between muscles, however. In hand muscles, the majority of motor units are recruited at relatively low forces (30% maximal voluntary contraction, MVC), whereas new units are recruited up to 80% MVC in biceps brachii (Kukulka and Clamann 1981; Milner-Brown et al. 1973). Inputs from supraspinal, intraspinal, and afferent sources all contribute to this recruitment and rate modulation of motor units (Binder et al. 1996). Since the synaptic input to different motor unit types has a nonuniform distribution in the uninjured spinal cord (Binder et al. 1996), disruption of part of this input by disease or trauma will alter the distribution of the synaptic inputs that remain in the motoneuron pool. These changes in input may influence the magnitude of force gradation by motor unit recruitment and rate modulation and the relative contribution of these two processes to voluntary force production after spinal cord injury.

Muscles that are left under some voluntary control by spinal cord injury are often controlled by a reduced number of motoneurons, both because the descending drive has been compromised and because some motoneurons die (Thomas et al. 1997a,b, 2002b). These changes may also alter both the strength and the distribution of the synaptic input within the motoneuron pool. Changes in the distribution of synaptic current (both background current and driving synaptic current) can modify the spacing between the recruitment thresholds of various motoneurons, and it can shift the numbers of motoneurons that are activated by a variation in excitatory drive to the pool (Binder et al. 1996; Kernell and Hultborn 1990). If the frequency–current relation of motoneurons is also altered, the magnitude of force gradation by motor unit rate modulation may change. Hence, it is quite possible that the manner in which motoneurons are managed during voluntary contractions has changed after spinal cord injury.

The first aim of this study was to document the relative contributions of motor unit recruitment and rate modulation during voluntary contractions of thenar muscles that have been paralyzed in part by chronic cervical spinal cord injury. We know that there are a reduced number of motor units in the thenar muscles of three of the subjects used in the present study (n = 35, 48, or 83 units; Thomas et al. 2002b). Since the injury also disrupted inputs from higher centers to the spinal cord, even fewer thenar motor units are under voluntary control in these particular muscles. Thus this situation provides a unique opportunity to document the levels of force at which different units are recruited and to follow the activity of these same motor units up to maximal muscle force. Data can be obtained during both weak and maximal voluntary contractions, a feat that is rarely accomplished in control muscles because too
many motoneurons are activated simultaneously. Our second aim was to compare the levels of voluntary force at which motor units were recruited and derecruited after chronic cervical spinal cord injury. If these motoneurons continue to be influenced by persistent inward currents, as would be expected from data obtained in animals (Bennett et al. 2001b; Eken et al. 1989) and humans (Collins et al. 2001; Gorassini et al. 2000; Zijdewind and Thomas 2001) with chronic cord injury, then these human motor units may change their recruitment–derecruitment thresholds (Heckman and Lee 1999) or show prolonged motor unit activity (Bennett et al. 2001a).

**Methods**

Five individuals (mean ± SD age: 46 ± 7 yr, 1 woman) with cervical spinal cord injury at C5 (\(n = 2\)), C6 (\(n = 2\)), or C7 were studied. These injuries occurred 11 ± 7 yr ago as a result of motor vehicle accidents (\(n = 2\)), a diving accident, a fall, or another cause. Only one hand was studied, that in which the subject could voluntarily contract the thenar muscles. This study had local ethical approval. Each subject gave informed written consent prior to participation in the experiment.

**Experimental setup**

Each subject sat in his or her wheelchair. As described before (Thomas 1997), the test forearm rested in a vacuum cast, palm up. The hand and fingers were immobilized in ther-a-putty and held in place with a metal plate and Velcro straps. The thumb rested against a custom-made transducer that registered the isometric abduction and flexion forces at right angles. Resultant force was calculated. Surface electromyographic (EMG) activity was recorded using wire electrodes strapped across the skin overlying the proximal, middle (common), and distal thenar muscles (Westling et al. 1990), which include m. abductor pollicis brevis, m. flexor pollicis brevis, and m. opponens pollicis. A custom-made monopolar tungsten electrode was used to record intramuscular EMG.

