Doublet Discharges in Motoneurons of Young and Older Adults

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Christie, Anita and Gary Kamen. Doublet discharges in motoneurons of young and older adults. J Neurophysiol 95: 2787–2795, 2006. First published February 1, 2006; doi:10.1152/jn.00685.2005. The purpose of this study was to investigate the occurrence of motor unit doublet discharges in young and older individuals at different rates of increasing force. Participants included eight young (21.9 ± 3.56 yr) and eight older (74.1 ± 8.79 yr) individuals, with equal numbers of males and females in each group. Motor unit activity was recorded from the tibialis anterior during isometric dorsiflexion using a four-wire needle electrode. Subjects performed three ramp contractions from zero to 50% maximal voluntary contraction (MVC) force at each of three rates: 10, 30, and 50% MVC/s. Overall, the occurrence of doublets was significantly higher in the young than in the older individuals. However, neither group showed differences in the occurrence of doublets across the three rates of force production. Doublet firings were observed in 45.6 (young) and 35.1% (old) of motor units at 10% MVC/s; 48.6 (young) and 22.5% (old) of motor units at 30% MVC/s; and 48.4 (young) and 31.4% (old) at 50% MVC/s. The maximal firing rate was significantly higher and the force at which the motor units were recruited was significantly lower for those units that fired doublets than those that did not. The force at which doublets occurred ranged from 3.42 to 50% MVC in the young subjects and from 0 (force onset) to 50% MVC in the older subjects. The results of this study suggest that the occurrence of doublets is dependent on both motor unit firing rate and force level. The lower incidence of doublets in older individuals may be attributable to changes in the intrinsic properties of the motoneurons with aging, which appear to play a role in doublet discharges.

INTRODUCTION

It is well understood that the human nervous system can increase force production of a muscle in one of two ways: 1) by increasing the number of active motor units or 2) by increasing the firing rates of motor units that are already active. During maximal voluntary contractions, motor unit firing rates typically peak at 25–60 pulses/s (pps) in young individuals and at 18–45 pps in older individuals, depending on the muscle (Bellemare et al. 1983; Connelly et al. 1999; Knight and Kamen 2004; Patten and Kamen 2000; Patten et al. 2001). However, “doublet” discharges, in which a motor unit discharges two action potentials close together in time, are often reported.

A doublet discharge has been defined as an interspike interval (ISI) that is <20 ms (Simpson 1969). However, ISIs as low as 2 ms have been reported (Van Cutsem et al. 1998), giving the motor unit an instantaneous firing rate of ≈500 pps, which far exceeds the reported maximal firing rates. Such doublet discharges are typically followed by a longer than average ISI, often lasting >100 ms (Bawa and Calancie 1983; Garland and Griffin 1999). This firing behavior has been described in numerous muscles of both the upper and lower limbs of healthy, young individuals (Bawa and Calancie 1983; Griffin et al. 1998; Kudina and Alexeeva 1992; Partanen and Lang 1978; Van Cutsem et al. 1998). However, the majority of studies to date have focused on muscles of the upper limb; doublet discharges have not been as well characterized in muscles of the lower limb.

Although their function is not fully understood, it is suggested that doublets are more than a “statistical anomaly,” and may act to augment both the rate and amount of force production (Binder-Macleod and Barrish 1992; Garland and Griffin 1999). It is also suggested that doublet discharges can help to slow development of muscular fatigue (Binder-Macleod and Barker 1991; Binder-Macleod et al. 1997; Griffin et al. 1998). Attempts to characterize the conditions under which doublet discharges are most likely to occur have produced equivocal results. Although doublets appear to occur most often at the initiation of a contraction, in some instances they have been reported to occur at a range of force levels and during both steady force and well as changing force conditions (Griffin et al. 1998; Van Cutsem et al. 1998). It has also been suggested that doublets occur most often during low force, ramp contractions and that as the rate of force production increases, the occurrence of doublets decreases (Bawa and Calancie 1983). However, Van Cutsem et al. (1998) have suggested the opposite, that the occurrence of doublet discharges increases with increasing contraction velocity.

