J Appl Physiol 138: 1050–1065, 2025.
First published March 17, 2025; doi:10.1152/japplphysiol.00863.2024

american physiological society

JOURNAL OF APPLIED PHYSIOLOGY

SYSTEMATIC REVIEW

Motor unit discharge behavior in human muscles throughout force gradation: a systematic review and meta-analysis with meta-regression

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Abstract

The analysis of motor unit (MU) discharge behavior provides an effective way of assembling information about the generation and control of movement. In this systematic review and meta-analysis, we identified and summarized the literature investigating MU discharge rate and discharge rate variability (CoV-ISI) during voluntary isometric contractions at various force levels. Databases were searched up to January 7, 2025, and a total of 262 studies were included. The meta-means of MU discharge rate and CoV-ISI were estimated and compared across human muscles. The influence of contraction intensity on MU discharge behavior was assessed through linear meta-regressions. At low-to-moderate forces [<60% maximal voluntary contraction (MVC)], the first dorsal interosseous, biceps brachii (BB), and forearm extensors (FEs) had the highest discharge rate, whereas the soleus had the lowest. At high force levels (>60% MVC), the tibialis anterior (TA) had the highest mean discharge rate compared with all other muscles, with the soleus maintaining the lowest. Regarding CoV-ISI results at low forces (<30% MVC), the TA had the lowest CoV-ISI values, except in comparison with the vastii. In addition, the vastii had lower CoV-ISI values than the FE, gastrocnemius medialis, and soleus. Contraction intensity was positively associated with the mean discharge rates in all muscles investigated, although some muscles showed steeper slopes than others. Similar results were observed for CoV-ISI meta-regressions, with muscle-specific differences in slope. These findings suggest potential variations in neural control strategies across muscles during force gradation, such as differences in the relative contribution of rate coding to facilitate increasing force demands.

coefficient of variation of the interspike interval; HDsEMG; intramuscular electromyography; neural control; rate coding

INTRODUCTION

Since the seminal work of Sherrington (1), the alpha motoneuron has been referred to as the final common pathway of the neuromuscular system, as it integrates the synaptic inputs generated from spinal and supraspinal pathways to generate muscle force. For this reason, analyzing the discharge behavior of motor units, consisting of the alpha motoneuron and all of the muscle fibers it innervates (2, 3), provides an effective way of assembling information about the generation and control of force production. From the pioneering works of Adrian and Bronk (4) and Denny-Brown and Sherrington's (5) use of concentric needle electrodes to the development of wire intramuscular (6, 7) and quadrifilar electrodes (8, 9), the recordings of single motor units opened new perspectives in the physiological mechanisms underlying voluntary muscle control. Decades later, the advancements in high-density electromyography (HDEMG) techniques (10–13) and motor unit decomposition algorithms (14–17) have led to recording large numbers of concurrently active motor units during voluntary contractions. Together, the use of the multichannel thin-filament intramuscular electrodes (14, 18) and HDEMG surface grid electrodes, combined with the advancements in motor unit decomposition algorithms (14–17), has given rise to a new line of research questions aimed to characterize motor unit discharge behavior under a variety of conditions. Considering the result of muscle contraction is the generation of force, it is fundamental to understand the relation between motor unit control strategies and the force generation capacity of the muscle throughout force gradation (6, 19–21).

The nervous system controls muscle force over most of the operating range of a muscle by concurrently modulating the motor unit discharge rate (rate coding) and the number of active motor units (recruitment) (22). However, the relative contributions of rate coding and recruitment vary across the force operating range and appear to differ between muscles (23–25). Experimental evidence indicates that during gradual increases in isometric force, which is an indicator of increased net excitatory synaptic input and may result from increases in persistent inward currents (PICs) (26–28), motor unit discharge rates initially increase with force and then stabilize (i.e., saturation stage) (6, 19, 29, 30). Discharge rate saturation is likely attributable to intrinsic mechanisms of the motoneurons (28, 31, 32), and the progressive involvement of inhibitory or excitatory inputs as contraction

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Submitted 5 November 2024 / Revised 3 December 2024 / Accepted 5 March 2025

intensity increases (33). The inhibitory and excitatory drive increases to the point where the dendrites saturate and can no longer respond to the synaptic drive. For these reasons, although the mechanisms underlying force gradation are well-established in the literature, the effect of contraction intensity on motor unit discharge behavior across different human muscles remains unclear.