**Protocol**

Each subject was asked to perform 5-s voluntary contractions at approximately 25, 50, 75, and 100% maximal by matching target levels on an oscilloscope. Each contraction was separated by 5–10 s of rest. Audio cues from a computer signaled when the subject was to contract and relax the thenar muscles. Data from these contractions were used to characterize the changes in surface EMG and motor unit firing frequencies that occurred with force. Subjects were then asked to perform a ramp voluntary contraction, taking 10 s to reach maximal force and 10 s to reduce the force to rest. These ramp contractions were primarily used to determine the forces at which the units were recruited and derecruited and the overall range of firing frequency modulation for each motor unit. After a 5-min rest, this contraction series was repeated. The intramuscular electrode was repositioned during this rest so that subsequent records came from different motor units (see following text).

**Data collection and analysis**

Force, surface EMG, and intramuscular EMG signals were filtered (DC–100 Hz, 30–1,000 Hz, and 300–10,000 Hz) and sampled on-line (400 Hz, 3,200 Hz, and 12,800 Hz, respectively) using a SC/Zoom system (Department of Physiology, University of Umeå, Sweden). For steady-level contractions, measurements were only made during the force plateau of each contraction. The resultant force at the start, middle, and end of the plateau was averaged. The surface EMG was rectified and integrated and then normalized by the time of the force plateau to provide an average EMG value for each contraction. Motor unit activity was only considered voluntary if the subject initiated the unit firing. Voluntarily activated potentials from the same motor unit were identified by amplitude and shape criteria. The potentials from each motor unit were overlaid to verify their identity. The shapes of the averaged proximal and distal surface EMG associated with the firing of each unit during different contractions was also used to confirm that the recordings came from the same unit (or different units when the intramuscular electrode was repositioned). The times between potentials belonging to any one motor unit was converted to instantaneous frequency and average firing frequency was calculated. During ramp contractions, the resultant force was measured every second until peak force. The firing frequency of each motor unit was averaged over these same intervals. Maximal unit frequency was also calculated as the average frequency for three consecutive interspike intervals because we wanted to define the absolute limits of firing modulation. The latter data are reported here because they did not differ significantly from the mean maximal motor unit firing rates computed over 1 s. Motor unit recruitment and derecruitment thresholds were defined as the forces at which the first and last potentials of a motor unit occurred, respectively. The levels of rectified and smoothed surface EMG at these same times were also measured to assess unit thresholds (Scutter and Turker 1998). Recruitment and derecruitment frequencies were calculated from the first and last interspike intervals, respectively.

Mean ± SD values are given. Force, proximal surface EMG, and motor unit firing frequency data were expressed relative to the values recorded during MVCs. Relationships between these parameters were described using least squares linear regression. Differences between units were compared using ANOVA. Posthoc tests were performed according to Bonferroni. Differences within the same unit were compared using paired t-tests. Statistical significance was set at \(P < 0.05\).

**Results**

Typical data obtained during steady-level voluntary contractions are shown in Fig. 1A. As the force was increased from 25% MVC to maximal, the thenar surface EMG increased (Figs. 1, B and C). The firing behavior of two motor units was followed during these same contractions. The average ± SD firing frequency of one motor unit rose from 8.9 ± 1.0 Hz during the 25% MVC to 12.7 ± 1.2 Hz during the 100% MVC, a 43% increase (Fig. 1B). In contrast, the other unit showed little rate modulation even though it was recruited first (7.2 ± 0.7 to 7.9 ± 0.7 Hz, a 10% increase; Fig. 1C).

