

ABSTRACT: The purpose of this review was to examine three issues that limit our understanding of motor unit physiology: (1) the range and distribution of the innervation ratios in a muscle; (2) the association between discharge rate and force; and (3) the variation in motor unit activity across contractions that differ in speed and type. We suggest that if more data were available on these issues, the understanding of neuromuscular function would be enhanced substantially, especially with regard to plasticity in the motor neuron pool, adequacy of the neural drive to muscle, and flexibility of activation patterns across various types of contractions. Current data are limited and these limitations influence our ability to interpret adaptations in muscle function in health and disease.

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MOTOR UNIT PHYSIOLOGY: SOME UNRESOLVED ISSUES

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Seventy-five years of research has enumerated many characteristics of the motor unit, from its anatomical description^{107,143} to the identification of a principle that appears to explain the functional organization within a population of motor neurons.^{38,80,82} From the beginning, progress in this field has relied on observations derived from both reduced preparations and intact animals, especially humans. Experimental studies on animals have provided considerable detail on the morphological and electrophysiological characteristics of the motor unit.^{10,22,79,81} In contrast, our understanding of motor unit activity during voluntary contractions has been derived largely from recordings obtained during a limited range of motor behaviors.^{52,126}

Despite these efforts, critical deficits remain in our understanding of motor unit physiology. Prominent among these deficits is our inability to explain

whole muscle function on the basis of motor unit properties and behavior. For example, Gardiner and Ohla⁶⁰ found the fatigability of the plantaris muscle in the rat hindlimb to be greater than that predicted from the fatigue properties of its constituent motor units. Similarly, ter Haar Romeny et al.¹⁵⁴ observed selective activation of motor units in the biceps brachii muscle of humans that depended on the direction of the net torque exerted by the elbow flexor muscles. Such findings indicate that muscle function can differ from the sum of its motor units,^{94,115,172} and that anatomically distinct muscles can comprise several functional populations of motor units.^{15,93,171,174,175}

The purpose of this review is to examine three examples of the limitations in our understanding of motor unit physiology: the number of muscle fibers innervated by motor neurons; the association between discharge rate and motor unit force; and variation in motor unit activity during the performance of different types of contractions. These examples address fundamental issues of motor unit physiology, which impact on our ability to interpret adaptations in muscle function across the lifespan. With such an approach, we provide both a review of relevant motor unit physiology and a conceptual foundation for subsequent studies in these areas.

Abbreviations: d_m , muscle moment arm; d_t , transducer moment arm; EMG, electromyogram; F_m , muscle force; F_t , transducer force; MVC, maximum voluntary contraction; R , ratio of innervation numbers; type FF, fast-contracting, fast-to-fatigue motor unit; type S, slow contracting motor unit; y_i , innervation number of motor unit i

Key words: anisometric contraction; contraction type; discharge rate; innervation ratio; lengthening contraction; motor unit; muscle fiber types

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INNERVATION NUMBER

The number of muscle fibers innervated by a single motor neuron varies across motor unit types and muscles (as reviewed elsewhere⁵²). In cat hindlimb muscles, for example, slow-contracting (type S) motor units innervate an average of about 100 fibers, whereas fast-contracting, fast-to-fatigue (type FF) motor units innervate an average of about 300 fibers.^{13,44,88,91} Similarly, the average number of fibers innervated by single motor neurons in human muscle ranges from about 5 for the lateral rectus (an eye muscle) up to about 2000 for the medial gastrocnemius muscle in the leg.^{57,165} The variation in innervation number is the most significant factor that contributes to differences in motor unit force.^{66,91,166}

The critical issue for muscle function is not the *average* differences in innervation ratio among motor units, but rather the *range* of innervation ratios within a given muscle. This property ultimately determines the proportions of the motor neuron pool that innervate the different muscle fiber types. However, such information on the number of fibers innervated across a pool of motor units is not directly available. The most common approach to determine the number of fibers innervated by a motor unit is the glycogen depletion technique.^{97,100} This procedure involves selectively activating a motor neuron or its axon for a duration that is adequate to reduce the level of glycogen in the innervated fibers. Subsequently, serial sections of the muscle are examined microscopically and the fibers with reduced levels of glycogen are counted. The main limitation of this technique is that only a single motor unit can be examined in each muscle, thereby providing limited information on the range and distribution of fiber number across the motor units of a muscle. Furthermore, not all the fibers may be depleted of glycogen, the accuracy of fiber enumeration can be influenced by muscle geometry, and the experimental data are limited to animals.^{3,25,120,124,164} Although single motor units can be selectively activated in humans by intramuscular^{49,150} and intraneural^{58,159,173} micro-

stimulation, there is not yet an imaging procedure that can discriminate the activated muscle fibers in humans.

Consequently, data on innervation numbers in humans have been derived mostly from cadaveric assessments.^{18,28,30,55,57,165} The typical approach has been to count the number of muscle fibers, estimate the number of motor axons innervating the muscle, and calculate the average number of muscle fibers innervated by each axon. The principal limitation of this approach is that the analysis yields only the average number of fibers innervated by the motor units in a muscle. Furthermore, there is uncertainty in distinguishing between sensory and motor axons in the nerve.