Most human studies have been limited to the investigation of a small fraction of motor units over a narrow force range due to technical limitations. As such, this has constrained our understanding of how the modulation of rate coding influences force gradation across its entire range. In addition, comparing motor unit discharge behavior across human muscles has been complicated by the broad range of methods applied across many studies, including variations in the methods used to record motor units, contraction intensities, and muscles being examined. Therefore, a systematic review and meta-analysis to pool the available data across many studies provides a more robust investigation of motor unit behavior in various human muscles. Although a number of excellent reviews have addressed anatomical and contractile properties of motor units (34, 35), how motor unit activity controls force production (22), the effect of aging on motor unit discharge rates (36), the effect of resistance training on motor unit behavior (37), and sex differences in motor unit behavior (38), no previous study has systematically reviewed and synthesized findings on motor unit discharge behavior across human muscles using a meta-analytic approach, particularly with a focus on the effects in individual muscles throughout the full spectrum of force gradation.

The primary aim of this systematic review and meta-analysis was to identify and summarize the findings from studies investigating motor unit discharge behavior during voluntary isometric contractions at various force levels. Specifically, we pooled data from studies published up to January 7, 2025, to estimate and compare the meta-means of motor unit discharge rate and discharge rate variability in a wide variety of human muscles. As a secondary aim, we conducted linear meta-regressions to assess whether the effect of contraction intensity on motor unit discharge behavior differed between muscles. Finally, this review discusses shortcomings in this area of study and where advancements are needed to propel the field of electrophysiology forward.

METHODS

This systematic review was conducted according to guidelines set forth by the Preferred Reporting Items for Systematic Review and Meta-Analysis (PRISMA statement 2020) (39). The PRISMA checklist is provided in Supplemental File S0. As our systematic review involved a meta-analysis of means rather than a meta-analysis of between-group or within-group differences (which is more common), certain PRISMA criteria were not applicable or required modification. For instance, we did not assess the risk of bias, as the primary tools available (e.g., ROBINS-I) are designed for studies of interventions. Consequently, we also did not evaluate the certainty of evidence. These deviations are explicitly marked as "N/A" in the PRISMA checklist.

Eligibility Criteria

The eligibility criteria for study inclusion were delineated using the PICOS framework (P: Population, I: Intervention, C: Comparator, O: Outcomes, and S: Study design). However, given the present review is a meta-analysis of means (i.e., estimating the overall mean of motor unit discharge behavior), the "Comparator" category was not applicable.

Population.

Studies where healthy adults between the ages of 18 and 65 yr old and without current or a history of neural or musculoskeletal disorders were included.

Intervention.

Studies included in this review investigated motor unit discharge behavior during isometric contractions in human muscles. Only studies assessing isometric voluntary sustained contractions were included; thus, studies focusing on evoked, automatic (e.g., postural), or dynamic contractions were not considered in this review. Studies where muscle contraction was not isometrically sustained around a target force (e.g., following a triangular profile or explosive contractions) were also excluded. There were no restrictions regarding the muscle or muscle group investigated.

The measurement tools considered for the assessment of motor unit discharge behavior were surface or intramuscular electromyographic myoelectric recording electrodes and complimentary decomposition software; therefore, studies that did not incorporate electromyographic recordings were excluded from this review. In addition, only studies that estimated motor unit discharge behavior were included.

Outcomes.