**Low motor unit firing frequencies during voluntary contractions**

For the five subjects, maximal voluntary force averaged 14.6 ± 5.6 N or 65.3 ± 32.6% of control force (Thomas 1997). The 25 to 100% MVC force increase was accompanied by a fourfold change in integrated surface EMG, on average. This resulted in a significant positive surface EMG–force relationship in the thenar muscles of each subject. Low mean firing frequencies were found for all the motor units recorded during both 25% MVCs (8.3 ± 2.2 Hz, \(n = 27\) units) and 100% MVCs (9.2 ± 3.1 Hz, \(n = 22\) units; Fig. 2A), values that were not significantly different from each other (\(P > 0.2\)). The mean maximal motor unit firing frequency for spinal cord-injured subjects was also significantly lower than the mean value recorded during MVCs performed by control subjects in an earlier study (34.1 ± 10.2 Hz; Fig. 2A (Thomas 1997). During the ramp contractions, the average firing fre-
Motor unit recruitment during strong voluntary contractions

During the ramp contractions, motor unit recruitment occurred up to 85% MVC force (range 0.36–85.0% MVC, n = 34 units). Fifteen of these units (44%) were recruited at forces > 30% MVC, while 9 units (26%) were recruited beyond 45% MVC force. When recruitment was expressed as a percentage of the maximal rectified and smoothed EMG, the corresponding numbers of motor units were 14 and 6, respectively. Motor unit recruitment at relatively high force levels (>45% MVC) occurred in both weak and stronger muscles (MVC force range 9.2–21.6 N). However, no correlation was found between unit recruitment thresholds and absolute MVC force ($r^2 = 0.01$). Those motor units with high recruitment thresholds (>30% MVC) had significantly higher maximal firing frequencies than the low-threshold units (14.6 ± 4.9 Hz, n = 15 units and 10.4 ± 3.9 Hz, n = 19 units, respectively, $P < 0.01$).

Motor unit recruitment versus derecruitment

Figure 3 shows an example of a motor unit (unit B) that was recruited and derecruited at similar forces (8.1 and 6.8 N, respectively). Another simultaneously active unit (unit A) had a lower derecruitment force (1.8 N) than recruitment force (15.1 N). For those units that stopped firing during the down ramp ($n = 28$ units), most had higher recruitment thresholds than derecruitment thresholds ($n = 21$ units, 75%), resulting in a significant difference in mean recruitment versus derecruitment force (30.20 ± 21.7 vs. 21.12 ± 17.9% MVC, $P < 0.001$). If recruitment and derecruitment thresholds were calculated as a function of the maximal rectified and smoothed surface EMG, the mean derecruitment threshold was also significantly lower than the mean recruitment threshold ($P < 0.001$). The mean motor unit firing rates of these units at recruitment (5.6 ± 2.7 Hz) and derecruitment (5.2 ± 2.0 Hz) were not significantly different, however.

**FIG. 1.** A: intramuscular electromyographic (EMG) activity, surface EMG activity, and force recorded during steady-level voluntary contractions performed by 1 subject. Also shown is the instantaneous firing frequency of 2 units that were identified in the intramuscular recording. Unit waveforms are overlaid to show accurate identification (right). B and C: surface EMG (●) and instantaneous firing frequency (+) for the two units active in A, in relation to force.

Frequency of these motor units at recruitment was 5.7 ± 2.5 Hz. The mean maximal motor unit firing frequency (mean of three interspike intervals) was significantly higher (12.8 ± 4.9 Hz, $n = 21$ units, $P < 0.001$), but it was still significantly lower than the control mean.

Figure 2B shows the relationships between force and firing frequency for all of the motor units that were followed during several steady-level contractions of differing intensities. These units also showed only modest or little firing frequency modulation. For the 11 units recorded during both submaximal (any intensity) and maximal voluntary contractions, the average change in firing frequency was 1.0 ± 1.9 Hz (range −2.5–4.2 Hz), representing an average increase of 25.6 ± 48.7% (range −29.3–154.3%). The mean maximal firing rate of these 11 units was also low (7.8 ± 2.2 Hz).