Alternatively, there have been some attempts to determine innervation ratios in humans with electrophysiological procedures.⁶⁴ This involves assessing the spatial territory of a motor unit and then obtaining an average measure of fiber density from measurements made at several locations within the territory.^{19,145} Motor unit territory can be determined from scanning electromyography (EMG), which involves inserting a concentric needle electrode deep into the muscle and then extracting it in 50- μ m steps while making recordings that are triggered from a single-fiber electrode.^{67,146} Similarly, fiber density can be determined from the number of action potentials detected with a single-fiber electrode that has a known detection area.¹⁴⁷ Such an approach, however, is limited to low-force contractions and has produced rather low innervation ratios.⁶⁴

Of the three techniques used to estimate innervation number, only the glycogen depletion procedure has provided data, albeit limited, on the range of innervation numbers in a muscle. Data for two hindlimb muscles in the rat and cat suggest a two- to ninefold range of innervation number (Table 1). The upper limit of these ranges, however, is substantially less than the average innervation number that has been reported for limb muscles in humans.⁵⁷

Table 1. Range of innervation numbers as determined by the glycogen depletion technique.

Reference	Species	Muscle	Innervation Number			Number of motor units
			Minimum	Maximum	Mean	
Bodine et al. ¹³	Cat	Tibialis anterior	60	379	200	11
Brandstater and Lambert ¹⁴	Rat	Tibialis anterior	55	172	118	36
Edström and Kugelberg ⁴⁷	Rat	Tibialis anterior	80	178	132	13
Kanda and Hashizume ⁹¹	Rat	Medial gastrocnemius	41	356	160	23
Tötösy de Zepetnek et al. ¹⁶⁶	Rat	Tibialis anterior	53	202	121	20

Given this discrepancy, it is necessary to obtain additional estimates of the range of innervation numbers in human muscles.

Estimates of Innervation Number. Because of the high correlation between innervation number and the maximum tetanic force of a motor unit,^{13,91,166} it is possible to estimate the range of innervation numbers in a muscle based on the range of motor unit forces. Such a strategy involves at least two steps: determining the range of tetanic forces; and estimating the number of muscle fibers required to achieve these forces.

In some cases, such as for human muscle, data on the tetanic forces of motor units may be limited, whereas there is ample information on the more easily measured range of twitch forces. For these circumstances, it is necessary first to predict the tetanic forces based on an estimate of the twitch–tetanus ratio. This ratio, however, varies across muscles and species. Furthermore, some studies have found a systematic change in twitch–tetanus ratios across motor unit types within a muscle, but this has not been a consistent finding. For example, one study found that the twitch–tetanus ratio in the rat medial gastrocnemius muscle ranged from average values of 0.16 for type S motor units to 0.45 for type FF motor units.⁹⁰ In another study on the same rat muscle, the average twitch–tetanus ratio was 0.14 for both type S and type F motor units.² This discrepancy may be related to differences in experimental protocols, such as tetanic stimulation prior to assessment of twitches. Because type F motor units usually exhibit greater potentiation after a tetanus,^{68,105} the twitch–tetanus ratio would likely be augmented for type F units compared with type S units after a preceding tetanic stimulation.

For human muscle, twitch and tetanus data have been reported for muscles that control the digits of the hand.^{58,156,158,161} These data can be represented by a linear function ($y = 0.322x$, where y = twitch force and x = tetanic force), which indicates that the twitch–tetanus ratio does not change systematically with tetanic force for these muscles (Fig. 1). The average twitch–tetanus ratio is indicated by the slope of the regression line and was about 0.322 for the data shown in Figure 1, which is similar to the value found for motor units in the cat tenuissimus¹⁰⁵ and cat medial and lateral gastrocnemius muscles.²³

As an example of the procedure to estimate the range of innervation numbers, we used data published on the first dorsal interosseous muscle of humans. According to estimates by Feinstein et al.,⁵⁷

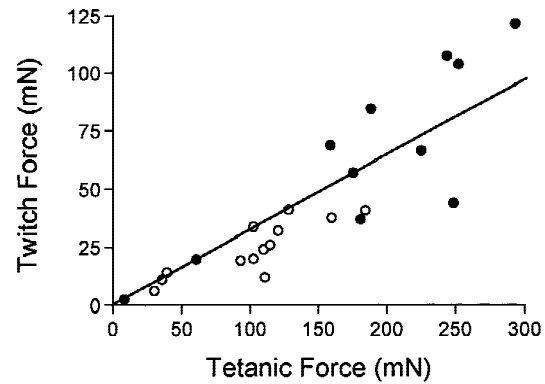


FIGURE 1. Relationship between the tetanic and twitch forces for motor units in muscles that control the digits in humans. The data were provided by Andrew J. Fuglevand, PhD (filled circles), and Christine K. Thomas, PhD (open circles). The relationship was characterized by a linear regression (twitch force = 0.322 tetanic force; $r^2 = 0.77$).

this intrinsic hand muscle comprises about 40,500 muscle fibers that are innervated by 120 motor neurons, which yields an average of 338 fibers innervated by each motor neuron. As determined by spike-triggered averaging^{36,116,163} and intramuscular microstimulation,⁴⁹ the twitch forces of motor units in first dorsal interosseous range from about 1 mN to 140 mN. From the regression line for the data in Figure 1, a motor unit with a measured twitch force of 1 mN would have a tetanic force of about 3 mN, and a motor unit in a first dorsal interosseous with a twitch force of 140 mN would have a tetanic force of 434 mN.

