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Influence of proprioceptive feedback on the firing rate and recruitment of motoneurons

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Abstract

We investigated the relationships of the firing rate and maximal recruitment threshold of motoneurons recorded during isometric contraction with the number of spindles in individual muscles. At force levels above 10% of maximal voluntary contraction, the firing rate was inversely related to the number of spindles in a muscle, with the slope of the relationship increasing with force. The maximal recruitment threshold of motor units increased linearly with the number of spindles in the muscle. Thus, muscles with a greater number of spindles had lower firing rates and a greater maximal recruitment threshold. These findings may be explained by a mechanical interaction between muscle fibres and adjacent spindles. During low-level (0% to 10%) voluntary contractions, muscle fibres of recruited motor units produce force twitches that activate nearby spindles to respond with an immediate excitatory feedback that reaches maximal level. As the force increases further, the twitches overlap and tend towards tetanization, the muscle fibres shorten, the spindles slacken, their excitatory firings decrease, and the net excitation to the homonymous motoneurons decreases. Motoneurons of muscles with greater number of spindles receive a greater decrease in excitation which reduces their firing rates, increases their maximal recruitment threshold, and changes the motoneuron recruitment distribution.

1. Introduction

Recently De Luca and Hostage (2010) have reported that the control scheme for motoneurons is invariant among such diverse muscles as the first dorsal interosseous (FDI), the tibialis anterior (TA), and vastus lateralis (VL). But, the values of the firing rates and recruitment thresholds of motor units vary among muscles. For example, motor units in the FDI muscle have been reported to have firing rates that reach 39 pulses per second (pps) and a maximal recruitment threshold of 67% of maximal voluntary contraction (MVC) (De Luca *et al* 1982a, Seki *et al* 2007, De Luca and Hostage 2010, among others). In contrast, motor units of the biceps brachii (BB) muscle have been reported to have lower firing rates, only reaching 26 pps and a maximal recruitment threshold of 90% MVC (Kukulka and Clamann 1981, Seki and Narusawa 1996, among others). There are three likely factors that can modulate the firing rate and recruitment range of motor units among muscles. They are: (a) the excitation/inhibition received from the central nervous system (CNS), (b) the excitatory/inhibitory feedback from the peripheral nervous system, or (c) a combination of the two.

The dominant candidates for the feedback influence are the Renshaw system, the proprioceptive system, consisting of muscle spindles and Golgi tendon organs (GTOs), and other sensors such as mechanoreceptors and joint receptors. Empirical evidence has been presented by Hultborn and Pierrot-Deseilligny (1979) and Piotrkiewicz *et al* (2004) indicating that Renshaw cells have minor influence at low

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force levels and an even lower influence at higher forces. These findings are supported by modelling studies by Shoemaker and Hannaford (1994) and Maltenfort *et al* (1998), which describe the gain of Renshaw cells as being negligible during constant force isometric contractions. It is also known that when the proprioceptive feedback from GTOs and spindles is blocked, the firing rate of motoneurons decreases (Macefield *et al* 1993). That finding infers that excitatory inputs from spindles have a stronger influence on motoneuron pool than inhibitory inputs from GTOs. If so, it is reasonable to hypothesize that the number of spindles present in a muscle would influence the motor unit firing rates. Consequently, we undertook to review the literature and explore if a relationship exists between the firing rates and the recruitment threshold range of motor units, with the number of spindles in a muscle.

2. Methods

2.1. Data collection

We searched the literature with two online journal search engines: Google Scholar and PubMed. The following keywords were used along with each muscle name: firing rate, recruitment, motor unit, isometric contraction, number of muscle spindles, muscle weight and human muscle. The keywords were combined in different sequences to retrieve the maximal number of sources. The publication dates of the over 500 found articles ranged from 1884 to 2008. From these, 79 studies that satisfied the following criteria were considered for data mining:

- Studies were published in peer-reviewed publications, with the exception of the muscle weight data from Theile (1884).
- Experiments were performed on healthy humans with no reported history of neurological disorders.
- Recording methods used to obtain the data were reported.
- Number, gender and age of subjects studied were provided.
- All electromyographic (EMG) data were collected from subjects less than 65 years of age.
- Data were collected from individual muscles.
- Number of observations made to determine the data values were reported. If the data were reported as an average of multiple observations, the standard deviation or standard error was provided.
- Motor unit firing rate data were acquired from EMG signals during non-fatiguing, targeted constant-force (or force plateau), isometric contractions.
- Motor unit recruitment data were acquired from EMG signals during non-fatiguing, isometric contractions ranging from 0% to 100% MVC level.

The following information from studies meeting the inclusion criteria were tabulated: authors, number of subjects, methods, muscle, contraction level and the standard deviation and number of observations of each parameter value. These tables were compiled for the following parameters: muscle weight, number of muscle spindles, motor unit firing rate, percentage of motor unit recruitment and maximum recruitment threshold.

Parameters for individual muscles were provided by multiple reports. The muscle weight was determined from the average value of dissected muscles from several human cadavers as outlined by Theile (1884). The number of spindles in a muscle was determined by microscopically counting each spindle from muscle slices (Cooper and Daniel 1949, Voss 1937, among others). Motor unit firing rate data were reported from constant-force isometric contractions at different force levels. The various studies reported the mean firing rate of each motor unit observed during the constant-force region of each contraction for each subject. Representative values of the firing rate at a specified force level from each report were obtained by averaging the reported individual mean firing rate values across all motor units and subjects in each report. Following the work of De Luca and Hostage (2010), this metric was selected because the averaged mean firing rate indicates the level of excitation received by the motoneuron pool and specifies the operating point of all active motor unit firing rates. These firing rate values were grouped into one of the following five force ranges: 1%–10% MVC, 20%–30% MVC, 40%–60% MVC, 70%–80% MVC, 100% MVC. These groupings were used because contractions studied in the literature were most frequently within these force ranges.

The distribution of motor unit recruitment across the entire range of contraction forces was obtained for different muscles from various reports. The specific methods used for different muscles are detailed by Kukulka and Clamann (1981), Duchateau and Hainaut (1990), Feiereisen *et al* (1997), among others. These histograms indicated the number or percentage of motor units recruited up to a certain force level. They were typically obtained from slow linearly varying isometric ramp contractions reaching 100% MVC. We grouped the percentage of recruited motor units in the following four force levels: 10% MVC, 25% MVC, 50% MVC and 75% MVC. The maximum recruitment threshold corresponds to the maximum force level beyond which no further motor unit recruitment occurred in the reported study.

2.2. Meta-analysis protocol

Each parameter was plotted as a function of the number of muscle spindles for all the muscles for which data were found in the literature. One example of more than 50 plots generated is shown in figure 1 which presents the motor unit firing rates at 100% MVC, plotted as a function of the number of spindles in different muscles. Each point plotted represents data from two independent sources. The size of the data points relates to the magnitude of a common weighting factor ($w_{x,y}$) assigned to that point. Because the data were mined from studies that were performed with varying number of subjects and contractions, the data for different muscles provided varying degrees of significance. In meta-analysis studies, this disparity is mitigated by assigning a singular weighting factor to both the independent (w_x) and dependent (w_y) variable on the x and y axes.

The singular weighting factor (w_x or w_y) was calculated as the inverse of the quotient of the coefficient of variation

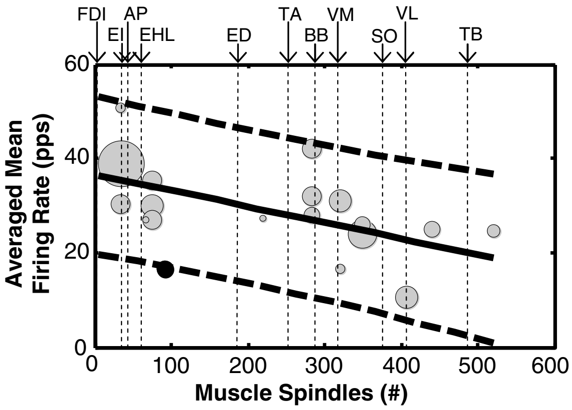

Figure 1. Example of the motor unit firing rates plotted against the number of spindles across muscles. Each data point represents an average of all mean motor unit firing rates reported in a single peer-reviewed reference for a muscle with a specified number of muscle spindles. Circle size indicates the magnitude of the weighting factor of that data point (see text for details). Muscles with data included in the plot are listed at the top of the plot and extended with dashed lines to the corresponding number of spindles on the horizontal axis. They are: FDI—first dorsal interosseous; EI–extensor indicis; AP–adductor pollicis; EHL—extensor hallucis longus; ED—extensor digitorum; TA—tibialis anterior; BB—biceps brachii; VM—vastus medialis; SO—soleus; VL—vastus lateralis; TB—triceps brachii. Confidence intervals of two standard deviations (95.45%) are illustrated by bolder, non-vertical dashed lines. Data points outside of the confidence intervals were marked as outliers (indicated by the black circle) and excluded from further analysis.

divided by the number of observations reported with each datum value. The coefficient of variation was used in place of the standard deviation to account for the presence of larger standard deviations with measurements of greater magnitude. In some studies, data were reported with a standard deviation of zero. In such cases it was assumed that a standard deviation could have been measured, but was rounded down to zero. In those cases we assigned a value of 0.49, the lowest two-significant figure value that would be rounded-off to zero. Other reported data values were measured from only one observation and did not have a standard deviation. In such cases, a singular weighting factor could not be assigned. These values were either excluded from the study, or kept if all data values in a category were obtained from one observation. For the number of muscle spindles parameter, all data in the set were considered singletons and singular weighting factors were not assigned to any of those data values.