The broad outcome domain of interest in this review was the assessment of motor unit discharge behavior in human muscles. The specific outcome domains included motor unit discharge rate and motor unit discharge rate variability (i.e., coefficient of variation of the interspike interval; CoV-ISI). CoV-ISI values were considered only if relative values were provided. Another outcome of interest was the contraction intensities at which the motor unit discharge was assessed. Only studies that directly provided the contraction intensity (or at least an approximation of the intensity) relative to the participant's maximal voluntary contraction (% MVC) were included. If a study assessed multiple contraction intensities, it was included only if the values were reported separately for each intensity.

Study design.

Considering our main review question (meta-analysis of means), the types of studies included were observational studies, either cross-sectional or longitudinal, where there was no intentional manipulation of the variables of interest. However, studies in which participants received an intervention (e.g., exercise, pain, and fatigue) were only included if baseline or control measures were available. In addition, only peer-reviewed studies published in English were included.

Information Sources and Search Strategy

Studies published up to June 27, 2023, were initially identified through a search conducted by one reviewer (H.V.C.). This search was subsequently updated on May 9, 2024, and again on January 7, 2025, by the same reviewer. The electronic databases used were MEDLINE (Ovid interface), PubMed, and Web of Science (Clarivate Analytics). Searching in databases may not retrieve all relevant studies, as reports may be missing or inadequately indexed due to insufficient detail in titles and abstracts (40). To complement the database searches, two reviewers (J.G.I. and H.V.C.) performed hand-searches of reference lists from selected studies and relevant reviews published in key journals (e.g., *The Journal of Physiology*, *Journal of Electromyography and Kinesiology*, *Journal of Neurophysiology*, and *Journal of Applied Physiology*).

The search strategy was designed by three reviewers (J.G.I., H.V.C., and C.C.), and the primary concepts were centered on the outcomes and measurement tools considered, which were structured as follows:

('Motor Unit Outcome') and ('Electromyography Technique').

"Motor unit outcome" identified the terms typically used in studies assessing motor unit discharge (e.g., 'discharge rate' or 'firing rate'). "Electromyography technique" encompassed the terms commonly used to describe the measurement tools used to evaluate motor unit activity (e.g., 'intramuscular electromyography' or 'high-density surface electromyography'). The search strategies used in each database are detailed in Supplemental File S1.

Selection and Data Extraction Processes

All search results were retrieved from databases and imported by one reviewer (H.V.C.) into EndNote v. 20 (Clarivate analytics), which facilitated the identification and removal of duplicates. Subsequently, the remaining citations and abstracts were imported into Rayyan (41), where the initial screening process (title and abstract) was independently conducted by two reviewers (J.G.I. and C.C.). The measure of agreement between the two reviewers was 0.94 (Cohen's kappa statistic), indicating almost perfect agreement (42). The disagreements were resolved through discussion, and a third reviewer (H.V.C.) was consulted for arbitration when necessary. Given the substantial number of eligible reports for the second stage of the screening (full text), this process was undertaken by three reviewers (J.G.I., C.C., and A.B.), with each reviewer assessing one-third of the eligible reports.

Like the full-text screening, the data extraction process was conducted by three reviewers (J.G.I., C.C., and A.B.). A customized excel spreadsheet was used for data extraction, and all extracted data were subsequently cross-checked for accuracy by two reviewers independently (J.G.I. and H.V.C.). In cases where multiple reports of the same study were identified, they were merged (43). The extracted data included participants' characteristics (e.g., sample size and age), intervention details (e.g., muscle assessed and measurement tool), task contraction intensity, and summary statistics (means and standard deviation) of the outcomes of interest (i.e., mean discharge rate and CoV-ISI). If a study provided interspike intervals (ms), the data were transformed into mean discharge rate (pps) (i.e., the multiplicative inverse of the interspike interval) and CoV-ISI (i.e., the standard deviation of the interspike interval divided by its mean). When the study results were solely presented in graphical form, WebPlotDigitizer software v. 4.6 (44) (retrieved from https://automeris.io/WebPlotDigitizer) was used to extract the data from the figures.