The characteristics of the motor units more likely to show doublets has also not been elucidated. It has been suggested that doublets occur most often in higher-threshold motor units, but it has also been suggested that any motor unit may be capable of firing doublets (Bawa and Calancie 1983; Garland and Griffin 1999; Kirkwood and Munson 1996). Therefore from the current literature, it is not clear which motor units are more likely to fire doublets. It is also not clear if there are certain muscles in which doublets are more likely to occur, or if there are particular tasks which make motor units more prone to doublet discharges. Investigation to gain a better understanding of this type of motor unit firing behavior is therefore warranted.

The mechanism responsible for doublet discharges seems to be the intrinsic properties of the motoneuron itself. Doublets are thought to arise as a result of delayed depolarization, most likely occurring in the dendrites of motoneurons (Calvin and Schwint 1972). Initial activation of the axon hillock of the motoneuron results in subthreshold antidromic signals traveling back toward the dendrites. The antidromic invasion of the...
dendrites increases the resting membrane potential of the dendrites, making them more susceptible to synaptic input, and thereby increases the likelihood of a second action potential (Calvin and Schwindt 1972; Granit et al. 1963; Kudina and Alexeeva 1992; Kudina and Churikova 1990).

With aging there are many changes in the neuromuscular system, which may impact the occurrence of doublet discharges. There is a decrease in the number of motoneurons, decreased excitability of motoneurons, and decreased maximal firing rate of motor units (Campbell et al. 1973; Granit et al. 1963; Kamen et al. 1995; Roos et al. 1997; Tomlinson and Irving 1977). It has also been shown that there is a decrease in membrane excitability of muscle fibers and decreased efficiency of the Na\(^+/K^+\) pump in muscle fibers (De Luca et al. 1990; Hicks et al. 1992; Klitgaard and Clausen 1989). Any combination of these changes may make doublet discharges less likely to occur in the aging neuromuscular system, which could contribute to the decrease in muscular force production with age that has been well documented (Backman et al. 1995; Clarkson et al. 1981; Kent-Braun and Ng 1999). Alternatively, the aging neuromuscular system may maintain, or even increase the occurrence of doublet discharges, to compensate for decreased maximal motor unit firing rates.

The purpose of this study was to investigate the occurrence of doublet discharges in older individuals; in an attempt to determine if this motor unit discharge behavior is maintained with age, despite the remodeling of the neuromuscular system. Comparisons between motor units that discharged doublets and those that did not were made in an attempt to characterize the recruitment patterns and maximal firing rates of motor units that discharge doublets in young and older individuals. Potential differences in the occurrence of doublets at different rates of force production were also investigated and compared between young and older individuals.

**Methods**

**Subjects**

All procedures in this study were reviewed and approved by the Human Ethics Review Board at the University of Massachusetts, Amherst. All subjects gave informed consent before participation. Eight young (21.9 ± 3.56 yr) and eight older (74.1 ± 8.79 yr) individuals, free of neurological, and cardiovascular disorders participated in this study. Each group (young and older) was comprised of four male and four female subjects. All subjects were inactive to sedentary, free of neurological, and cardiovascular disorders participated in this study. Each group (young and older) was comprised of four male and four female subjects. All subjects were inactive to sedentary, free of neurological, and cardiovascular disorders.

**Procedures**

Subjects visited the Exercise Neuroscience Laboratory on one occasion for testing. Data were obtained from the dominant leg while subjects performed isometric dorsiflexion of the ankle. A custom-designed chair (Fig. 1) was used to isolate the tibialis anterior (TA) during dorsiflexion. The knee and ankle were positioned at 90° and straps were placed across the hips, thigh, and knee to ensure no movement of the leg. Additional padding was placed around the foot to avoid any antero-posterior or medio-lateral movement of the foot. A padded metal bar was secured across the top of the foot at the distal metatarsals, providing an immovable resistance for isometric dorsiflexion. The nondominant foot was placed on a padded box to prevent subjects from using resistance in this leg to enhance force.

**FIG. 1.** Experimental set-up for isometric dorsiflexion. Subjects were seated with the knee and ankle at 90°. Straps were secured over the knee, thigh, and foot to isolate the dorsiflexors. The four-wire needle electrode was inserted into the belly of the tibialis anterior.