The common weighting factor ($w_{x,y}$) of each point in a plot was calculated from the x-axis data set singular weighting factor (w_x) and y-axis data set singular weighting factor (w_y) as

$$w_{x,y} = \left(w_x^{-2} + w_y^{-2}\right)^{-1/2}.$$

If the data set plotted on the x-axis (independent variable) did not have an assigned singular weighting factor (w_x) due to the previously described statistical limitations, the final common weighting factor ($w_{x,y}$) of each datum point in the plot was set equal to the singular weighting factor of w_y. If neither variable had an assigned singular weighting factor, a unity common weighting factor ($w_{x,y} = 1$) was assigned to all data points in the plot. The final common weight of each datum point was normalized to the mean common weighting factor of the data set and then plotted.

A weighted linear regression was performed on the weighted data points. Confidence intervals were calculated at two standard deviations (95.45%) about the regression line as illustrated by the dashed lines in figure 1. Data points outside the confidence intervals were excluded from further consideration. An example of excluded data is shown as a black datum point in figure 1. This method of exclusion prevented outlier data from extraneous literature reports from influencing the grouped data. A final weighted linear regression was performed on the remaining data points. The parameters of the second regression analysis (not shown in figure 1) are reported in section 3 and were used for further analysis.

3. Results

Data for the parameters used in this study are listed in table 1. A total of 26 muscles are included. The sources from which the data were obtained are listed in the appendix.

3.1. Firing rate ($\hat{\lambda}_{\text{avg}}$)

Figure 2 presents the firing rate values at each of the five force levels as functions of the number of spindles across different muscles. The linear regression lines were calculated as discussed in section 2. Excluding figure 2(d), the R^2 values did not exceed 0.5. Such values are not uncommon for meta-analysis studies due to the unknown, but likely considerable, variability that exists across studies performed using different methods on different subjects by different researchers. According to Rosenthal and Rosnow (1991), low R^2 values in a meta-analysis do not limit the validity of the correlations and relationships portrayed by the data. In the plots, an inverse relationship between the firing rate and the number of spindles was progressively more evident with increasing force levels. With the singular exception of the lowest force level, the regressions demonstrated that muscles containing more spindles had lower firing rates than muscles with fewer spindles.

The regression lines from all force ranges studied were plotted together in figure 2(f) where a progression of the slope of the regression lines can be seen clearly. The regression lines were plotted with a solid line over the region for which spindle data were available from the literature. The dotted extensions of the regression lines are included to visually indicate the complete pattern of the behaviour of the firing rates as a function of number of spindles in the muscles. It is apparent that the behaviour of the regression lines in figure 2(f) changes with force level. Therefore, the firing rate of motor units in a muscle is a function of both the number of muscle spindles in that muscle and the force level of isometric contraction. It can be modelled according to the following equation:

$$\hat{\lambda}_{\text{avg}}(\varphi, s) = m(\varphi)s + b(\varphi), \tag{1}$$

Table 1. Summary of all data collected in the meta-analysis performed in this study. The abbreviations refer to the following muscles: masseter (MA), orbicularis oculi (OO), lateral pterygoid (LP), platysma (Plat), trapezius (Trap), abductor digiti minimi (ADM), abductor pollicis brevis (APB), adductor pollicis (AP), anconeus (Anc), biceps brachii (BB), brachioradialis (BR), deltoid (DE), extensor carpi radialis (ECR), extensor carpi ulnaris (ECU), extensor digitorum (ED), extensor indicis (EI), flexor carpi radialis (FCR), first dorsal interosseous (FDI), triceps brachii (TB), extensor hallucis longus (EHL), gastrocnemius (GA), rectus femoris (RF), soleus (SO), tibialis anterior (TA), vastus lateralis (VL), vastus medialis (VM). Each number in parentheses refers to the source reference listed in the appendix from which the data were obtained.

Muscle	Number of muscle spindles	Weight (g)	Averaged firing rate (pps)					Max REC threshold (% MVC)	Percentage of MU recruitment (%)			
			<10% MVC	20%–30% MVC	40%–60% MVC	70%–80% MVC	100% MVC		<10% MVC	20%–30% MVC	40%–60% MVC	70%–80% MVC
MA	114 (40)	27.4 (69)						35 (58)	52 (58)	97 (58)	100 (58)	100 (58)
	160 (27)											
OO		4 (69)		18.3 (13)								
LP	6 (40)	8.3	7.4 (54)	17.8 (54)								
				14.8 (3)								
Plat		12.8 (69)			28.6 (13)							
Trap	437 (75)	201.2 (69)	11.2 (77)	17.8 (78)								
			12.9 (79)	17.2 (22)								
			14.7 (78)									
ADM		8.6 (69)	11.9 (67)	13.2 (67)	16.4 (67)	17.4 (67)	20.3 (67)	90 (68)	32 (68)	49 (68)	67 (68)	91 (68)
APB	80 (57)	6.3 (69)						69 (70)	25 (70)	75 (70)	98 (70)	100 (70)
AP	75 (57)	5.5 (69)					29.9 (4)	30 (19)	75 (19)	98 (19)	100 (19)	100 (19)
							26.9 (6)	50 (42)	41 (42)	86 (42)	100 (42)	100 (42)
							35.4 (6)					
Anc		11.2 (69)	10.3 (43)	10.5 (43)								
BB	320 (39)	163.9 (69)	11.4 (12)	9.8 (33)	10.8 (32)	14.3 (32)	16.5 (32)	90 (42)	6 (42)	47 (42)	80 (42)	96 (42)
			13 (65)	18 (60)	20.8 (60)	26.2 (60)	31.1 (4)					
				16 (46)	21.6 (60)							
BR	70 (76)	67.4 (69)		18.3 (46)								
				19.1 (8)								
DE	182 (37)	355.7 (69)		14 (18)								
ECR	74 (76)	44.3 (69)	9.6 (66)	12.6 (14)	21 (15)							
ECU	157 (76)	25.3 (69)		15.2 (14)	23 (15)							
ED	219 (76)	42.8 (69)					27.4 (50)					
EI	68 (76)	7.1 (69)					27.1 (50)					
FCR	129 (76)	28.8 (69)		12 (64)	19 (64)							
FDI	34 (63)	9.3 (69)	10.4 (61)	18.3 (20)	19.4 (60)	32.3 (15)	29.3 (28)	35 (19)	65 (19)	92 (19)	100 (19)	100 (19)
			10.2 (62)	13.5 (38)	26.1 (20)	31.1 (60)	30.4 (7)	78 (71)	42 (71)	79 (71)	93 (71)	98 (71)
			13.2 (78)	16.7 (60)	21.4 (9)		50.9 (36)	52 (17)				
				16.1 (78)	20.9 (15)		39 (59)	60 (36)				
				18.7 (1)	24.3 (36)			67 (16)				
				17.6 (15)	20.6 (45)							
					25.7 (60)							
					18.7 (72)		24.6 (72)					
TB	520 (39)	346.4 (69)	10.9 (43)	11.1 (29)								
				10.7 (31)								
				15.3 (43)								
EHL	92 (74)	30.6 (69)					16.7 (44)					
GA	156 (74)	390.2 (69)	9.7 (53)	12.1 (53)								
RF	232 (76)	254.9 (69)	10.2 (49)	12.1 (49)								
				11.9 (48)								
SO	408 (74)	402.3 (69)		7.4 (41)	10.6 (41)		10.7 (4)					
TA	284 (74)	133.7 (69)	11.5 (53)	16.1 (11)	16.2 (21)	21.8 (5)	32.1 (5)	90 (26)	39 (26)	63 (26)	89 (26)	98 (26)
			12.2 (11)	12.7 (24)	16.7 (5)	28 (11)	41.9 (11)	70 (21)				100 (21)
			12.7 (73)	11.3 (23)	15.5 (10)	31.3 (15)	28.1 (55)	90 (16)				
			10.2 (25)	14.7 (53)	22 (11)	23.8 (21)						
				14 (73)	15.7 (13)							
				15.6 (15)	19.1 (15)							
					21.4 (21)							
					16.3 (73)							
VL	440 (76)	607.3 (69)	8.7 (30)	9.1 (2)	18.5 (34)	20.8 (34)	25 (34)	95 (16)				
				15.7 (34)	12.6 (35)	16.4 (35)						
				10.1 (35)	14.1 (47)							
					16 (56)							
VM	350 (76)	427.5 (69)	8.8 (52)	10.5 (52)	14 (52)	18.5 (52)	23.8 (51)					
							26 (52)					

where $\hat{\lambda}_{\text{avg}}$ is the firing rate in pps, s is the number of muscle spindles in a muscle: $34 \leqslant s \leqslant 440$ and φ is the normalized MVC force: $0 < \varphi < 1$.