Data Synthesis and Meta-Analysis

All analyses were conducted in R (v. 4.4.2; R Foundation for Statistical Computing, Vienna, Austria) using the RStudio environment (v. 2024.12.0 + 467). Meta-analysis and moderator (meta-regression) analysis were performed using the *metafor* package (45).

The primary aim of this systematic review was to estimate and compare motor unit discharge rate and discharge rate variability across human muscles. To achieve this, we combined data from individual studies in a multilevel meta-analysis of means. Specifically, we used a two-level hierarchical model using the restricted maximum likelihood (REML) method. This approach was chosen because the included studies often reported multiple estimates for the same muscle (e.g., different contraction intensities within the same study). The two-level meta-analytic model accounts for the clustering of multiple estimates within the same group of participants (46–48) and has been previously applied in meta-analyses of similar data (36). Meta-analytic models were conducted separately for the three different force ranges (low < 30% MVC; moderate 30%–60% MVC; and high > 60% MVC) with "muscle" included as a moderator to assess differences in motor unit discharge behavior between muscle groups within each force range. Importantly, only muscles with at least five estimates within a specific force range were included in the analysis.

Results from the meta-analyses are presented graphically using orchard plots [*orchard* package (49)]. These plots illustrate the estimated meta-analytic means for each level of the moderator (muscle), depicted as central circles (the 'trunk'), with confidence intervals represented by thick horizontal lines (the 'branches') and prediction intervals by thin horizontal lines (the 'twigs'). Individual estimates are shown as transparent circles, with their size proportional to precision (1/standard error), meaning larger circles indicate more precise estimates. Importantly, the estimated meta-analytic means are derived from the two-level hierarchical model, meaning they do not necessarily coincide with any single data point but rather represent the model-based estimate that accounts for individual estimates variance as well as clustering within studies. This explains why, in some cases (e.g., Fig. 3 vastus medialis, abductor digiti minimi, gastrocnemius medialis, and soleus at low intensity), the meta-analytic mean may appear outside the range of individual estimates. Finally, in cases where the standard deviation of an estimate was not reported in the study, missing standard deviations were imputed separately for each muscle using the coefficient of variation from all complete cases, following the method proposed by Bracken (50).

To explore whether the experimental method (surface or intramuscular electromyography) influenced reported motor unit discharge behavior, we conducted an additional analysis using the experimental method as a factor in the two-hierarchical meta-analytic model. This analysis was restricted to the low force range (0%–30%), as it included the largest number of muscles, estimates, and methodological variations.

The secondary aim of this review was to determine whether contraction intensity influenced motor unit discharge rate or discharge rate variability to a different degree between muscles. For this purpose, we conducted a linear meta-regression using a two-level hierarchical model. The interaction between “contraction intensity” and “muscle” was included as moderator to assess whether the slope of the relationship between contraction intensity and motor unit discharge behavior varied among muscle groups. Meta-regression analyses were performed only for muscles with at least 10 estimates, ensuring sufficient data for robust statistical analysis. Results are presented graphically using bubble plots (Figs. 4, 5, and 6), which display the regression slope for each muscle and the relative weight of individual estimates based on their precision (i.e., 1/standard error). Pairwise comparisons between muscles for both the meta-analyses and meta-regressions were performed using the *emmeans* package (51) with Tukey’s adjustment for multiple comparisons.

All individual estimates extracted from each study (i.e., sample size, contraction intensity, means, and 95% confidence intervals of motor unit discharge behavior) are provided at https://doi.org/10.6084/m9.figshare.27325089 and as supplemental material, separated by muscle. The estimates of mean discharge rate (Supplementary File S3) and CoV-ISI (Supplementary File S4) are provided for all muscles, including those not included in the meta-analyses.