**Force**

Force exerted during dorsiflexion was measured by a strain gauge force transducer (Interface Model MB-10, Scottsdale, AZ) secured to each side of the immovable metal strap. The force signal was low-pass filtered at 2 Hz and was amplified using a custom-built bridge amplifier. The signal was sent through an A/D converter (Data Transition Model DT 2801) to a personal computer, where it was sampled at 50 Hz and displayed on a personal computer using DasyLab software (Data Acquisition System Laboratory, DasyTec USA, Amherst, NH) to provide real-time feedback to the subjects. The force signal was also sent through a second A/D converter (WIN-30 data acquisition board, United Electronics, Watertown, MA) and sampled at 25.6 kHz using DasyLab software (Data Acquisition System Laboratory, DasyTec USA) and stored for off-line analysis. This signal was subsequently digitally down-sampled to 50 Hz before analysis.

After familiarization with the set-up, subjects were asked to perform three maximal voluntary contractions (MVCs) of the dorsiflexors, with 2 min of rest between contractions. The highest value obtained across the three trials was deemed the MVC, and all subsequent tasks were scaled to this value. Subjects viewed a computer screen with real-time feedback of their force, and a separate line that gradually increased from 0 to 50% MVC. The slope of this line corresponded to one of three rates of force production: 10, 30, or 50% MVC/s. Subjects were asked to match their force to the line on the screen as closely as they could. Three trials at each of the three rates of force production were completed by each subject.

**Motor unit activity**

Intramuscular EMG activity of the TA was recorded using a 25-gauge, stainless steel, four-wire needle electrode. The location of the needle within the muscle was manipulated between each trial in an attempt to obtain a different sample of motor units with each trial. The cannula of this needle houses four platinum-iridium wires, each of which is 50 μm in diameter and terminates at a side port. This
arrangement provides three channels of differential recordings of motor unit action potentials (MUAPs). The intramuscular EMG signal was filtered between 1 and 10 kHz, amplified using a Dantec Counterpoint Electrography (Dantec Electronik Medicinsk, Skovlunde, Denmark), and viewed on a digital oscilloscope. The three channels of MUAP signals were also sent from the amplifier through an A/D converter (WIN-30 data acquisition board, United Electronics, Watertown, MA) to a personal computer, where they were sampled at 25.6 kHz using DasyLab software (Data Acquisition System Laboratory, DasyTec USA, Amherst, NH), and stored for off-line analysis.

Custom written software was used to automatically identify individual motor units based on the shape of the MUAPs, using a template-matching algorithm. After this computerized identification, each file was inspected manually to resolve multiple MUAPs that were temporally superimposed on one another. Computational errors and misidentifications made by the automatic identification program were also corrected by trained operators. This procedure for identifying motor units has been reported previously (Kamen et al. 1995; Knight and Kamen 2004) and has been shown to have high reliability (Lacourse et al. 1993).

The recruitment force, total number of firings, maximal firing rates, and occurrence of doublets were determined for each identified motor unit. Doublet firings of individual motor units were defined as any ISI ≤10 ms (Partanen and Lang 1978). The occurrence of doublets was identified as the number of motor units that discharged at least one doublet. The recruitment level of each motor unit was defined as the force level at which the first firing of that motor unit occurred. The maximum firing rate of each identified motor unit was calculated by taking the mean of the five shortest consecutive ISIs. Any sequence of MUAPs that included doublet firings (<10 ms) or long ISIs (>200 ms) were excluded from the analysis (Kamen et al. 1995). The number of doublets, the ISI of each doublet, and the ISI after each doublet were calculated for each identified motor unit in each trial. The firing rate immediately preceding a doublet discharge was calculated by taking the mean of the three ISIs before a doublet discharge. The firing rate immediately before a doublet was not calculated if there were not three ISIs before the doublet (i.e., if the doublet occurred in the first two firings of that motor unit) or if one doublet was preceded by another doublet. The force (%MVC) at which the doublet firings occurred was also determined. Finally, the peak-to-peak amplitude of the first and second MUAPs of each doublet discharge was calculated.