The slope, $m(\varphi)$, from figure 2(f) was plotted as a function of normalized contraction force in figure 2(h). This force level was determined as an average of all force levels from each data point in one plot (e.g. figure 2(a)). The standard error obtained from the slope of each regression line in figure 2(f) is indicated by the vertical lines in figure 2(h). The slope increases in a linear fashion as a function of contraction force, and may be described as

$$m(\varphi) = A\varphi + B. \tag{2}$$

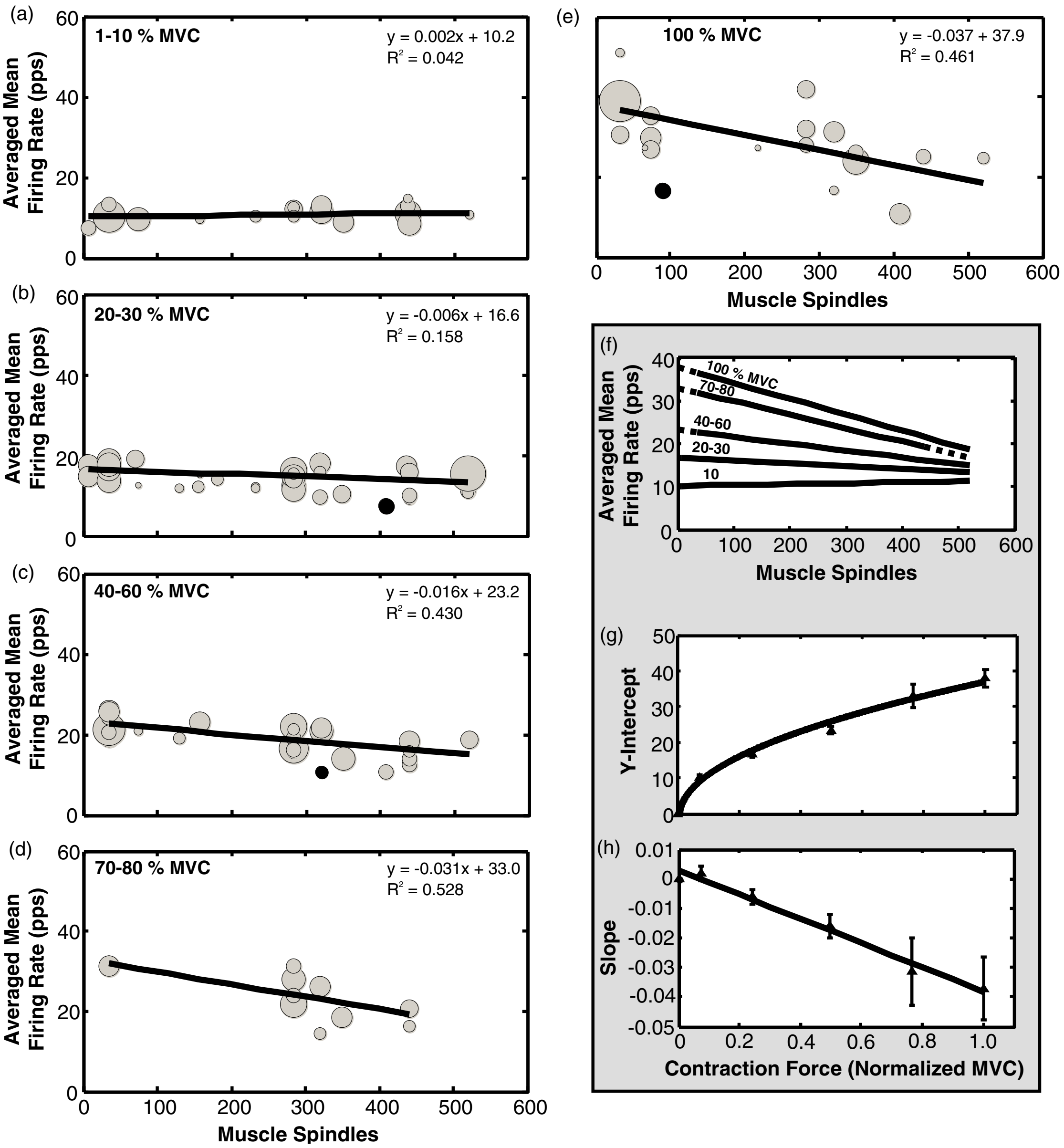

Figure 2. Motor unit firing rates plotted as a function of the number of spindles across muscles. (a–e) Plots of the firing rate versus the number of spindles at each of five different force levels are presented. Circle size indicates the data point weight; black circles represent outliers excluded from the analysis. The force level, regression equation and R^2 values are indicated on each plot. Note that each plot has data points for different muscles, depending on the data that could be mined from the literature. (f) The regression lines for the various force ranges are grouped together. The dashed continuations of some of the lines represent regions where no data were available. (g, h) The slope and y-intercept of each regression line plotted as functions of normalized isometric contraction force. Vertical bars indicate the value of ± standard error. Regression statistics are described in the text and listed in table 2.

Table 2. Regression statistics of the y-intercept-force and slope-force regressions in figure 2 and equation (4) as well as those in figure 4 and equation (9).

Averaged firing rate and recruitment regression statistics						
$A = -0.041 \pm 0.004$	$B = 0.003 \pm 0.002$	$C = 37 \pm 2.8$	$D = -0.60 \pm 1.8$	$E = 0.13 \pm 0.005$	$F = 0.17 \pm 0.008$	$G = 9.8 \pm 0.9$

The MATLAB Curve Fitting Toolbox was used to obtain the values of the parameters A and B. The values which provided the best fit are presented in table 2. The R^2 value for the fit was 0.981.

The intercepts of the regression lines in figure 2(f) were also plotted as a function of normalized contraction force in figure 2(g). The intercepts increase as a function of the square root of the force, and may be described as

$$b(\varphi) = C(\varphi)^{1/2} + D. \tag{3}$$

The values of C and D were obtained with the MATLAB Curve Fitting Toolbox and are presented in table 2. The R^2 value for the fit is 0.989.

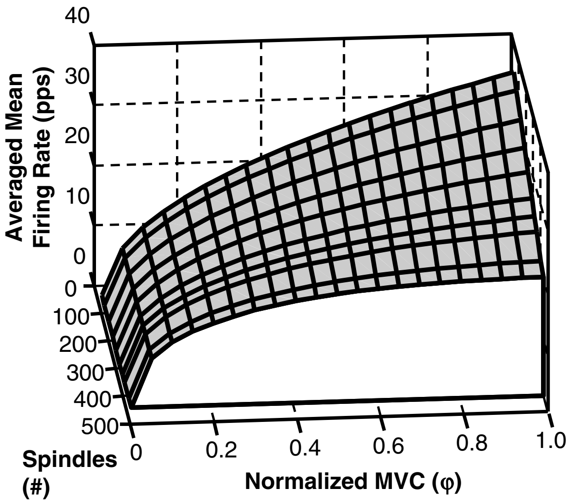

Figure 3. Firing rates of motor units as a function of the number of spindles in a muscle and the normalized contraction force level. Data plotted comes from the model of motor unit firing rates in equation (5). The resolution of forces plotted is 0.05 normalized MVC.

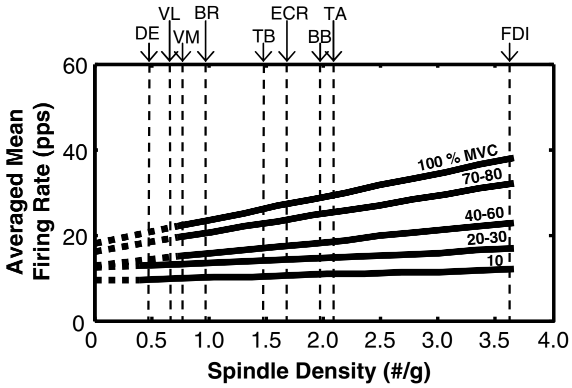

Figure 4. Firing rates of motor units plotted against the spindle density. The force range of each regression line is shown on the plot. Muscles included in the plot are illustrated by vertically dashed lines and denoted by abbreviations listed above the plot. They are: DE—deltoid; VL—vastus lateralis; VM—vastus medialis; BR—brachioradialis; TB—triceps brachii; ECR—extensor carpi radialis; BB—biceps brachii; TA—tibialis anterior; FDI—first dorsal interosseous. The dashed extensions of some regression lines indicate regions where no data were available from the literature.