These estimates for first dorsal interosseous, however, are based on the abduction force exerted by the index finger and not the tensile force of the muscle. The actual forces transmitted through the distal tendon depend on the ratio of two moment arms¹¹¹: the moment arm from the force transducer to the metacarpophalangeal joint (d_t) and the moment arm from the muscle tendon relative to the joint (d_m). The force exerted by a motor unit (F_m) will be approximately equal to the force detected by the transducer (F_t) multiplied by the ratio of two moment arms:

$$F_m = F_t \times \frac{d_t}{d_m} \quad (1)$$

We estimate a typical ratio of moment arms to be about 3.0. Therefore, the actual motor unit forces in first dorsal interosseous are probably at least three times greater than the measured values, which would yield a range of 9–1304 mN.

Next, it is necessary to determine the number of muscle fibers required to achieve the minimum and maximum motor unit forces. The number of requisite fibers depends on the average cross-sectional area of the fibers and the intrinsic capacity of the fibers to generate force, a property known as specific tension. Based on biopsy samples obtained from the first dorsal interosseous muscle of healthy women,³⁷ the fiber diameter data indicate the average cross-sectional area of type I fibers to be 2140 μm^2 compared with 3685 μm^2 for type II fibers. Estimates of specific tension, however, are more problematic. Although specific tension may vary across the different types of muscle fibers^{76,77,103} and motor units,^{13,25,29,90,91} we assume a constant specific tension of 0.0002 mN/ μm^2 (20 N/ cm^2).^{46,91,110,128}

Accordingly, the tetanic force exerted by a single muscle fiber will be equal to the product of its cross-sectional area and its specific tension. Therefore, the force of a type I muscle fiber in the first dorsal interosseous would be 0.428 mN (2140 $\mu\text{m}^2 \times 0.0002$ mN/ μm^2) and for a type II muscle fiber it would be 0.737 mN (3685 $\mu\text{m}^2 \times 0.0002$ mN/ μm^2). Likewise, the tetanic force of the weakest motor unit would require 21 muscle fibers (9 mN/0.428 mN) compared with 1770 muscle fibers (1304 mN/0.737 mN) for the strongest motor unit. This represents an 84-fold range of innervation ratios.

In addition to the range of forces and innervation numbers across a population of motor units, it is also necessary to consider its distribution. One aspect of motor unit organization that seems consistent across muscles and species is the skewed distribution of various properties, including motor unit force. The frequency distribution of motor unit force comprises many units that exert small forces and relatively few units that exert large forces.^{49,116,123} Such a distribution can be represented as an exponential in the form:

$$y_i = a e^{[(\ln R)/n] \cdot i} \quad (2)$$

where y_i indicates the force or innervation number of unit i , a is the force or innervation number for the smallest unit (unit 1), n is the number of units, and R is the ratio of the innervation numbers for the largest and smallest units ($R = y_n / y_1$).⁵⁹ For the first dorsal interosseous muscle, which is innervated by about 120 motor neurons,⁵⁷ the exponential distribution of innervation ratios can be characterized by (Fig. 2A):

$$y_i = 21 e^{[(\ln 84)/120] \cdot i} \quad (3)$$

Based on this estimated distribution of innervation

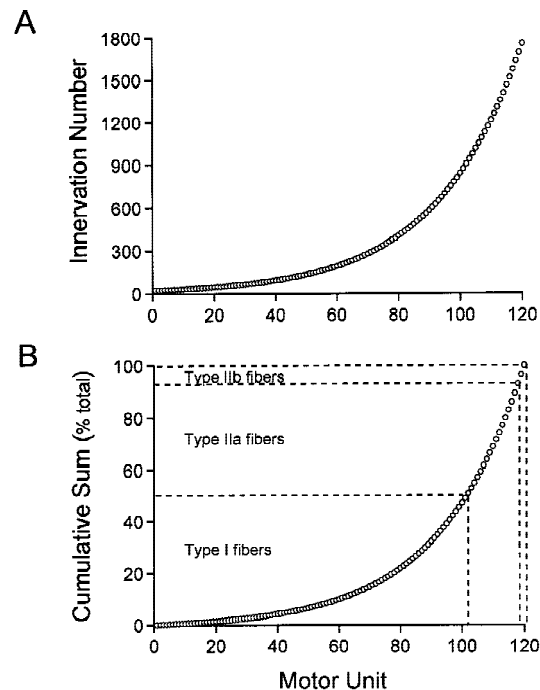


FIGURE 2. Proportions of motor units in the first dorsal interosseous muscle that innervate the different muscle fiber types. **(A)** The distribution of innervation numbers for the 120 motor units. **(B)** The number of motor units that innervate the different fiber types based on eq. (3).