**FIG. 2.** A: mean (+SD) motor unit firing rates recorded during 25% maximal voluntary contractions (MVCs) (range 2.1–13.1 Hz, $n = 27$ units) and 100% MVCs (5.4–16.1 Hz, $n = 23$ units) performed by spinal cord–injured subjects compared with MVC data from control subjects (18.3–57.9 Hz, $n = 28$ units) (Thomas 1997). B: force-frequency relations for motor units followed during several contractions ($n = 21$). Data from each unit are represented by the linear regression line of best fit ($P < 0.05$ for 18/21 regression lines).
Prolonged motor unit firing

Four of five subjects were unable to stop the activity of some motor units after the voluntary contractions, even with the help of both visual and acoustic feedback. Figure 4 shows an example of one motor unit that exhibited this prolonged, contraction-induced activity. Of the 33 units that were identified during the voluntary contractions, 8 units (24%) showed prolonged, involuntary firing at a mean frequency of 5.9±0.8 Hz.

The force produced by this sustained involuntary unit activity varied between 0.4 and 7.2% MVC (mean 2.7±2.5% MVC) and the activity could last for more than 10 min. At least 10 other units with small action potentials fired repetitively after the cue to end the voluntary contraction but their activity could not be followed throughout the voluntary contractions.

The mean recruitment threshold, firing frequency at recruitment, and maximal firing frequency of units that showed contraction-induced prolonged firing (17.0±19.2% MVC, 6.1±1.9 and 9.6±3.9 Hz, respectively) were not significantly different from the corresponding values obtained for other units that were stopped voluntarily (30.2±21.7% MVC, 5.6±2.7 and 13.1±4.9 Hz).

Unit rate modulation during spasms exceeds that during voluntary contractions

Figure 5 compares the firing behavior of a motor unit during a maximal voluntary contraction (Fig. 5A) and a muscle spasm that just occurred spontaneously (Fig. 5B). This motor unit showed little or no rate modulation as the voluntary force was increased to maximum (10.1±0.1 N) and its firing frequency during the MVC force plateau was low (8.0±0.8 Hz; n=3 interspike intervals). Yet, at the peak of the muscle spasm, both the whole muscle force (23.8±0.4 N) and the firing frequency of this same unit had increased significantly (14.9±2.2 Hz, n=3 interspike intervals). Unfortunately, the activity of other units could not be followed during this spasm because the contraction was too strong.

DISCUSSION

The present data show that motor unit firing rates were low during both submaximal and maximal voluntary contractions of thenar muscles that have been weakened by chronic spinal cord injury. These reductions in motor unit firing rates occurred irrespective of whether the subjects performed steady-level or ramp voluntary contractions. This relatively modest or sometimes absent motor unit rate modulation with force, despite fourfold increases in integrated surface EMG, suggests that recruitment of motor units must contribute strongly to the

FIG. 3. Activity of 2 units (A and B) during a ramp force increase, a MVC, followed by a ramp force decrease to rest. Dotted lines with arrowheads indicate the recruitment and derecruitment forces for each unit. Notice unit B was recruited and derecruited first. Ten overlaid potentials for each unit show how they were identified accurately (right).

FIG. 4. Sustained involuntary unit activity after the ramp decrease in voluntary force. One unit was identified throughout the contraction (10 overlaid potentials, left), although at least 3 units were active.

FIG. 5. Activation of the same motor unit during a MVC (A) and a spasm (B) of the same thenar muscles. This unit fired at a higher rate during the spasm (+) than during the MVC (△).
force produced during voluntary contractions of these muscles. Indeed, new motor units were recruited during strong voluntary contractions of every muscle evaluated. Those motor units that could be stopped voluntarily also had significantly lower de-recruitment forces than recruitment forces. In contrast, other motor units showed prolonged, contraction-induced motor unit firing after the voluntary contraction that could last for minutes.