By substituting equations (2) and (3) into equation (1) we obtain the following equation that describes the relationship for the motor unit firing rate as a function of the number of muscle spindles and normalized isometric contraction force:

$$\hat{\lambda}_{\mathrm{avg}}(\varphi, s) = (A\varphi + B)s + C(\varphi)^{1/2} + D. \tag{4}$$

When the parameter values from table 2 are replaced, the equation reduces to

$$\hat{\lambda}_{\mathrm{avg}}(\varphi, s) = (-0.041\varphi + 0.003)s + 37(\varphi)^{1/2} - 0.60. \tag{5}$$

This equation predicts the firing rate of motor units in a muscle as a function of the isometric contraction force level, and the number of muscle spindles in that same muscle. Note that the equation is not precise because it is derived from a meta-analysis. For example, it fails at $\varphi = 0$, where it predicts -0.5 pps for $s = 34$ (the FDI muscle) and 0.76 pps for $s = 440$ (the VL muscle). Nonetheless, it does provide a description of the relationship between the firing rate and the number of muscle spindles in the muscles.

Equation (5) was used to compute the approximate firing rate data for muscles with different numbers of spindles across all levels of contraction force. The resulting distribution is shown in figure 3. The lowest computed firing rate is limited by the 5% MVC incremental resolution of the force data available from the literature. Ten muscles were used to generate the surface in figure 3. These are: the first dorsal interosseous (FDI) with 34 spindles, the adductor pollicis (AP) with 75 spindles, the flexor carpi radialis (FCR) with 129 spindles, the deltoid (DE) with 182 spindles, the rectus femoris (RF) with 232 spindles, the tibialis anterior (TA) with 284 spindles, the biceps brachii (BB) with 320 spindles, the vastus medialis (VM) with 350 spindles, the soleus (SO) with 408 spindles and the vastus lateralis (VL) with 440 spindles.

The distributions of firing rates of three of these muscles, the FDI, TA and VL, have been studied by De Luca and Hostage (2010). While the absolute values of the firing rates extracted from their plots differ slightly from those shown in figure 3, their relative values demonstrate consistent behaviour with the data herein. At low forces, all muscles, independent of the number of spindles, demonstrate the greatest increment in firing rate. At greater force levels, muscles having a relatively low number of muscle spindles, such as the FDI, have large increments in firing rates, with diminishing but still substantial increments at greater force levels (figure 3). In contrast, muscles with a relatively larger number of spindles, such as the VL, maintain consistently smaller firing rate increments as shown by the diminishing slope of the firing rate distribution in figure 3.

A similar regression analysis was performed for the firing rate as a function of spindle density. Figure 4 shows the summary of five regression lines, each representing the previously specified force ranges. Note that the domain of spindle density plotted was limited to 0–4 spindles per gram. Data lying beyond this range were not available for all force levels studied.

3.2. *Motor unit recruitment*

Figure 5 presents the percentage of motor units in a muscle reported to be recruited at each of the four force levels analysed as functions of the number of spindles present in the muscle. A weighted linear regression analysis was performed on each data set. The regression lines for the different force levels are plotted together in figure 5(e). As in the previous figures, the dotted extension of the regression lines are included to visually indicate the complete pattern of the behaviour of the percentage of recruited motor units as a function of number of spindles in the muscles. As the number of spindles in a muscle increases, the percentage of recruited motor units at a specific force level decreases, and the slope decreases with increasing force levels. At the highest force level considered (75% MVC), where most motor units in some muscles and

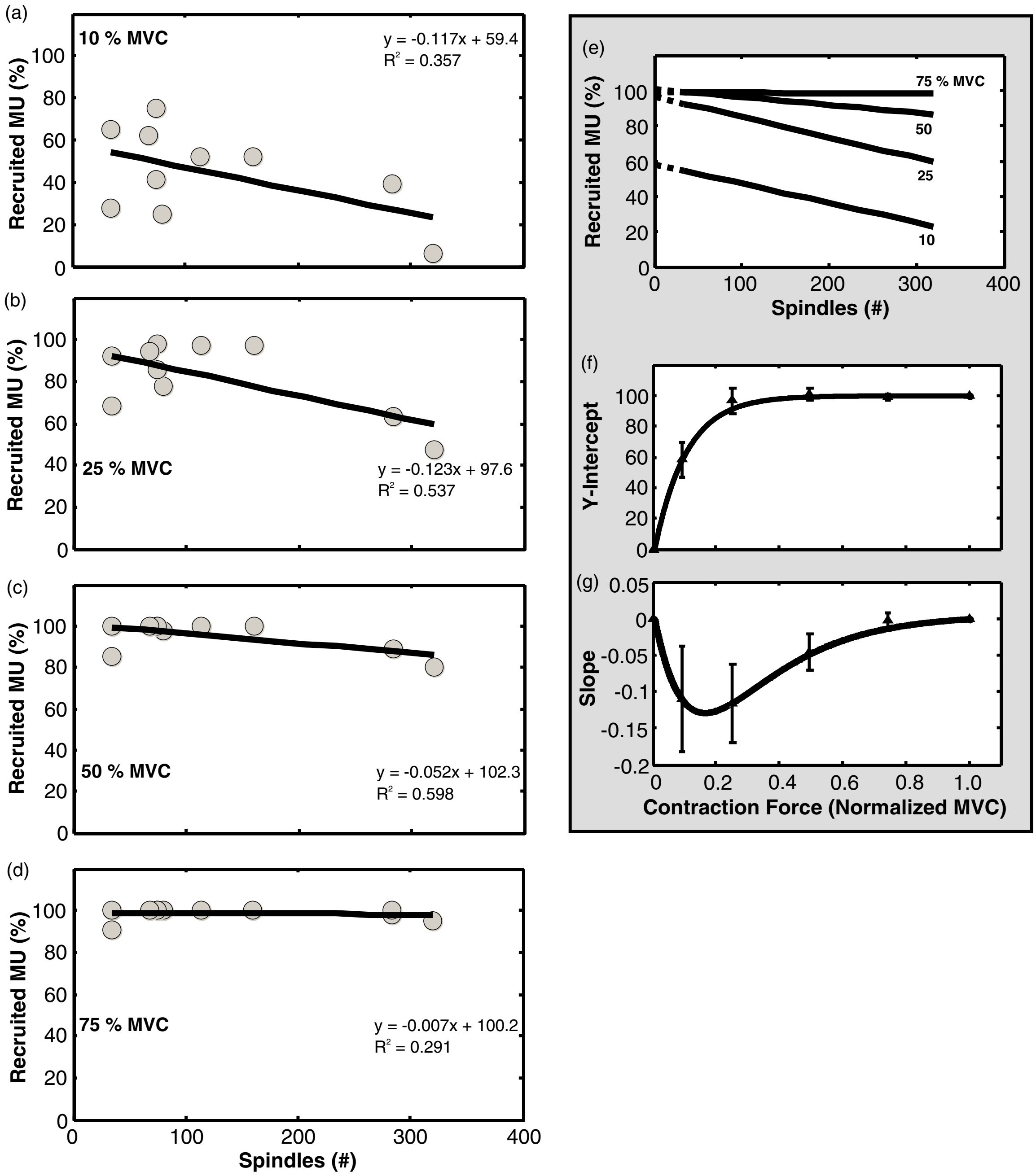

Figure 5. Percentage of motor units recruited plotted as a function of the number of spindles across muscles. (a–d) Plots for the motor unit recruitment versus the number of spindles at each of four different force levels are presented. Circle size indicates the data point weight; black circles represent outliers excluded from the analysis. The force level, regression equation and R^2 value are indicated on each plot. Note that some plots have data points for different muscles, depending on the data that could be mined from the literature. (e) Regression lines are grouped together with each force level indicated. (f, g) The slope and y-intercept of each line were plotted as functions of isometric contraction force. Error bars indicate value ± standard error. Regression statistics are described in the text and shown in table 2.

all the motor units in other muscles have been recruited, the slopes of regression lines decrease and approach zero.

Consequently, the percentage of motor units recruited in a muscle during a given isometric contraction is a function of both the number of muscle spindles in that muscle and the force level of contraction. The relationship may be modelled according to the following equation:

$$\%\mathrm{MU}(s, \varphi) = m(\varphi)s + b(\varphi) \qquad (6)$$

where %MU is the percentage of motor units recruited, s is the number of muscle spindles in a muscle: $34 \leqslant s \leqslant 320$ and φ is the normalized MVC force: $0 < \varphi < 1$.