numbers, the total number of fibers in the muscle would be 47,976, which is similar to the 40,500 fibers counted in the first dorsal interosseous by Feinstein et al.⁵⁷ For comparison, a linear distribution of innervation numbers would produce a muscle with 604,442 fibers. According to the fiber-type proportions reported by Dennett and Fry,³⁷ 50.3% (24,132) of the fibers in first dorsal interosseous would be type I, 44.7% (21,445) would be type IIa, and 5% (2399) would be type IIb. If we assume that the smallest motor units in the population innervate type I fibers, and cumulatively sum the number of fibers belonging to individual motor units from the smallest to largest (Fig. 2B), then motor units 1–101 would comprise type I fibers, motor units 102–118 would innervate type IIa fibers, and only two units, numbers 119 and 120, would supply type IIb fibers. Although the muscle comprised equal numbers of type I and II fibers, the skewed distribution of innervation numbers resulted in about 84% of the motor units comprising type I muscle fibers and only about 16% containing type II fibers.

If the range and distribution of innervation numbers derived for first dorsal interosseous is similar for other muscles, then the relations between fiber-type and motor neuron pool percentages can be esti-

mated for other muscles with different proportions of fiber types. The results for three muscles that span the range of fiber-type proportions in humans are shown in Table 2. The relative proportions indicate that, even in a muscle that has few type I muscle fibers, most of the motor neurons innervate, and hence motor units comprise, type I muscle fibers. Furthermore, the number of type I fibers in a muscle has to decline to about 10% before half of the motor neurons innervate type II muscle fibers.

Clinical Significance. The reason for presenting this example on the range of innervation numbers in a muscle is to emphasize that, even though a muscle might comprise 50% type II muscle fibers, most of the motor neurons innervate the type I muscle fibers. Based on data for the first dorsal interosseous muscle, we estimate that 84% of the motor neuron pool innervates type I muscle fibers, which comprise half of the fibers in the muscle, and only two motor neurons innervate the type IIb fibers. These proportions provide some insight into the adaptations that occur in the spinal cord when fiber-type proportions change due to an intervention or a disease.

For example, a number of studies have reported that there is considerable remodeling of motor unit territories with advancing age,^{27,42,54,113} which largely appears to involve a decrease in the number and size of type II muscle fibers^{103,106} and an increase in the number of muscle fibers innervated by low-threshold motor units.^{48,88,90} The results shown in Figure 2 suggest that, depending on the distribution of innervation numbers for the involved muscle, this adaptation may involve the loss of only a few motor neurons. Similarly, the proportion of the motor neuron pool involved in the progression of a disease^{50,71,133,141} depends on the recruitment thresholds of the motor units that exhibit the adaptations. For example, if a disease influences mostly high-threshold motor units, this may involve rela-

tively few motor neurons. Conversely, a disease that focuses on low-threshold motor units would likely involve a large fraction of the pool. Furthermore, it is not appropriate to infer the proportion of motor neurons involved in a disease based on changes in fiber-type proportions.^{1,75,114}

This example also serves to underscore the difficulty associated with obtaining a complete characterization of the contractile properties of the motor units in a muscle. Because there can be so few motor neurons innervating type II muscle fibers, the chances of sampling the entire range of motor units are less than what is suggested by the fiber-type proportions of the muscle. This limitation may contribute to the differences in the relationships between motor unit properties that have been reported for human and animal data.⁸

The range and distribution of innervation numbers in a muscle provide fundamental information about the relative distribution of activity in the motor neuron pool. Nonetheless, there are few such data in the literature, especially for human muscles.

DISCHARGE RATE AND FORCE

In addition to the number of fibers innervated by a motor neuron, the rate at which the motor neuron discharges action potentials has a pronounced influence on the force that the motor unit exerts. This effect is typically characterized as the force–frequency relationship, which indicates a sigmoidal association between variation in average discharge rate and force.^{58,111,158} The shape of the relationship for a motor unit depends on the time course of its twitch response and the quantity of contractile proteins included in the innervated muscle fibers. The force–frequency relationship can be characterized by such measures as the amplitude of the peak force, the frequency required to achieve peak force, the frequency needed to achieve 50% force, and the frequency at which the peak slope occurs (Table 3). The functional significance of the force–frequency relationship is that it represents how the neural code, in terms of motor neuron discharge rate, is transformed into a mechanical response (force) and then applied to the external surroundings through the skeleton.

One of the unresolved issues involving the modulation of discharge rate during voluntary contractions is the discrepancy between the observed maximum rates and those that are required to achieve maximum tetanic force. For example, intraneural stimulation of single motor units indicates that it requires rates of 30–100 Hz, with average values closer to 100 Hz (Table 3), to achieve peak force for

Table 2. Proportion of the motor neuron pool that innervates the different muscle fiber types in muscles with different percentages of muscle fiber types.