RESULTS

Study Selection

The PRISMA flow diagram for the studies’ selection process is presented in Fig. 1. From the initial 16,096 records retrieved through database searches, and after duplicates were removed, 9,919 records underwent title and abstract screening. Following the removal of 9,185 (including 24 that were not retrievable), 736 records (707 from databases and 29 from hand-searching) proceeded to the full-text screening. After further excluding 456 reports (440 from databases and 16 from hand-searching) due to the lack of population, outcome, or interventions of interest, and after collating multiple reports of the same study (Supplemental File S2), a total of 262 studies were included in the review.

Study Characteristics

The 262 studies included a total of 3,547 participants with ages ranging from 18 to 65 yr old (11 studies did not report age), average height from 152 ± 6 to 184 ± 7.1 cm (138 studies did not report height), and average mass from 57.9 ± 10.6 to 96.8 ± 15.7 kg (132 studies did not report mass). Intramuscular electromyography was used in 123 studies, surface electromyography in 132 studies, and 7 studies used both measurement techniques. The muscles assessed in the studies included (in order of prevalence): tibialis anterior ($n = 66$), vastus lateralis ($n = 59$), biceps brachii ($n = 40$), first dorsal interosseous ($n = 39$), vastus medialis ($n = 28$), soleus ($n = 18$), triceps brachii ($n = 13$), gastrocnemius medialis ($n = 12$), gastrocnemius lateralis ($n = 10$), abductor digiti minimi ($n = 9$), forearm extensors ($n = 8$), forearm flexors ($n = 8$), thenar