Statistical analysis

Differences between young and older individuals in MVC force and in the number of motor unit firings at each force level were assessed using an independent samples t-test. A two-way ANOVA was used to study differences between groups and across the different rates of force production for the following measures: number of trials with doublet discharges, ISIs of the doublet, the ISIs following doublet discharges, and the force at which doublets occurred. A two-way repeated measures ANOVA was used to test for differences between groups in the amplitudes of the MUAPs between the first and second discharge in the doublet (repeated measure). A three-way ANOVA was used to study potential differences in motor unit recruitment levels and maximal firing rates between groups, across rates of force production, and between those units that discharged doublets and those that did not. Post hoc analysis was performed using Tukey’s least significant differences tests when significant differences were noted among the different rates of force production. The relationship between recruitment force level and the force at which doublets occurred, and the relationship between firing rate immediately before the doublets and the maximal motor unit firing rates, were explored through the calculation of Pearson correlations.

RESULTS

MVC

Mean dorsiflexion MVC force was assessed in the young and older subjects. The young group had a significantly higher mean MVC (223.2 ± 47.15 N) than the older group (152.2 ± 60.61 N; P < .001).

Motor unit firings

The number of motor unit trains contributing to the mean number of firings for young and older individuals, respectively, were 100 and 65 at 10%MVC/s, 80 and 62 at 30% MVC/s, and 69 and 46 at 50%MVC/s. The number of motor unit firings within these trains was not significantly different between young and older individuals at 10% MVC/s (60.3 ± 36.9 and 49.8 ± 29.7 firings, respectively; P = 0.057) or 30% MVC/s (34.9 ± 16.9 and 30.6 ± 16.21 firings, respectively; P = 0.13). However, there were significantly fewer motor unit firings in the older group (22.7 ± 10.3 firings) than in the younger group (33.8 ± 17.4) at 50% MVC/s (P < 0.001). This suggests that, at least in the 10 and 30% MVC/s conditions, potential differences in the occurrence of doublets between young and older subjects, was not confounded by differences in the total number of motor unit firings analyzed.

A sample recording of force and the discharge behavior of a motor unit showing doublets is shown in Fig. 2. In total, there were 503 doublet discharges in the young subjects and 140 in the older subjects. All but one (older) of the subjects showed at least one doublet discharge over the nine contractions. The percentage of motor units that demonstrated doublets ranged from 45.6 to 48.6% across the three rates of force production in young subjects and from 22.5 to 35.1% in the older subjects (Fig. 3A). There were no significant differences in the occurrence of doublet discharges across the three rates of force production.
production (P = 0.38). There was, however a significant difference between groups, with older subjects showing doublet discharges in fewer trials than the young subjects (P < 0.001). There was no significant interaction between rate of force production and age (P = 0.36).

Doublet discharges and muscular force

The force levels at which doublet discharges occurred ranged from 3.42 to 50% MVC in the young subjects and from 0–50% MVC in the older subjects. Figure 3B shows these mean values at each of the three rates of force production in the young and older groups. There were no significant differences in the force at which doublets occurred between groups (P = 0.92) or among rates of force production (P = 0.80). A significant group × rate of force interaction was found (P = 0.027). The interaction effect appeared to be due to the observation that the force at which doublets occurred was greater for the young than the older group at 30% MVC/s (P = 0.13) and 50% MVC/s (P = 0.44), but greater for the older subjects at 10% MVC/s (P = 0.069).

The force level at which motor units were recruited is shown in Fig. 4. Mean values are shown for both motor units that discharged doublets and those that did not, in both the young and older groups. Those motor units that showed doublet discharges had significantly lower recruitment thresholds, on average, than those units that did not fire any doublets (P < 0.001). Mean recruitment threshold was not significantly different across the different rates of force production (P = 0.26), but was significantly different between age groups (P = 0.003), with the older subjects having a slightly lower mean recruitment force overall. A significant group × rate of force interaction (P = 0.001) was found for the recruitment force level. As seen in Fig. 4, for the young subjects, the difference in recruitment force threshold for those motor units that exhibited doublets was appreciably different from motor units without doublets (P < 0.001). However, no such difference was observed for the older adults (P = 0.26).

Weak, although significant, correlations were found between recruitment force and the force at which doublets occurred (P = 0.001). This was true in both the young (r^2 = 0.16, P < 0.001) and older (r^2 = 0.18, P = 0.001) individuals.

Doublet discharges and motor unit firing rates

Doublet ISIs (the time between the first and second discharge of the doublet) ranged from 1.6 to 9.3 ms in younger subjects and from 1.4 to 8.6 ms in older subjects. Mean doublet ISIs for each group at each rate of force production are shown in Fig. 6A. There were no significant differences in doublet ISIs between groups (P = 0.068). However, there was a significant difference in doublet ISIs among rates of force production (P = 0.034). Post hoc analysis revealed a tendency toward longer doublet ISIs at 50% MVC/s than those at 30% MVCs (P = 0.08).