	Fiber types (%)			Motor neuron pool (%)		
	I	IIa	IIb	I	IIa	IIb
Soleus	70.4	29.7	0	92.5	7.5	0
First dorsal interosseous	50.3	44.7	5.0	84.2	14.2	1.7
Triceps brachii	32.9	49.6	17.6	75.0	20.8	4.2

Fiber type data for soleus and triceps brachii were taken from Harridge et al.⁷⁶

Table 3. Characteristics of the force–frequency relationship for human motor units (data expressed as mean \pm SD and range).

Study	Muscle	Peak force (mN)	Discharge rate		
			Peak force (Hz)	50% force (Hz)	Peak slope (Hz)
Fuglevand et al. ⁵⁸	Forearm and hand Group 1 ($n = 8$)	200 \pm 59 (110–293)	83 \pm 22 (50–100)	9 \pm 1 (8–10)	8 \pm 1 (7–9)
	Group 2 ($n = 5$)	223 \pm 220 (8–571)	90 \pm 22 (50–100)	16 \pm 1 (14–17)	14 \pm 2 (13–18)
Macefield et al. ¹¹¹	Toe extensors ($n = 13$)	89 \pm 17 (30–188)	50*	10 \pm 1 (7–14)	11 \pm 1
Thomas et al. ¹⁵⁸	Thenar ($n = 19$)	80 \pm 38 (22–166)	— (30–100)	12 \pm 4	—

Groups 1 and 2 (Fuglevand et al.⁵⁸) were distinguished on the basis of the stimulation rate needed to achieve the 50% force.
*Median.

a motor unit. In contrast, the average discharge rates of motor units during high-force contractions are much lower (Table 4). These data suggest that either the force is not maximal during these presumed maximal contractions or that the force exerted by a motor unit does not depend solely on its average discharge rate.

Early on in the description of motor unit behavior, it was recognized that the discharge pattern might have a significant effect on the force exerted by the motor unit.^{33,39,45,109,140} This expectation was corroborated by the observation that brief intervals (5–55 ms) between successive action potentials can increase the rate of force production during a rapid contraction^{161,168} and may temporarily enhance motor unit force during submaximal contractions.^{24,63,111,176} Such brief intervals are referred to as double discharges or doublets. Furthermore, the use of such an activation pattern during a fatiguing contraction can reduce the decline in force.^{6,9,11,12}

One feature of this phenomenon that is often overlooked is the time course of the enhanced force after the brief interval (double discharge). Macefield et al.¹¹¹ found that a brief interval delivered at the onset of low-frequency trains of stimuli (<20 Hz) increased motor unit force, but that the enhancement dissipated within 1–2 s. Also, there was no increment in force when the brief interval preceded higher frequency trains. Similarly, Thomas et al.¹⁶¹ showed that the inclusion of additional short intervals in a train of stimuli does not lead to further enhancement of the force. They suggested, therefore, that the double discharge by a motor neuron probably has little effect on the force exerted during a long-lasting contraction at a relatively strong intensity.¹⁶¹

These observations suggest that the interpretation of discharge rates must involve consideration of

both the intensity and the duration of the contraction.⁷⁰ For example, the force exerted by motor units during brief contractions at low intensity can be markedly affected by subtle variation in the pattern of activity independent of average discharge rate. This is an important consideration because many natural motor behaviors do involve such contractions. In contrast, it is principally the average discharge rate that determines the force exerted by the motor units during strong contractions that last more than a few seconds. Furthermore, once a motor unit has achieved its peak force, discharge rate can decline substantially without causing force to decrease.¹⁶¹ Consequently, the discrepancy between the discharge rates recorded during a maximum voluntary contraction (Table 4) and the stimulus rates needed to achieve maximal force in human motor units (Table 3) implies that the maximal *voluntary* force is not equivalent to the maximum force *capacity* of a muscle or muscle group.⁵³

This interpretation, however, must be tempered by consideration of differences between the two types of experiments. Because most of the tension generated by muscle fibers is transmitted laterally through the cytoskeletal and connective tissue networks to the tendon,^{142,148} the tensile state of surrounding fibers will influence the force that can be registered externally by a single motor unit. The force–frequency relationship for a motor unit, therefore, will vary depending on the compliance of the muscle in which it is embedded. The relatively low activation rates that are necessary to achieve one half of the peak force (Table 3) suggest that this effect is significant. Nonetheless, it remains unclear whether the average discharge rates recorded during a maximum voluntary contraction are adequate to evoke the maximum force that a muscle can exert.

Table 4. Average discharge rates of human motor units during high-force contractions (data expressed as mean \pm SD and range).