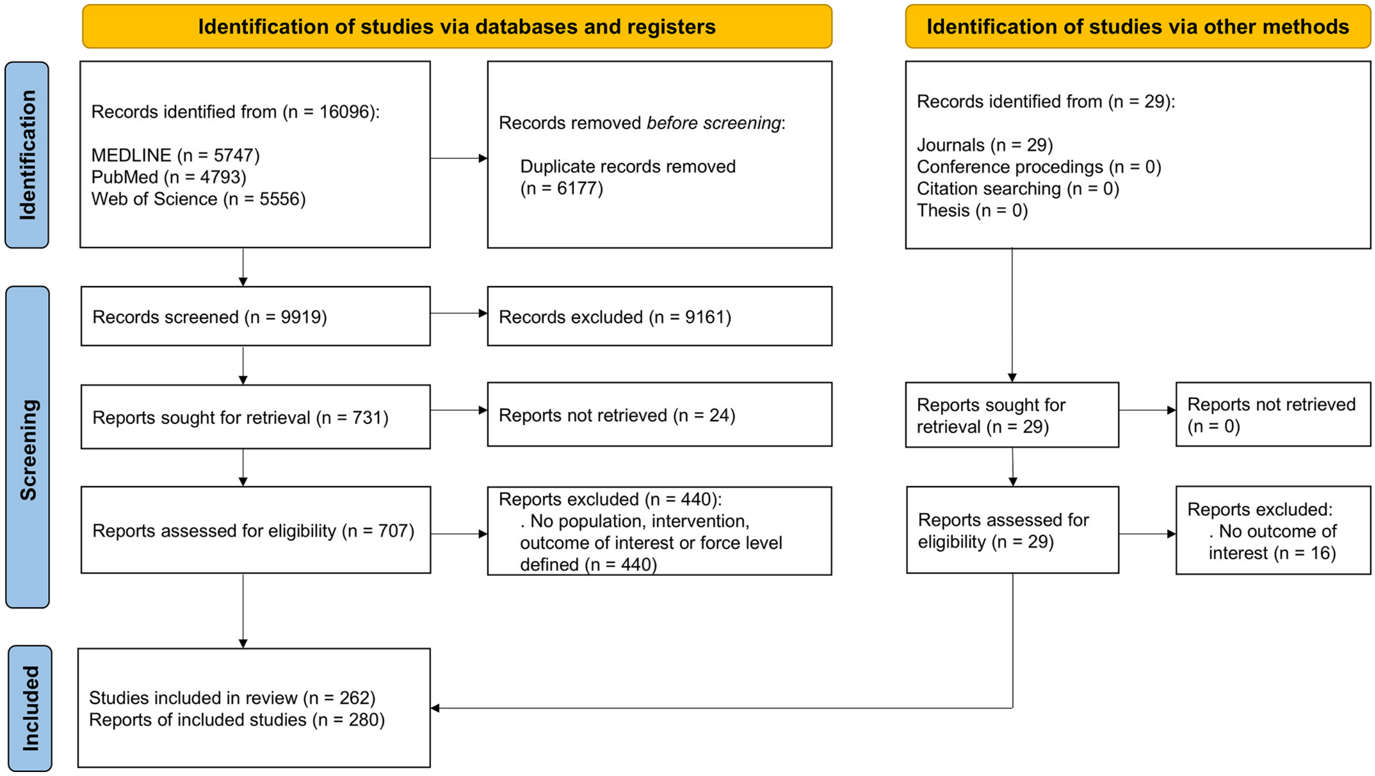

Figure 1. PRISMA flow diagram. PRISMA, preferred reporting items for systematic reviews and meta-analyses.

($n = 5$), biceps femoris ($n = 4$), adductor pollicis ($n = 4$), trapezius ($n = 4$), brachioradialis ($n = 3$), semitendinosus ($n = 3$), masseter ($n = 2$), abductor hallucis ($n = 2$), anconeus ($n = 2$), rectus femoris ($n = 2$), peroneus ($n = 1$), pectoralis major ($n = 1$), semispinalis cervicis ($n = 1$), brachialis ($n = 1$), dorsal interosseus ($n = 1$), erector spinae ($n = 1$), extensor hallucis longus ($n = 1$), occipitofrontalis ($n = 1$), and sternocleidomastoid ($n = 1$). In addition, several contraction intensities were assessed in the studies, including lower than 10% MVC ($n = 49$), 10% MVC ($n = 115$), 11%–19.9% MVC ($n = 24$), 20% MVC ($n = 90$), 21%–29.9% MVC ($n = 51$), 30% MVC ($n = 70$), 35% MVC ($n = 7$), 40% MVC ($n = 33$), 50% MVC ($n = 77$), 60% MVC ($n = 23$), 70% MVC ($n = 30$), 75% MVC ($n = 19$), 80% MVC ($n = 11$), 90% MVC ($n = 4$), and 100% MVC ($n = 43$).

Results of Syntheses

Overall pooled effect (meta-means).

The pooled mean discharge rates, along with 95% confidence interval (CI) and 95% prediction intervals for each muscle, are shown in Fig. 2, separated by force ranges (low, moderate, and high). In addition, Table 1 provides all meta-estimates of the mean discharge rates for the muscles included within each force range. Overall, there was a significant effect of "muscle" on the pooled mean discharge rate across all force ranges (test of moderators; $P < 0.001$ for all). Detailed contrasts, including estimated mean differences in mean discharge rate between muscles and corresponding P values, are provided in Supplemental File S5.

At the low force range (<30% MVC; Fig. 2*A*), the motor units of the first dorsal interosseous, biceps brachii, and forearm extensors presented the highest mean discharge rates compared with other muscles ($P < 0.007$ for all), with no significant differences between these three muscles ($P > 0.11$ for all). In contrast, soleus motor units had the lowest mean discharge rates compared with all other muscles ($P < 0.001$ for all) except for the biceps femoris ($P = 0.731$) and forearm flexors ($P = 0.294$). In addition, the abductor digiti minimi showed higher mean discharge rates than the triceps surae ($P < 0.001$ for all) and vastus lateralis ($P = 0.012$). The triceps brachii also showed significantly greater mean discharge rates than both the vastii ($P < 0.001$ for both) and the gastrocnemii ($P < 0.001$ for both). Furthermore, tibialis anterior motor units presented higher discharge rates compared with the gastrocnemii ($P < 0.001$ for both). Finally, the gastrocnemius medialis had higher mean discharge rates than the vastus medialis ($P = 0.002$).