The slope, $m(\varphi)$, from figure 5(e) was plotted as a function of normalized contraction force in figure 5(g). In a manner similar to that used in the firing rate data, the force level was determined as an average of all force levels from each data point in one plot (e.g. figure 5(a)). The standard error obtained from the slope of each regression line in figure 5(e) is

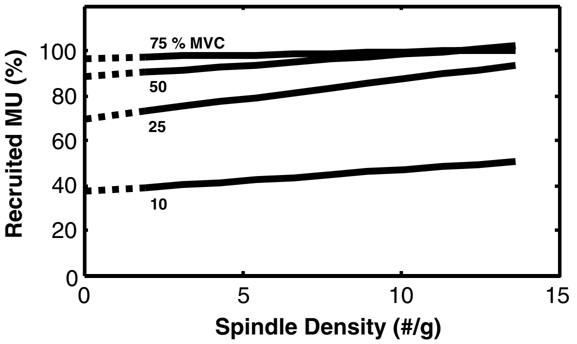

Figure 6. Percentage of motor units recruited plotted against the spindle density. The force level of each regression is indicated on the plot. The dashed extensions of some regression lines indicate regions where no data were available from the literature.

indicated by the vertical lines in figure 5(g). The slope may be approximated by exponential functions of the following form:

$$m(\varphi) = E\varphi/F\left(\mathrm{e}^{(1-1/F)} - \mathrm{e}^{(1-\varphi/F)}\right). \tag{7}$$

The MATLAB Curve Fitting Toolbox was used to obtain the values of the parameters E and F. The values which provided the best fit are presented in table 2. The R^2 value for the fit was 0.994.

The intercepts of the regression lines in figure 5(e) were also plotted as a function of normalized contraction force in figure 5(f). The intercept also varies as an exponential function of the contraction force, and may be described as

$$b(\varphi) = 100(1 - \mathrm{e}^{-G\varphi})\big/(1 - \mathrm{e}^{-G}). \tag{8}$$

The value of G is listed in table 2. The R^2 value for the fit was 0.995.

By substituting equations (7) and (8) into equation (6) we obtain the following equation that describes the relationship for the percentage of motor units recruited as a function of the number of muscle spindles and normalized isometric contraction force:

$$\begin{aligned}\%\mathrm{MU}(s,\varphi) &= E\varphi s/F\left(\mathrm{e}^{(1-1/F)} - \mathrm{e}^{(1-\varphi/F)}\right)\\ &\quad + 100(1-\mathrm{e}^{-G\varphi})/(1-\mathrm{e}^{-G}).\end{aligned} \tag{9}$$

When the average parameter values from table 2 are replaced, the equation reduces to

$$\%\mathrm{MU}(s,\varphi) = 0.0058s\varphi(1-360\mathrm{e}^{-5.9\varphi})+100(1-\mathrm{e}^{-9.8\varphi}). \tag{10}$$

This equation predicts the approximate percentage of the total number of motor units recruited in a muscle as functions of the isometric contraction force level and the number of muscle spindles in that same muscle.

The percentage of motor units in a muscle that is recruited at each of the four force levels was also examined as a function of spindle density. The plot in figure 6 shows a reverse relationship to that obtained with the number of spindles.

3.3. *Maximum recruitment threshold ($\tau_{\max}$)*

Plots of the maximum recruitment threshold versus the number of spindles and spindle density are shown in figure 7. Weighted linear regressions were determined for each data set. Both plots have low R^2 values due to the high variability of the available data. The regressions indicate that the maximum recruitment threshold is directly related to the number of spindles in a muscle (figure 7(a)) and is inversely related to the muscle spindle density (figure 7(b)). Using figure 6(a), the maximum recruitment threshold was defined as a function of the number of spindles in a muscle by the following equation.

$$\tau_{\max} = 46 + 0.11s, \tag{11}$$

where $\tau_{\max}$ is the maximum motor unit recruitment threshold and s is the number of muscle spindles $34 \leqslant s \leqslant 440$.

The relationships between the firing rate and the maximum recruitment threshold of 22 different muscles, for which these parameter values were available, and the number of spindles and spindle density are shown collectively in figure 8. The bar plot (figure 8(a)) indicates the spindle density versus the number of spindles. The vertical dashed lines indicate the location of the individual muscles along the spindle spectrum. Figures 8(b) and (c) present the firing rates and the maximum recruitment threshold, respectively. Muscles like the FDI, which have fewer spindles and greater spindle density, have higher motor unit firing rates and lower maximum recruitment threshold. Muscles like the BB, with more spindles and less spindle density, have lower motor unit firing rates and a higher maximum recruitment threshold.

3.4. *Density of motor unit recruitment as a function of number of spindles*

Given equation (10), the incremental percentage of motor units recruited at any force level as a function of muscle spindles may be predicted. Figure 9 presents a graph of the relationship. In this figure, the trajectories are bounded by the maximal recruitment threshold presented in figure 7(a). In figure 9 the lowest force threshold of motor unit recruitment is limited by the 5% MVC resolution of contraction forces available from the literature.

The same ten muscles used to present the firing rate distribution in figure 3 were also used to generate the surface relating density of motor unit recruitment with the number of muscle spindles and isometric force level. The densities for four of these muscles, the FDI, AP, BB and TA, have been obtained empirically by Duchateau and Hainaut (1990), Kukulka and Clamann (1981) and Feiereisen *et al* (1997). Their recruitment histogram (density functions) are comparable to our calculated data for the same four muscles in figure 9 and provide an indication that equation (10) is reasonably valid, given the limitations of the scattered data sources. The progression of recruitment densities relative to increasing number of spindles in muscles shown in figure 9 is useful for illustrating the change in the density function. (Note that a more accurate representation would require a set of empirical data obtained under uniform conditions.)

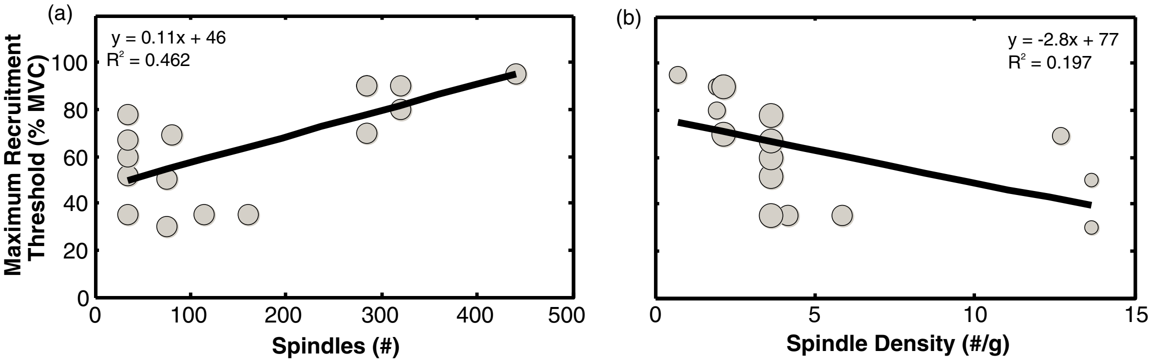

Figure 7. Regression analysis of the maximum recruitment threshold as a function of: (a) the number of muscle spindles, and (b) spindle density. Circle size indicates the data point weight; filled circles represent outliers excluded from the analysis. The regression equation and R^2 value are indicated on each plot.

It may be seen in figure 9 that muscles having a relatively low number of muscle spindles, such as the FDI and the AP, have a recruitment threshold density function that may be approximated by an exponential; meaning that the largest increment of motor units is recruited at the lower (near zero) force threshold, with diminishing increments recruited at increasingly greater thresholds as shown by Freund *et al* (1975) and Duchateau and Hainaut (1990). Such muscles also have a maximum recruitment threshold of about 50% to 60% MVC (Kukulka and Clamann 1981, De Luca *et al* 1982a, De Luca and Hostage 2010). In contrast, muscles with relatively large number of spindles, such as the soleus and VL, have a recruitment threshold density function that peaks at approximately 25% MVC, with decreasing increments on either side, which are similar to the empirical data presented by Kukulka and Clamann (1981). These muscles also have a maximum recruitment threshold up to 95% MVC as seen in both the predicted values in figure 9 and the empirical observations by De Luca and Hostage (2010).

4. Discussion

Meta-analysis studies have an inherent limitation due to the lack of control over the homogeneity of the source and quality of the data. It is therefore impressive to find substantial correlations with acceptable R^2 values among separately measured parameters. The reasonable R^2 values and the orderly progression of the regression lines suggest that a relationship exists between the regressed variables and the number of spindles across muscles. These orderly relationships are a gratifying outcome of data points which are obtained from different sources. The noise in the data due to the diversity of the sources would tend to obscure relationships among parameters. The fact that the regressions of the data are not obliterated by the noise is an indication that the relationships are sound and may be taken as representing physiological relationships.

The dominant finding of the study is the indication of relationships between muscle spindle feedback, contraction force, motor unit firing rates and recruitment. Specifically, muscles with fewer spindles exhibit higher firing rates and lower recruitment threshold range. In muscles with more spindles, motor units have lower firing rates and a greater recruitment threshold range. These observations are summarized in figure 8.