Study	Muscle	Force (%MVC)	Discharge rate (Hz)
Bellemare et al. ⁵	Adductor pollicis (<i>n</i> = 300 trains)*	100	29.9 \pm 8.6 (12–60)
	Biceps brachii (<i>n</i> = 270 trains)	100	31.1 \pm 10.1 (12–60)
	Soleus (<i>n</i> = 270 trains)	100	10.7 \pm 2.9 (5–20)
Connelly et al. ³¹	Tibialis anterior (<i>n</i> = 175 trains)		
	Young adults	~100	41.9 \pm 8.2 (27–65)
	Old adults	~100	31.0 \pm 8.5 (20–62)
Conwit et al. ³²	Vastus medialis (<i>n</i> = 82 trains)	75	14.9 \pm 4.8 (8–30)
De Luca et al. ³⁵	Deltoid (<i>n</i> = 34 MUs)	80	29.4 \pm 3.4
	First dorsal interosseous (<i>n</i> = 38 MUs)	80	41.4 \pm 9.6
Duchateau and Hainaut ⁴³	Adductor pollicis (<i>n</i> = 55 MUs)	100	22.6 \pm 7.4
	First dorsal interosseous (<i>n</i> = 39 MUs)	100	31.0 \pm 8.9
Gydikov and Kossarov ⁷³	Biceps brachii (<i>n</i> = 17 MUs)	100	— (12–24)
Hannerz ⁷⁴	Tibialis anterior (<i>n</i> = 63 MUs)	100	— (25–65)
Jakobi and Cafarelli ⁸⁷	Vastus lateralis (<i>n</i> = ~200 APs)	100	27 (15–47)
Kamen et al. ⁸⁹	First dorsal interosseous		
	Young adults (<i>n</i> = 51 MUs)	100	50.9 \pm 19.5 (21–92)
	Old adults (<i>n</i> = 57 MUs)	100	31.1 \pm 11.8 (13–64)
Kukulka and Clamann ¹⁰¹	Adductor pollicis (<i>n</i> = 4 MUs)	60–100	— (17–32)
Leong et al. ¹⁰⁴	Rectus femoris		
	Old weight lifters (<i>n</i> = 28 MUs)	100	23.8 \pm 7.7
	Old adults (<i>n</i> = 26 MUs)	100	19.1 \pm 6.3
Macefield et al. ¹¹¹	Tibialis anterior (<i>n</i> = 10 MUs)	100	20.3 \pm 2.3
Monster and Chan ¹¹⁷	Extensor digitorum communis (<i>n</i> = 60 MUs)	80	— (20–25)
Rice et al. ¹²⁹	Vastus medialis (<i>n</i> = 555 trains)	100	23.8 \pm 6.1
Roos et al. ¹³⁰	Vastus medialis (<i>n</i> = 300 trains)	100	26.4 \pm 7.6 (15–47)
Seki and Narusawa ¹³⁶	Biceps brachii (<i>n</i> = 166 trains)	80	26.2 \pm 9.2 (7–51)
	First dorsal interosseous (<i>n</i> = 187 trains)	80	31.1 \pm 10.2 (10–62)
Thomas ¹⁵⁷	Thenar (<i>n</i> = 28 trains)	100	36.0 \pm 10.2 (18–58)
Thomas and de Valle ¹⁶⁰	Triceps brachii (<i>n</i> = 23 trains)	100	24.6 \pm 7.1 (15–37)
Van Cutsem et al. ¹⁶⁹	Tibialis anterior (<i>n</i> = 528 MUs)	100	33.2 \pm 14.7 (10–67)

*Number of motor units (MUs), action potential trains, or action potentials (APs).

DIFFERENT TYPES OF MUSCLE CONTRACTIONS

A common approach used to assess the limits of the size principle is to compare the activity of motor units across various behaviors. Such comparisons, however, can be compromised by anatomical and functional variations among muscles. For example, because muscles have distributed and off-center attachments on the skeleton, they can generally contribute to several actions about a joint.^{17,41,121,177} For some muscles, such as biceps brachii¹⁷¹ and lateral gastrocnemius,^{174,175} this has led to the observation of discrete populations of motor units that appear to be activated selectively for specific actions. Similarly, the distribution of activity within a group of muscles can vary across actions, such as isometric and anisometric contractions.^{16,69,152,153,170} In this section, however, we consider the evidence that the activation of a given population of motor units varies with the type of muscle contraction performed.

Shortening Contractions. Most studies of motor unit behavior have been based on recordings obtained during isometric contractions. Under these conditions, the gradation of force is accomplished by the concurrent modulation of the number of active motor units and discharge rate.^{38,127,140} The operating range of this strategy, however, varies across muscles. For example, the upper limit of motor unit recruitment, which denotes the transition to reliance on modulation of discharge rate, appears to be about 50% maximum voluntary contraction (MVC) for some hand muscles, compared with 85% for limb muscles.^{35,101,116,149}

When subjects perform slow movements that involve shortening contractions, both the distribution of activation among synergist muscles^{151–153} and the level of activation for individual muscles^{69,155,167} can differ from that observed during isometric contractions. The greater EMG amplitude appears to be due

to an increase in the number of motor units recruited to perform the shortening contraction. For example, Theeuwens et al.¹⁵⁵ had subjects place an arm in a transverse plane and recorded the activity of motor units under various conditions while maintaining a constant force at the wrist. Activation of the biceps brachii, brachioradialis, and anterior deltoid muscles varied with the direction of the load torque and the task being performed. For each direction examined, they found that the EMG amplitude for slow movements was greater compared with isometric contractions, and that the recruitment thresholds of motor units were lower for the movements, but that there was no difference in the initial discharge rates between the two conditions. Similarly, Kossev and Christova⁹⁶ observed a reduction in the recruitment threshold of motor units in biceps brachii for a slow shortening contraction against an elastic load compared with an isometric contraction. Furthermore, motor unit behavior was similar for isometric contractions and an intended isometric contraction that the investigators permitted to become a slow shortening contraction.¹⁵³