At the moderate force range (30%–60% MVC; Fig. 2*B*), motor units in the first dorsal interosseous exhibited the highest mean discharge rates compared with all other muscles ($P < 0.003$ for all), except for the biceps brachii ($P = 0.965$). In contrast, soleus motor units showed significantly lower mean discharge rates than those of other muscles ($P < 0.049$), except for the vastii ($P > 0.250$ for both). In addition, biceps brachii and vastus medialis motor units had significantly higher discharge rates than those in the vastus lateralis ($P < 0.010$ for both). The biceps brachii also showed higher discharge rates than the gastrocnemius medialis ($P = 0.003$).

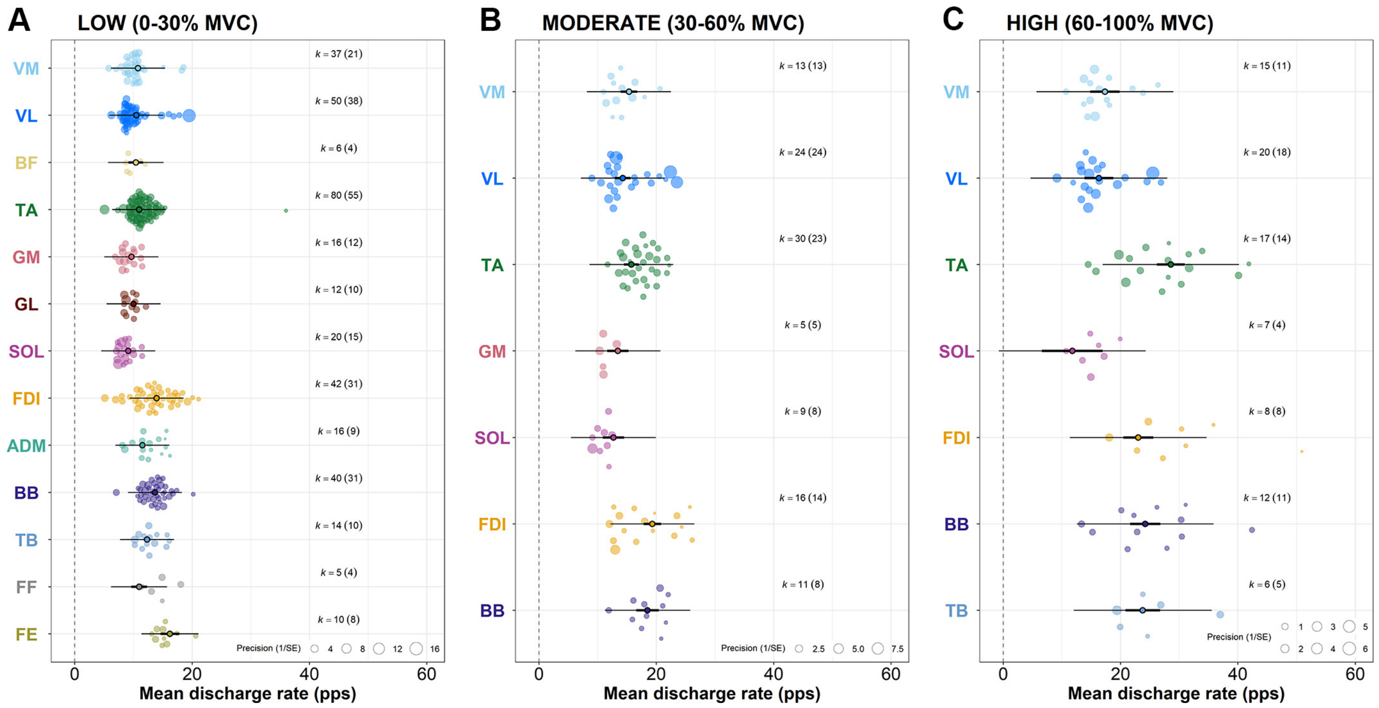

Figure 2. Orchard plots displaying the meta-analysis of means for motor unit discharge rates across different human muscles (*y*-axis), separated by low (*A*), moderate (*B*), and high (*C*) force ranges. Each circle represents individual estimates. The central circle (trunk), ticker horizontal line (branch), and thinner horizontal line (twig) represent the meta-mean estimate, 95% confidence level interval, and prediction interval, respectively. For each muscle, k indicates the total number of estimates with the total number of studies in brackets. Muscle abbreviations: ADM, abductor digiti minimi; BB, biceps brachii; BF, biceps femoris; FDI, first dorsal interosseous; FE, forearm extensors; FF, forearm flexors; GL, gastrocnemius lateralis; GM, gastrocnemius medialis; SOL, soleus; TA, tibialis anterior; TB, triceps brachii; VL, vastus lateralis; VM, vastus medialis.

Table 1. *Meta-estimates of mean discharge rate (pps)*

	Low (<30% MVC)			Moderate (30%–60% MVC)			High (>60% MVC)		
Muscle	**Meta-mean**	**95% LCI**	**95% UCI**	**Meta-mean**	**95% LCI**	**95% UCI**	**Meta-mean**	**95% LCI**	**95% UCI**
Forearm extensors	16.22	14.62	17.82						