Mechanisms of force gradation

In control muscles, the orderly recruitment of motor units and their rate modulation are important mechanisms for force gradation that are not controlled independently. Rather, these processes are strongly related in that an increase in excitatory synaptic current to a motoneuron pool results in the recruitment of new motor units and increases in the firing frequencies of already active units. Thus any alterations in the number and the effectiveness of the synaptic connections to motoneurons as a consequence of spinal cord injury, and any associated long-term neuromuscular changes, may well influence motoneuron recruitment and rate modulation. The relative importance of these two force-generating processes may also be modified by changes in the intrinsic properties of motoneurons, such as input resistance, current threshold, and afterhyperpolarization (e.g., Kernell 1993). After chronic spinal cord transection in animals, some motoneurons show small but significant changes in the duration of their afterhyperpolarization potential and their threshold for spike initiation (Bennett et al. 2001b; Cope et al. 1986; Hochman and McCrea 1994; Munson et al. 1986). It is uncertain whether these changes also occur in human motoneurons influenced by chronic injury to the cerebral spinal cord. F-wave analysis suggests that motoneurons to completely paralyzed thenar muscles with reduced numbers of motor units have comparable excitability to motoneurons that innervate muscles of control subjects (Butler and Thomas 2003). In contrast, the thenar motoneurons studied here have only been denervated partially. That is, these motoneurons remain under some voluntary control. However, they do receive a reduced amount of supraspinal input and many of them also produce stronger than usual force, probably because their axons sprout to innervate denervated muscle (Thomas et al. 2002b).

Low unit firing frequencies during voluntary but not involuntary contractions

After spinal cord injury, thenar motor unit firing frequencies at recruitment were similar to those recorded from many other muscles in control subjects (Person and Kudina 1972; Tanji and Kato 1973). However, little or only modest increases in firing rate occurred in these units as the spinal cord–injured subjects increased their voluntary force to maximum. This impaired unit rate modulation in all thenar units after injury contrasts with control data (Fig. 2) (Thomas 1997) and with the high unit firing rates typically recorded during maximal voluntary contractions of triceps brachii muscles paralyzed partially by spinal cord injury (Thomas et al. 2002a). This difference in motor unit behavior between muscles, even in the same subject, may relate to differences in the distribution of various inputs within the motoneuron pool that arise from the injury itself (Calancie 1991) or naturally. In control subjects, hand muscles are supposed to receive stronger monosynaptic corticospinal input compared with the triceps brachii.

Other studies on motor unit behavior after spinal cord injury report relatively high or low unit firing rates during submaximal voluntary contractions of various muscles (Little et al. 1996; Wiegner et al. 1993). As these contractions were submaximal, it is unclear whether additional motor unit rate modulation would have occurred during stronger contractions.

The one motor unit that we could follow through both a maximal voluntary contraction and a spasm showed much higher firing frequencies during the spasm. This difference in voluntary and involuntary firing rates showed that this thenar motoneuron could respond to inputs from other sources and that the motoneuron itself was capable of firing at high frequencies (see also Zijlstra and Thomas 2001). Together, these data suggest that the voluntary drive to thenar muscles is impaired after spinal cord injury.

Motor unit recruitment at high voluntary forces

In thenar muscles of spinal cord–injured subjects, motor unit recruitment was observed up to 85% maximal voluntary force. Recruitment of motor units also occurred at >45% MVC in all the thenar muscles studied. Yet in intrinsic hand muscles of control subjects, most units are recruited by 30% MVC force, with further force production accomplished by increases in motor unit firing rates (Kukulka and Clamann 1981; Milner-Brown et al. 1973). If the widening of the recruitment range was just a result of an equal decline in effective excitatory synaptic current to the whole motoneuron pool after spinal cord injury, one would expect the highest recruitment thresholds in the weakest muscle and relatively normal recruitment thresholds in the stronger muscles. However, no significant relationship was observed between thenar unit recruitment thresholds and voluntary strength. This expansion in the range of recruitment forces is consistent with data from Davey et al. (1999) that suggest that fewer thenar motor units are activated by voluntary input at low forces after spinal cord injury. With transcranial magnetic stimulation, they showed that less thenar motor unit activity was evoked during low-force voluntary contractions performed by spinal cord–injured subjects compared with control subjects. At higher force levels, relatively larger increases in motor-evoked potentials occurred in the thenar muscles of spinal cord–injured subjects compared with controls.