As a constant-velocity, shortening contraction progresses, the magnitude of the surface EMG increases.^{26,69} Although some of the increase in EMG is due to the effect of muscle fiber length on the detected signal^{62,65,78,85} and shifts of fiber length along the length–tension relationship,¹⁰⁸ there is also a change in the amount of motor unit activity. Because these contractions are performed at slow velocities, the force–velocity relationship presumably has a minimal effect on the observed differences. For example, Kato et al.⁹² found that, when subjects used the dorsiflexor muscles to displace the foot against a constant torque, the increase in EMG for tibialis anterior was accompanied by the recruitment of motor units. The discharge rate of the active motor units, however, remained relatively constant throughout the range of motion. Similar findings have been reported for motor units in biceps brachii⁹⁶ (Fig. 3A) and first dorsal interosseus¹⁰² during a shortening contraction. The absence of modulation of discharge rate contrasts with the control strategy used to grade force in isometric contractions.^{125–127}

These findings suggest two fundamental differences in motor unit activity between isometric contractions and slow shortening contractions. First, differences in the recruitment threshold indicate that, at the onset of the contraction, there is some feature of the input to the motor neuron pool that distinguishes between the two tasks. Second, the relative contributions of recruitment and discharge rate vary for the two tasks. These suggestions, however, should

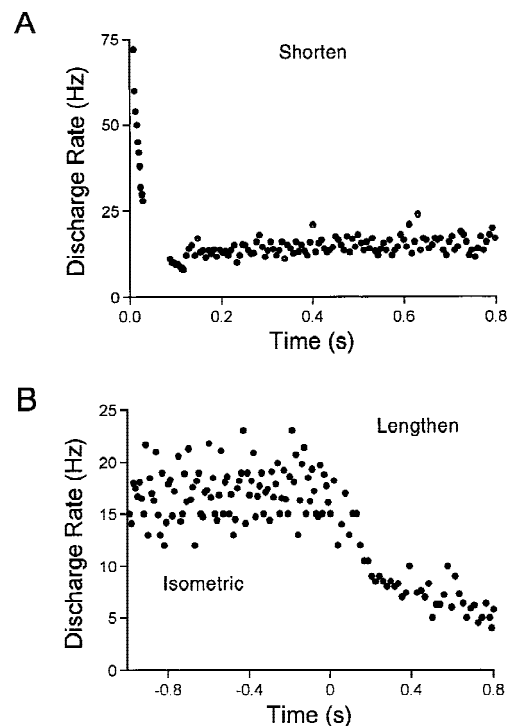


FIGURE 3. The instantaneous discharge rate of a motor unit in biceps brachii when stretching and releasing an elastic band. Each data point indicates the time between successive action potentials, and data from several trials of each task are superimposed on the same graph. **(A)** The muscle performed a shortening contraction, beginning at 0 s, to stretch the elastic band. The contraction began at 0 s and ended at about 0.9 s. **(B)** After holding the elastic band at a stretched length (isometric contraction), the muscle performed a lengthening contraction to release the band. The lengthening contraction began at 0 s. For this motor unit, the discharge ended at about 15 Hz for the shortening contraction and also began the lengthening contraction from about 15 Hz. The data were taken from Kossev and Christova.⁹⁶

be considered tentative until they have been examined more systematically.

Lengthening Contractions. In the last decade or so, considerable attention has been focused on the observation by Nardone et al.¹¹⁸ that lengthening contractions appear to involve alterations in the order that motor units are recruited. Subjects were seated and performed slow shortening and lengthening contractions with the plantarflexor muscles that involved raising and lowering an inertial load. The distribution of activity among the involved muscles (soleus, lateral and medial gastrocnemius, peroneus, tibialis anterior) was usually different for the lengthening contraction compared with the shortening and isometric contractions,¹¹⁹ and the motor units active during the lengthening contraction were usually different from those used during the shortening

contraction.¹¹⁸ This observation led to the conclusion that lengthening contractions are controlled by high-threshold motor units, which is contrary to the orderly recruitment phenomenon.

Subsequently, a similar finding has been reported on one other occasion,⁸⁴ but only rarely by most investigators who have examined this issue.^{4,61,96,102,144} It appears, therefore, that lengthening contractions may involve alterations in recruitment order, but this is not a general strategy. One of the difficulties associated with studying lengthening contractions is that they are not simply the converse of shortening contractions. By definition, the performance of a lengthening contraction requires that the net torque exerted by the involved muscles must be slightly less than the load torque, which appears to involve heightened levels of feedback from muscle receptors.^{21,131} As a consequence, a comparison of motor unit behavior in shortening and lengthening contractions requires that the anatomical and biomechanical details be similar across tasks and experiments. For example, recordings could be made from functionally different groups of motor units across experiments or there might be slight changes in the direction of the net force vector.