The mean time to the next firing, following a doublet discharge is depicted in Fig. 6B, for young and older individ-
uals at the three rates of force production. In young subjects the ISI following the doublet ranged from 12 to 283 ms, and in older subjects it ranged from 17 to 425 ms. There were no significant differences in the ISI after doublet discharges between groups \((P > 0.22)\). There was, however, a significant difference in the ISI following a doublet among rates of force production \((P < 0.004)\), but, no significant interaction effect \((P > 0.19)\). Posthoc analysis revealed that at 10% MVC/s the ISI following doublets was significantly longer than at 30 or 50% MVC/s \((P < 0.02)\).

Figure 7 shows the maximum firing rates of motor units in young (A) and older (B) subjects during the three conditions. Those motor units that showed doublet discharges and those that did not are both depicted in this figure. There were no significant differences in maximal motor unit discharge rates between groups \((P > 0.11)\) or among rates of force production \((P > 0.43)\). However, those motor units that fired doublets had significantly higher maximal firing rates than those that did not fire doublets \((P < 0.001)\). It is important to reiterate here that doublet discharges were removed from the discharge histories before the calculation of maximal firing rates.

We also sought to determine how the firing rate of the motor units immediately before a doublet discharge related to the maximal firing rate during the contraction. In young individuals, a weak, but significant, correlation was found \((r^2 = 0.12, P = 0.003)\). In older individuals a stronger significant correlation was found \((r^2 = 0.66, P < 0.001)\). The stronger correlation in the older individuals appeared to be due in part to the motor units of the older individuals being close to their maximal discharge rates when the doublets were fired. This was not the case in the young individuals (Fig. 8).

**Amplitude of doublet MUAPs**

The mean amplitude of the first and second firings of the doublets, respectively, was \(0.94 \pm 0.73\) and \(0.90 \pm 0.71\) mV in the young subjects, and \(0.86 \pm 0.95\) and \(0.80 \pm 0.57\) mV in the older subjects. There were no significant differences in amplitude between the young and older groups \((P = 0.19)\). There was, however, a significant difference in amplitude between the first and second firings \((P = 0.023)\), with the second firings being slightly, but significantly smaller in amplitude than the first. The effect size for this difference in amplitude, however, was small \((0.05)\), indicating that the magnitude of the difference \((0.043\) mV) was too small to be of practical significance.

**DISCUSSION**

**Age differences**

Doublet discharges were observed in all but one subject during a task requiring increased force production. The findings of this study therefore provide support (although indirect) for a role of doublet discharges during tasks which require increasing force. Previous studies, however, have been restricted to young individuals. With advanced age there are several changes in the characteristics of the neuromuscular...
system that are suggested to contribute to the observed decline in muscular force and contraction velocity. It is possible that changes in the occurrence of doublets with age may also contribute to the decreased force producing capabilities of the muscles. A novel finding in this study was a lower occurrence of doublets in older individuals than in young, at all rates of force production studied.

Those units that discharged doublets had higher maximal firing rates than those that did not (dark) are presented. Maximal firing rates were not significantly different between groups or among rates. Those that discharged doublets had a significantly higher maximal firing rate than those that did not.

An interesting finding in this study was that the motor units of older individuals seemed to be close to maximal firing rates when the doublets occurred. This was not the case in the young subjects. The higher firing rates of older individuals before the doublet suggests that the motoneurons of older individuals require higher levels of descending drive to produce doublets.

The apparent requirement of greater descending drive to produce doublets in older individuals could potentially be related to the excitability of the motoneurons. H-reflex studies have suggested that the excitability of motoneurons is lower in older individuals, compared with young (Angulo-Kinzler et al. 1998; Robertson and Koceja 2003; Scaglioni et al. 2002). It is therefore possible that even if delayed depolarization is occurring in the motoneurons of older individuals, it may take a greater amount of synaptic input to elicit the second potential. It is tempting to also suggest that greater inhibition on the motoneuron pool of the older adults may contribute to the lower occurrence of doublets. This seems to be an unlikely mechanism, however, as older adults have been shown to have similar, or even lower, levels of recurrent inhibition than their younger counterparts (Chalmers and Knutzen 2004; Earles et al. 2001).