In contrast, the relationship between spindle density, firing rate and recruitment threshold range was generally, but not consistently, the opposite of that found with the number of spindles in individual muscles. This is likely due to the fact that larger muscles, which have a greater number of motor units, also have a smaller spindle density. Figure 8(a) shows this trend, with the apparent exception of the FDI and the lateral pterygoid muscles. Even though larger muscles have a greater number of spindles, they have a proportionally larger mass that does not necessarily bear a progressive relationship to the number of spindles. Thus, the spindle density does not constitute a reliable independent variable for the spindle feedback. This point is accentuated by the relationship between the FDI muscle and the AP muscle. The FDI has a relatively low spindle density compared to the AP muscle, but still possesses a greater firing rate value and lower maximal recruitment threshold value. Consequently, the spindle number provides a better association with the motor unit control parameters.

Although, it is beyond the ability of a meta-analysis to establish causal relationships, the consistency of the correlations, across a diverse range of muscles, of the firing rates and recruitment threshold ranges with the degree of spindle involvement provides a reasonable basis for suggesting the existence of a mechanism for their interaction. An insight into the behaviour of firing rates and mechanisms associated with the recruitment of motor units has been provided by the work of Broman *et al* (1985) and of Westgaard and De Luca (2001). Both studies found that when a motor unit was recruited during slow varying isometric contractions, the firing rates of previously active motor units decreased. The observation was more apparent when the rate of force increase was relatively slow ($<1\%$ MVC s^{-1}). They suggested that this phenomenon could result from the influence of the feedback from the GTOs and muscle spindles.

When the primary and secondary endings in the muscle spindles are stretched they provide an excitatory (positive) feedback, via the type Ia and type II fibres, to virtually all of the motoneurons in the homonymous motoneuron pool

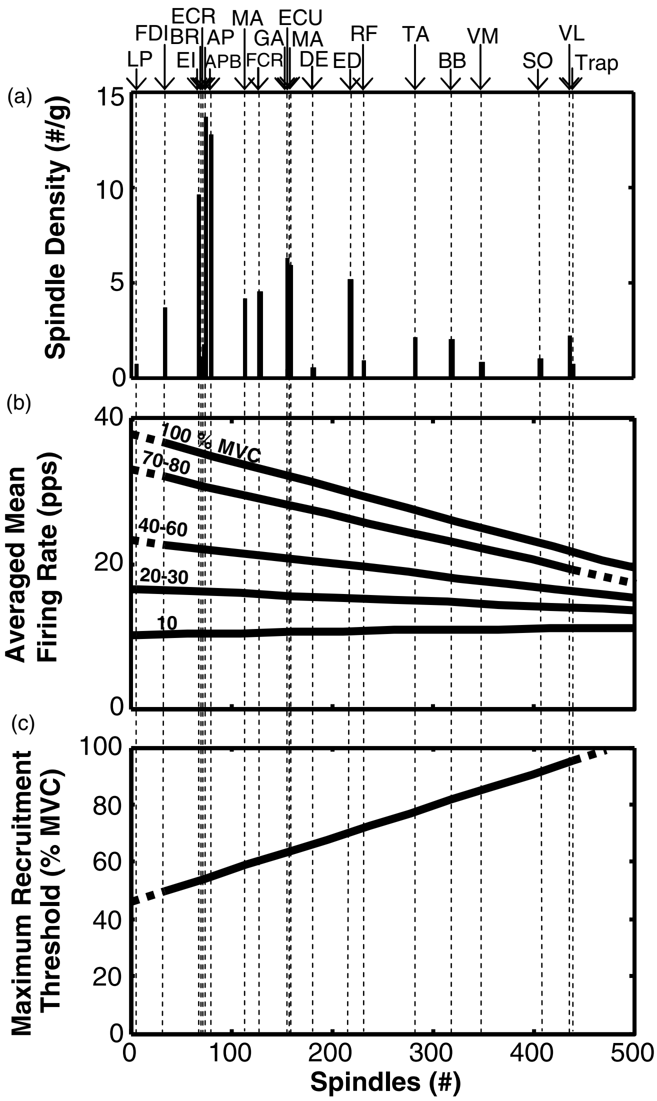

Figure 8. Muscle spindle density, firing rate, and maximum recruitment threshold plotted against the number of spindles in a muscle. (a) The bar plot includes spindle data from each of 20 human muscles, which are indicated by arrows above the bar plot. The abbreviations refer to the following muscles: LP—lateral pterygoid; FDI—first dorsal interosseous; EI—extensor indicis; BR—brachioradialis; ECR—extensor carpi radialis; AP—adductor pollicis; APB—abductor pollicis brevis; MA—masseter; FCR—flexor carpi radialis; GA—gastrocnemius; ECU—extensor carpi ulnaris; DE—deltoid; ED—extensor digitorum; RF—rectus femoris; TA—tibialis anterior; BB—biceps brachii; VM—vastus medialis; SO—soleus; VL—vastus lateralis; Trap—trapezius. (b) Firing rate and (c) maximum recruitment threshold plots were taken from the data in figures 2(f) and 8(a), respectively. Vertical dashed lines are superimposed to show the observed motor unit firing rates and maximum recruitment threshold of the motor units of several muscles in the bar plot.

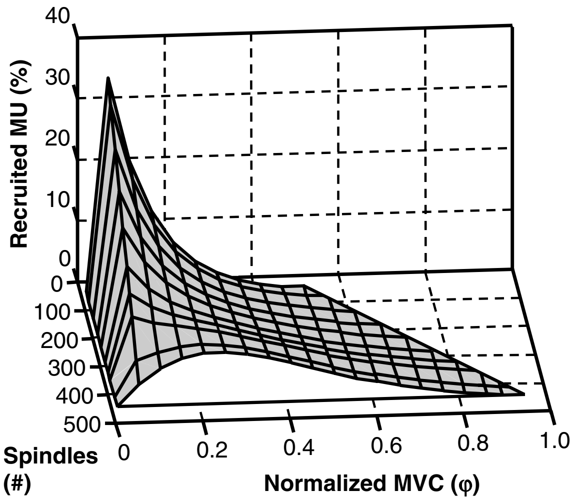

Figure 9. Motor unit recruitment density as a function of the number of spindles in a muscle and the normalized contraction force level. Data plotted come from the model of motor unit recruitment in equation (10) and adjusted for noise by the regression equation of maximal recruitment threshold in figure 6(a). The resolution of forces plotted is 0.05 normalized MVC.

(Mendell and Henneman 1971, Scott and Mendell 1976, Watt *et al* 1976, among others). It is also known that when the GTOs are stretched they provide a disynaptic non-reciprocal inhibition (negative) feedback, via type Ib fibres, to the homonymous motoneurons. It has been shown by Binder *et al* (1977) and verified by Edin and Vallbo (1990) that the Ib fibres respond to tension generated by individual motor units. We cannot estimate the relative contribution of the GTOs to the proprioceptive negative feedback because virtually no information is available on their performance in humans. However, it is known from the work of Gandevia *et al* (1990) and Macefield *et al* (1993) that the disynaptic feedback path of the Ib fibres from the GTOs is less effective than the monosynaptic path of the Ia fibres from the spindles. For these reasons and because reports of spindle counts are readily available for many muscles, we will continue the discussion by expressing the influence of the proprioceptive feedback as a function of the number of spindles in a muscle.

There are several other aspects of the spindle mechanism that might influence the excitation to the motoneuron pool, but they also are not well understood. For example, the involvement of the type II spindle afferents is also uncertain. While type II spindle afferents connect to motoneurons in a yet unclassified array of mono-, di- and polysynaptic connections, and could have disparate influence on the motoneuron pool, studies by Stauffer *et al* (1976) and Munson *et al* (1982) suggest that their inputs elicit effects consistent with those of primary spindle afferents. Other inputs such as those from presynaptic inhibition of spindle afferents are also present within a motoneuron pool, but according to Hultborn *et al* (1987) and Pierrot-Deseilligny (1997) they are weak amongst motoneurons of active muscles; only having a strong effect on the synapses of motoneurons of surrounding inactive muscles. Heteronymous primary spindle afferent input to the contracting muscle may also be influential. Increases in spindle feedback tend to be excitatory when originating from synergists and inhibitory when from antagonists (Ashby and Labelle 1977, Mao *et al* 1984, Bayoumi and Ashby 1989, among others). However, Chalmers and Bawa (1977) have shown that primary muscle spindle input does not exist between all synergists. Meunier *et al* (1990) and Creange *et al* (1992) have demonstrated that this feedback is not limited to muscles acting on the same joint, but can originate from muscles across two joints. These few characterizations notwithstanding, a quantifiable classification of heteronymous muscle spindle input has yet to be determined. An additional variable is the size and quanta of excitatory post synaptic potentials (EPSPs) released by each spindle synapse on a motoneuron. Although an all-inclusive distribution of EPSPs in motoneurons has yet to be documented, studies by Mendell and Henneman (1971) and Sypert *et al* (1980) indicate that EPSPs are stronger in primary than secondary afferents and their overall strength is related to the afferent's conduction velocity.