Nevertheless, there are features of lengthening contractions that distinguish them from shortening and isometric contractions.⁵¹ When an individual goes from performing a shortening contraction to a lengthening contraction, there is a reduction in EMG amplitude^{7,26,69} that corresponds to a decline in the net muscle torque. The decrease in EMG is largely due to a decline in the average discharge rate of the active motor units rather than a change in the population of motor units.^{96,102,144} As the lengthening contraction progresses, there is a further decline in both the EMG amplitude and the discharge rate of the motor units. For example, Kossev and Christova⁹⁶ found that when subjects performed a lengthening contraction against an elastic load with the elbow flexor muscles, the decrease in force was accomplished by a gradual reduction in the discharge rate of the involved motor units (Fig. 3B). In contrast, the gradation of force during the shortening contraction was achieved by recruiting additional motor units rather than increasing discharge rate (Fig. 3A). This example demonstrates that when the biceps brachii muscle was used to decrease force during a lengthening contraction, the modulation of motor unit activity was different from that used for the converse task of increasing force during a shortening contraction.

When lowering inertial loads, however, the discharge rate of motor units does not decline gradu-

ally during the lengthening contraction. Rather, the average discharge rate is reduced at the onset of the lengthening contraction and the average value remains relatively constant as the load is lowered.¹⁰² Old adults, however, exhibit a marked increase in the variability of discharge rate during the lengthening contraction,¹⁰² which may account for their reduced steadiness during lengthening contractions compared with shortening contractions.^{26,69}

Another property of motor unit activity that appears to differ across contraction types is the relative timing of the discharge of action potentials among motor units. The concurrent discharge of action potentials is known as synchronization, and is usually measured with a cross-correlation histogram derived from the trains of action potentials discharged by pairs of motor units. The strength of synchronization depends on the pattern of shared synaptic input onto the motor neurons^{95,135} and, therefore, reveals details about the distribution of input to the motor neuron pool.^{34,122,135} Motor unit synchronization is influenced by such factors as learning, handedness, and recovery from a lesion.^{56,132,134,138,139} It now appears that synchronization is greater during anisometric contractions compared with isometric contractions, and may be greatest during lengthening contractions.¹³⁷

These findings indicate that the modulation of motor unit activity during lengthening contractions can exhibit greater variations than those observed during isometric and shortening contractions. Although the recruitment order of motor units does not appear to be violated consistently during lengthening contractions, the modulation of discharge rate can vary across loading conditions and with chronic adaptations, such as aging. Furthermore, the distribution of synaptic input to a motor neuron pool appears to differ across contraction types.

Rapid Contractions. When subjects perform fast contractions, the recruitment order of motor units remains the same as that for slow contractions.^{40,41,86,112,162,168} Furthermore, when subjects perform rapid contractions with the triceps brachii muscle, the same motor units in the lateral head of triceps brachii are activated to produce a similar EMG–time profile in isometric contractions and movements.⁸⁶ However, the recruitment threshold, as measured during slow isometric contractions, shifts for fast isometric contractions and rapid movements to account for the fixed delay between the action potential and the mechanical response.^{20,86,168}

Rapid changes in muscle force, during both isometric and anisometric contractions, are often asso-

ciated with the appearance of double discharges of action potentials.^{41,63,72,98,99} This phenomenon refers to two action potentials that are discharged within 20 ms of each other.⁸³ For example, Van Cutsem et al.¹⁶⁸ had subjects train the dorsiflexor muscles for 12 weeks with rapid contractions against loads that were 30–40% of maximum. The training program increased muscle strength, the maximum speed of the rapid contractions, the average discharge rate of the motor units, and the incidence of double discharges. The double discharges were distributed throughout the contraction, but mainly at the beginning of the contraction, and were exhibited by motor units with different recruitment thresholds. However, the appearance of double discharges in a train of action potentials does not always confer a beneficial mechanical effect. For example, the reduced ability of old adults to perform steady contractions with first dorsal interosseous while exerting low forces and lifting light loads has been associated with a greater incidence of double discharges.¹⁰² Furthermore, the double discharges were distributed throughout each contraction, especially at the transition from a shortening contraction to a lengthening contraction. These findings underscore the mixed evidence on the role of double discharges as an activation strategy.⁶³

Although this discussion of task strategies has identified several features of motor unit activity that appear to differ across tasks, most of these descriptions are based on limited data. Therefore, we emphasize that it is premature to formulate general principles about the behavior of motor units across the movement spectrum. The most consistent finding seems to be the reliability of orderly recruitment. In contrast, there are data that suggest the relative roles of recruitment and discharge rate can vary with task, but this issue needs to be examined over a broader range of movement conditions and in different muscles. Furthermore, identifying significant differences in motor unit behavior will require that each condition be characterized by a thorough biomechanical assessment of the involved elements.

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