Another property of the motoneuron that has been cited as a main factor affecting the occurrence of doublets is the length of the AHP after an action potential (Granit et al. 1963). Granit et al. (1963) suggest that motoneurons with longer AHP after an action potential are less able to generate a state of delayed depolarization, and are therefore less likely to show doublet discharges. It has been shown in animals that the duration of AHP in motoneurons is increased with age (Engelhardt et al. 1989; Roos et al. 1997). It is therefore quite possible that longer AHPs can account for the lower occurrence of doublets in the older individuals. Unfortunately the discharge histories in this investigation were too short to perform analysis of motoneuronal after-hyperpolarization using published methods (Matthews 1996).

**Rate of force production**

Many studies of doublet discharges have used a ramp and hold protocol for force production. These studies have revealed system that are suggested to contribute to the observed decline in muscular force and contraction velocity. It is possible that changes in the occurrence of doublets with age may also contribute to the decreased force producing capabilities of the muscles. A novel finding in this study was a lower occurrence of doublets in older individuals than in young, at all rates of force production studied.

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**Rate of force production**

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that doublet discharges are more prevalent at the start of the contraction (during the ramp up to a target force) and less prevalent later in the contraction (while subjects are holding force steady) (Andressen and Rosenfalck 1980; Bawa and Calancie 1983). Other studies have shown that doublet discharges can occur not only at the initiation of force production, but throughout the course of a ballistic or movement contraction (Griffin et al. 1998; Van Cutsem et al. 1998). This suggests that doublets play a greater role in force production when the task involves changing levels of force than when the task involves maintaining a steady force. All but one subject showed at least one doublet discharge during the ramp contractions in the current study. The results of this study therefore support a role for doublets during tasks that require changes in force.

In particular, it has been suggested that doublet discharges are more prevalent during slow ramp contractions (Bawa and Calancie 1983; Garland and Griffin 1999). A main finding in the present study was that there were no significant differences in the occurrence of doublets at the different rates of force production. This contradicts the findings of Bawa and Calancie (1983), who suggested that as the rate of force development increased, the incidence of doublet discharges decreased. It is possible, however, that a rate of force development of 50% MVC/s was not fast enough to detect a change in the occurrence of doublets. Bawa and Calancie (1983) noted decreased doublet discharges when subjects were reaching target forces over a 100-ms period. This is a much faster rate of increase in force than that used in this study. Other authors have suggested that increased contraction velocity actually increases the occurrence of doublet discharges (Van Cutsem et al. 1998). This also contradicts these findings of no differences in doublets at different rates of force production. However, the Van Cutsem et al. (1998) protocol involved ballistic contractions at maximal volitional velocities. Therefore again, the 50% MVC/s paradigm may not have been fast enough to note differences in the occurrence of doublets. It may also be the case that doublet discharges are dependent on the peak level of force. Both the Bawa and Calancie (1983) and the Van Cutsem et al. (1998) protocols involve forces that are higher than the 50% MVC used in this study. It is possible that at higher levels of force greater differences in the occurrence of doublet discharges would be observed. Further study is needed to determine whether the occurrence of doublet discharges is in fact dependent on rate of force production and/or on the peak level of force obtained by the subjects.

Amplitude of doublet MUAPs

The results of this study show that the amplitude of the second MUAP of doublet discharges was smaller than the amplitude of the first, as has been suggested previously (Bawa and Calancie 1983; Kudina and Alexeeva 1992). Because of the short period of time between MUAPs in a doublet discharge, incomplete recovery of Na+ and/or K+ channels may reduce the amplitude of the second MUAP. However, the results of previous studies are anecdotal, with no statistical analysis of MUAP amplitude. The results of this study include statistical analysis of MUAP amplitude of over 400 motor unit discharge histories, with over 600 doublet discharges. Although the amplitude of the second MUAP of the doublet discharges was found to be significantly smaller that the amplitude of the first, the size of the effect was quite small. The effect size for the difference in amplitude was 0.05, indicating that magnitude of the difference was quite small. It was determined that with these data, a difference in amplitude of 0.15 mV would be required to obtain even a effect size of 0.2, considered to be small (Cohen 1988). The difference in amplitude in this case was 0.043 mV, suggesting that the finding of a significant difference was due in large part to the large sample size (over 600 motor units). While these results provide inferential support of a difference in amplitude, the difference is quite small.