While these and other variables exist within a motoneuron pool, the extent of their presence is weakly substantiated in the literature, and some remain speculative. Therefore, while acknowledging the existence of other spindle variables that could affect the firing behaviour of motor units, our discussion will focus on the currently characterized and substantially classified neural interactions; that is, those between primary muscle spindle afferents and motoneurons.

We now propose an explanation for our data based on a mechanical interaction between muscle fibres and nearby spindles, with special emphasis on the characteristics of the mechanical coupling when a muscle fibre is recruited, as part of a motor unit, and when it is substantially activated as the contraction increases. Consider the following plausible sequence of events unfolded in figure 10. When a motor unit is recruited during a contraction, including an isometric contraction, muscle fibres of the recruited motor unit fire at a low firing rate and they cycle through a series of contractions and relaxations where the sequential force twitches do not overlap, as shown in figure 10(a). The nearby muscle spindles, greater than 90% of which are arranged in parallel to the muscle fibres (Binder and Stuart 1980, Burke *et al* 1987), slacken as the muscle fibre contracts and lengthen as the muscle fibres relax. The diagrams in figure 10(a) show three states that occur throughout the duration of a muscle fibre contraction induced by a force twitch. In state (1) the muscle fibres are at rest and the spindle is at rest. As a new α-motoneuron is recruited, a pulse activates the muscle fibres of the associated motor unit. It has been suggested by Vallbo (1974), Burke *et al* (1979), Edin and Vallbo (1990), and others that the γ-motoneurons are excited along with the α-motoneuron. This simultaneous occurrence is also predicted by the 'common drive' property proposed by De Luca *et al* (1982b) and De Luca and Erim (1994) and confirmed independently by Semmler and Nordstrom (1997), Marsden *et al* (1999), among others. Thus, γ-motoneurons to spindles adjacent to the newly recruited muscle fibres are also activated causing the intrafusal fibres of the spindle to contract. When a pulse arrives from the α-motoneuron, the muscle fibre(s) begin to shorten, the nearby spindle(s) slacken (state 1–2) and the Ia fibres are positioned to respond to a stretch of the intrafusal fibres. In the transition from state 2 to 3, the muscle fibre relaxes to its original length. In so doing, it stretches the taught spindle. The intrafusal fibres are stretched and the Ia fibres fire.

At low force levels, the earlier-recruited motor units are not tetanized and influence the length of adjacent spindles. The spindle shortening produces the fast increasing excitatory feedback to the homonymous motoneurons, as reported by Macefield *et al* (1991) and shown by the solid line in the cartoon of spindle feedback in figure 10(c). In this non-overlapping region (the shaded regions in the range of 0 to 10% MVC) the work of Broman *et al* (1985) displayed as a cartoon in figure 10(d) showed that during a very-slow increasing (1.5% MVC s^{-1}) isometric contraction, the firing rates of motor units #1 and #2 increased continuously up to 10% MVC. This behaviour indicates that the excitation from the spindle was additive to the slow increasing excitation from the CNS.

As the excitation to the motoneuron increases, the firing rates of the motor units increase and the force twitches overlap (figure 10(b)). The muscle fibres assume a shorter length and the adjacent spindles slacken (state 1–2 in figure 10(b)). The sequence in figure 10(a) is repeated, except that the degree of shortening and lengthening of the muscle fibres and spindles becomes increasingly smaller as the firing rate increases. The intrafusal fibres are stretched over a shorter distance and the Ia firings decrease, as shown in figure 10(b). According to Macefield *et al* (1991), in this range the firings of the Ia fibres decrease and the excitatory feedback to the homonymous motoneurons decreases. (See dashed line segment and non-shaded regions in figure 10(c).) The effects of this behaviour are seen in the non-shaded regions of figure 10(d). When the excitation to motor unit #2 passes the 10% MVC level, the firing rate of the previously recruited motor unit #1 decreases with respect to that of motor unit #2; and when motor unit #3 is recruited at above 10% MVC, the firing rates of motor units #1 and #2 begin to decrease as the force continues to increase slowly. This behaviour occurs while the rate of force increase is similar to where motor units #1 and #2 were recruited. Thus, with similar increases of excitation from the CNS, the firing rates of motor units #1 and #2 decrease, implying that excitation from the spindles is decreasing. This interpretation is consistent with the presence of decreasing excitation from the spindles as reported by Macefield *et al* (1991) and shown by the dashed line in figure 10(c).

The above explanation may seem to be in conflict with the 'common drive' property (De Luca *et al* 1982b, De Luca and Erim 1994, De Luca and Hostage 2010 among others) which states that when the net excitation (central and peripheral, including from spindles) increases the firing rates of earlier recruited motor units should increase rather than decrease as in the example reported by Broman *et al* (1985) shown in figure 10. This apparent inconsistency may be explained as follows. In the special force paradigm used by Broman *et al* (1985) the target force was increased slowly (less than 0.1% MVC s^{-1}). During this interval, at least one (observed) and possibly other (unseen) motor units were recruited. They influence the spindles near their fibres to provide negative feedback and cause the firing rates of previously active motor units to decrease. The newly recruited motor units have greater force twitches and provide the necessary force to overcome the reduced force of the earlier recruited motor units. This phenomenon is evident because in figure 10 the rate of increase of the excitation is very slow. This is a discrete micro effect