Several factors are probably important in explaining the relatively broad force range seen for recruitment of units in thenar muscles after spinal cord injury. For example, a change in the range of forces produced by thenar motor units (Thomas et al. 2002b) could alter the absolute recruitment thresholds. The distribution and efficiency of the synaptic inputs to the thenar motoneuron pool may also have changed. Interlimb reflexes that only become evident months after human cervical spinal cord injury are consistent with the idea of new spinal connections (Calancie et al. 2002, but see Zehr et al. 2001).

Prolonged motor unit firing

Several motor units continued to fire after the voluntary contractions. Subjects were unable to stop this prolonged involuntary motor unit activity, as described for motor units in
thenar muscles completely paralyzed by spinal cord injury (Zijdewind and Thomas 2001). This self-sustained unit firing may result from a maintained input from the periphery. However, no striking differences were observed in the amount of afferent input to cervical motoneurons in subjects with a chronic spinal cord injury compared with healthy subjects (Thomas and Westling 1995).

Prolonged motor unit activity may relate to changes in the synaptic strength or efficiency after spinal cord injury. For example, a decline in the amount of inhibition (Calancie et al. 1993) could increase the membrane potential of motoneurons that are close to their spike-initiating threshold. These units may then be activated by synaptic noise (Matthews 1996; see Zijdewind and Thomas 2001), although one would expect more variable motor unit firing patterns than observed here (Fig. 4).

The prolonged unit firing may also arise from the activation of persistent inward currents in motoneurons and/or spinal interneurons. These currents may account for the significantly lower derecruitment compared with recruitment thresholds of units that could be stopped voluntarily. This suggestion is consistent with the activation of persistent-inward currents in rat motoneurons after chronic spinal cord injury (Bennett et al. 2001b; Eken et al. 1989).

In humans, it is impossible to evaluate the mechanisms that underlie this prolonged unit firing directly. However, sustained motor unit firing after muscle vibration and electrical stimulation is seen in control subjects (Collins et al. 2001 2002; Gorassini et al. 1998, 2002; Kiehn and Eken 1997) and in individuals with spinal cord injury (Collins et al. 2001; Gorassini et al. 2000; Zijdewind and Thomas 2001). After spinal cord injury, both the amount of supraspinal excitation and inhibition are probably reduced. Lack of inhibition could therefore result in the more frequent occurrence of prolonged motor unit activity.

Functional implications

Motor unit recruitment at high voluntary forces was a finding common to all the thenar muscles examined. It may relate to changes in the amount, distribution, or function of the synaptic inputs to the motoneuron pool and/or be a consequence of the relatively low motor unit counts typically found in thenar muscles influenced by chronic cervical spinal cord injury (Thomas et al. 2002b). If the latter is the case, effective reinnervation of denervated muscle by local axon sprouting will produce stronger than usual motor units. Recruitment of one of these strong thenar units will thus make a greater force contribution to the whole muscle force than the activation of a typical unit in control muscles. If these stronger units are not recruited at voluntary higher forces, possibly reflecting poor adaptation between motoneuron and muscle fibers properties, then voluntary force gradation will also be coarser than usual.

The relatively low maximal motor unit firing rates after spinal cord injury suggest that motoneurons receive just enough input to be activated voluntarily but insufficient excitation to be activated at the maximal possible firing rates. The combination of a smaller than usual descending input together with a persistent-inward current (and/or reduced inhibition) may provide just enough excitation to a motoneuron for it to reach its spike-generating threshold. Persistent-inward currents (and/or reduced inhibition) may also be beneficial in keeping motoneurons active despite declines in central drive during fatiguing contractions (Thomas and Del Valle 2001).

Some motor units in thenar muscles weakened by spinal cord injury also continued to fire long after the voluntary contraction that induced their activity. It is important to study the possible mechanisms that contribute to this prolonged unit firing in relation to the initiation of motoneuron firing and to involuntary contractions. Equally important is the need to evaluate the influences that various medications have on these processes and thus on muscle force production and relaxation.

In conclusion, all of these data support the idea that spinal cord injury does not only result in weak voluntary contractions. Voluntary contractions of thenar muscles are now produced by motoneuron recruitment over an increased range of force and by a lower than usual amount of motor unit rate gradation.

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