Motor unit types

Overall, doublet discharges were observed in ~25% of the motor units analyzed for older individuals and in ~46% of those analyzed for young individuals. Previous reports on the percentage of motor units that discharge doublets are equivocal, with reports ranging from 7 to ≤97% (Hicks et al. 1992; Kudina 1974). One limitation to these previous reports is a general inconsistency in the definition of doublets in terms of ISI, with this definition ranging from 10 to 20 ms (Hicks et al. 1992; Kudina 1974). These reports also involved study of a variety of different muscles. The percentage of motor units that showed doublet discharges in this study, however, falls in the middle of these previously reported ranges. Van Cutsem et al. (1998) observed doublet discharges in 32% of motor units in the TA of younger individuals during ballistic contractions, which fits nicely with these results.

In these findings, motor units that showed doublet discharges had lower recruitment thresholds in young individuals. In both young and older subjects, motor units that fired doublets had higher maximal firing rates than those that did not fire doublets. On average, those motor units that fired doublets had recruitment thresholds of 20% MVC in young subjects and 19% MVC in older subjects. These values closely match reports by Griffin et al. (1998) who suggest that those units that showed doublet discharges had recruitment threshold ranging from 20 to 50% MVC. Previous reports have suggested that doublets are more likely to occur in “higher-threshold” motor units (Bawa and Calancie 1983; Garland and Griffin 1999; Kudina and Alexeeva 1992). It is important to note, however, that these studies, like this study, have used protocols that typically do not require force production above 50% MVC. The “high-threshold” qualification is therefore relative, as the majority of motor units at these low forces are likely to be of the small, slow-twitch type.

Induction of doublet discharges through current injection in the cat, have shown that there is a higher occurrence of doublets in slow motor units, compared with fast motor units (Spielmann et al. 1993). Single fiber H-reflex testing has shown that those motor units capable of doublet discharges have a higher excitability than those that are incapable of doublet discharges (Kudina and Churikova 1990). This also suggests a higher tendency for slow motor units to discharge doublets, as slow motor units have a higher excitability than fast motor units (Hammelsbeck and Rathmayer 1989). These findings suggest a mechanism by which slow motor units may be more likely to discharge doublets, as slow motor units typically have lower recruitment thresholds and higher maxi-
nal firing rates than fast motor units (Henneman 1957; Kamen et al. 1995). Intracellular studies of membrane potentials have revealed that there is less delayed depolarization in motoneurons as the ISI lengths, making the motoneuron less likely to discharge a doublet (Granit et al. 1963). This supports the finding of higher maximal firing rates in those motor units that showed doublets in this study (Fig. 7).

In conclusion, an important and novel finding in this study was a lower incidence of doublet discharges in older individuals than in young. This suggests that the incidence of doublets is not maintained throughout the aging process. The most likely cause of the lower incidence in the older individuals is a change in the intrinsic properties of the motoneurons that occur with aging. Future studies could focus on the further characterizing the changes in intrinsic properties of the motoneurons with age and how they related to doublet discharges. This would afford a better understanding of the underlying mechanisms of doublets.

A contribution to the characterization of doublets was that those motor units that showed doublets had a lower recruitment threshold in young subjects and higher maximal firing rate in both young and older individuals. This suggests that this discharge behavior is occurring primarily in slow motor units. In older adults, higher maximal firing rates were observed in those units that discharged doublets; however, the recruitment thresholds of those units that discharged doublets and those that did not were fairly uniform. This finding along with the significant correlation between the firing rate immediately before doublets were observed and maximal recorded motor unit firing rate suggests a dependence of doublet discharges on motor unit firing rates.

Further comparisons should be done with a similar protocol among different muscle groups to gain better insight as to whether the occurrence of doublets is muscle-specific. Comparisons at a wider range of rates of force production could also help to elucidate the dependence of doublet discharges on contraction velocity. Future studies should also investigate the relationship of doublet discharges to force production to gain a better understanding of the specific contribution of doublets to increasing force.

GRANTS

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REFERENCES