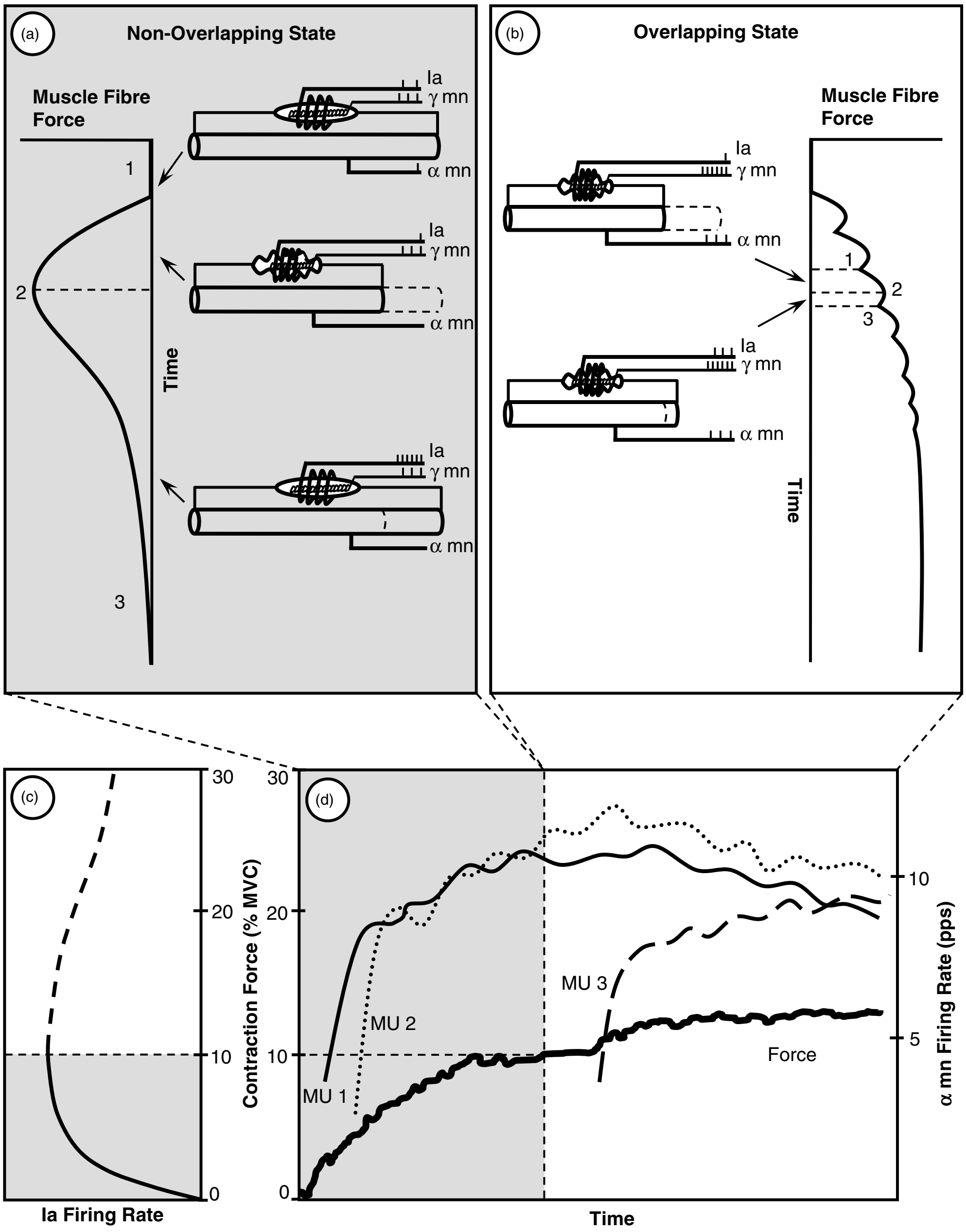

Figure 10. Sequence of events that connects the mechanical influence of newly recruited muscle fibres on the near-by spindles. Note that as a matter of convenience the force level of 10% MVC is used as a demarcation point between non-overlapping and overlapping force twitches. Motoneuron (mn) and spindle behaviour below the 10% MVC level are shaded grey while activity above the 10% MVC point is not shaded. The actual MVC cut-off level would depend on the force twitch duration and the firing rate characteristics of the muscle. (a) When a motoneuron is recruited it fires with low firing rates. At firing rates that correspond to average inter-pulse intervals longer than the time duration of the force twitches (commonly at force levels $<$10% MVC), muscle fibre force twitches contract without sequential interaction. The muscle fibres shorten and lengthen with each subsequent excitation. A mechanically coupled spindle in the vicinity of the muscle fibres first shortens (slackens) and then is stretched with each sequential excitation. As the spindle stretches, the Ia excitation increases. We refer to this situation as the non-overlapping state. (b) As the excitation to the motoneuron increases, the firing rates increase and when average inter-pulse intervals become shorter than the time duration of the force twitches (commonly at force levels $>$10% MVC), subsequent muscle fibre force twitches overlap and the spindle shortens (slackens) because the force twitch cycle does not return to the resting state. The muscle fibres shorten, the spindles slacken, and the Ia excitation decreases. We refer to this as the overlapping state. (c) The cartoon describes the observation of Macefield *et al* (1991). Note that the Ia excitation (shaded regions and solid line) increases up to about 10% MVC and subsequently decreases (non-shaded regions and dashed line). The increasing Ia excitation is caused by the stretching of the spindle in the non-overlapping state. As the spindle enters the overlapping state, the range of the stretching decreases and the Ia excitation decreases, as shown with the dashed line. (d) A cartoon of firing rates of motor units recruited during slow increasing isometric force in the TA muscle as observed by Broman *et al* (1985). Note that in the shaded regions of the plot, when motor unit #2 is recruited, below 10% MVC, the firing rates of both motor units #1 and #2 increase. In the non-shaded regions, when motor unit #3 is recruited above 10% MVC, the firing rates of both motor units #1 and #2 begin to decrease. The firing rate profiles behave according to the profile of the Ia excitation in (c). (Note: (c) is a cartoon of figure 2 from Macefield *et al* (1991) and (d) is redrawn from figure 5 of Broman *et al* (1985).

that is temporarily inconsistent with the general concept of the common drive when expressed on a macro scale. It is noteworthy to point out that the micro effect is quickly overridden when the excitation increases to provide additional force as may be seen in figure 1 in Broman *et al* (1985). In so doing, the relationship of the common drive becomes evident.

Although they are mostly considered as secondary factors, the GTOs also respond to the muscle fibre shortening by stretching, and the Ib fibres increase their firing rate. This action provides an increasing inhibitory or negative feedback to the homonymous motoneurons. Therefore, the combined negative feedback from the muscle spindles and the GTOs elicited by the recruitment of a motoneuron decreases the total excitation to the motoneuron pool. As a result the rate of increase of the firing rate will decrease.

A similar explanation involving the proprioceptive feedback from spindles was also used by De Luca *et al* (2009) to explain the modulation of the common drive during sustained isometric contractions. In the light of this explanation, the involvement of the Renshaw system for explaining the decrease in the firing rate of motor units subsequent to the recruitment of new motor units in Westgaard and De Luca (2001) needs to be reconsidered.

Now let us return to the data in figure 2. Note that in figure 2(a) the firing rate values at the force levels of 1% to 10% MVC remain essentially invariant to the number of spindles. Considering the above argument, as the force level increases in the 10% MVC range, most active spindles in a muscle exist in the dynamic state and send positive feedback (increasing excitation) to the homonymous motoneuron pool. According to Freund *et al* (1975) and Duchateau and Hainaut (1990), and as may be seen in figure 9, in muscles such as the FDI, about 50% of the motor units in the muscle are recruited in the 0%–10% MVC range. In contrast, in muscles with more spindles, like the BB, only 5%–10% of the motor units are recruited in the same force range (Kukulka and Clamann 1981). This difference between the FDI and the other muscles is clearly seen in figure 9. Although the BB has nearly ten times the number of spindles of the FDI, only one-tenth of its population is recruited resulting in about the same number of spindles activated in both muscles at forces within the 10% MVC range. Hence, the amount of positive feedback to the respective motoneurons is more or less similar. Consequently, in the 10% MVC range the firing rates of the motoneurons remain unaffected by the number of spindles in the muscle.

As the excitation to the motoneuron pool increases further, the firing rates increase and the muscle fibre force twitches begin to overlap; the spindles become fixed in a slackened state (figure 10(b)). The excitatory feedback from muscle spindles is now less than it was previously during the dynamic spindle state. This decrease in excitation is equivalent to a negative feedback to the homonymous motoneurons. The degree of the negative feedback increases with increasing overlap of the force twitches. It follows that the greater the number of spindles in the muscle, the greater the negative feedback, the lower the firing rate and the greater the maximal motor unit recruitment threshold. The inverse relationship between the firing rate and number of spindles is evident in figures 2(b)–(e) at each force level above 10% MVC and it is defined by equation (5).

Equation (5) also predicts that if a muscle has approximately 700 spindles, the firing rates of the motor units in the force range of 10% to 100% MVC would converge at 12 pps, as is evident in figure 2(f). At this point, the decreasing excitation from the spindles activated below the 10% MVC range is approximately equal to the increasing excitation of the common drive (described by De Luca *et al* (1982b), and De Luca and Erim (1994)) to the motoneuron pool. This interpretation indicates that the interplay between the increasing and decreasing excitations of approximately 700 spindles in one muscle is approximately equal to the net increase of excitation from the CNS between 10% and 100% MVC. It would be interesting to test this prediction, but no such muscle exists. The longissimus thoracis muscle has been reported to have 1193 spindles (Voss 1963). But that muscle receives innervations from several spinal cord levels and is best described as having several motoneuron pools, thus it does not provide a test case for the inference. The one muscle that approximates the condition is the gluteus maximus, which has 629 spindles (Voss 1959). We found no firing rate data for this muscle in the literature.

The slope of the inverse relationship between the firing rate and the number of spindles increases as the contraction level increases (see figure 2). This behaviour may be accounted for by the motor unit recruitment densities shown as a function of the contraction force in figure 9. In muscles with a low number of spindles, the negative feedback to the motoneuron pool is greater at lower force levels, diminishes quickly and ends at relatively lower force levels where the maximal recruitment threshold is reached. For muscles with a relatively large number of spindles, the negative feedback persists throughout a greater force range, thus reducing the firing rate of the earlier recruited motor units to a greater extent. This behaviour is evident in the firing rate equation (5) which states that muscles with smaller number of spindles, such as the FDI, would have on average a maximum mean firing rate of 35.1 pps, and for those with relatively larger number of spindles, such as the VL, the maximal firing rate would be 19.7 pps.

The relationship between the maximal recruitment threshold and the number of spindles in a muscle is provided by equation (11). According to this equation, if a muscle contains no spindles (or if the spindles were dysfunctional) the maximal recruitment threshold would be approximately 50% MVC, a number not too far from that reported in muscles with relatively few spindles such as the FDI. Those with large number of spindles, such as the VL, would have higher maximal recruitment threshold, in the range of 95% MVC, a value consistent with that observed by De Luca and Hostage (2010).

The data for the recruitment of motor units collected also enabled the derivation of the density function of the number of recruited motor units as a function of number of muscle spindles and force level. The values of the density function compare well with those reported by Freund *et al* (1975) and

Duchateau and Hainaut (1990) for the FDI which has the form of a negative exponential function as may be seen in figure 9 for low values of spindles (34), and by Kukulka and Clamann (1981) for the BB, which has the form of a more widely distributed function having a peak at the lower end of the spindle distribution, as may be seen in figure 9 when the value of the spindle is 320.

In conclusion, motoneurons of muscles with greater number of spindles receive greater negative feedback which reduces their firing rates, increases their maximal recruitment threshold and changes the distribution of motoneuron recruitment over the force range.

Acknowledgments

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Appendix

Database sources

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(5) Bigland-Ritchie B, Furbush F, Gandevia S C and Thomas C K 1992 Voluntary discharge frequencies of human motoneurons at different muscle lengths *Muscle and Nerve* **15** 130–7

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(8) Calder K M, Stashuk D W and McLean L 2008 Physiological characteristics of motor units in the brachioradialis muscle across fatiguing low-level isometric contractions *J. Electromyography Kinesiology* **18** 2–15

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