Forearm flexors	10.95	9.6	12.3						
Abductor digiti minimi	11.53	11.01	12.06						
Biceps brachii	13.67	13.22	14.11	18.49	16.58	20.41	24.2	21.63	26.77
Biceps femoris	10.4	9.14	11.65						
First dorsal interosseous	13.94	13.4	14.47	19.33	17.83	20.82	23.01	20.46	25.57
Gastrocnemius lateralis	10.02	9.5	10.54						
Gastrocnemius medialis	9.64	9.15	10.13	13.44	11.61	15.28			
Soleus	9.1	8.62	9.58	12.67	10.84	14.49	11.78	6.6	16.96
Tibialis anterior	10.95	10.55	11.36	15.74	14.47	17.01	28.57	26.19	30.95
Triceps brachii	12.31	11.75	12.86				23.78	20.81	26.75
Vastus lateralis	10.48	9.98	10.98	14.35	12.96	15.62	16.31	13.85	18.78
Vastus medialis	10.78	10.28	11.29	15.4	13.96	16.72	17.33	14.85	19.82

LCI, lower confidence interval; MVC, maximal voluntary contraction; UCI, upper confidence interval.

At the high force range (>60% MVC; Fig. 2C), motor units in the tibialis anterior showed the highest mean discharge rates compared with all other muscles ($P < 0.028$ for all). Similar to the pattern observed at moderate force levels, soleus motor units displayed significantly lower mean discharge rates than all other muscles ($P < 0.003$), except for the vastii ($P > 0.450$ for both). In addition, the vastus medialis showed higher discharge rates than the vastus lateralis ($P = 0.008$). Moreover, both the biceps brachii and triceps brachii motor units presented higher discharge rates than the vastii ($P < 0.025$ for all). The first dorsal interosseous also showed greater discharge rates than the vastii ($P < 0.034$ for both).

The pooled CoV-ISI values, along with 95% CI, are presented in Fig. 3 and Table 2, separated by force ranges (low, moderate, and high). At high force ranges (Fig. 3C), the only muscle with at least five estimates was the tibialis anterior, making it not feasible to perform comparisons between muscles.

At the low force range (<30% MVC; Fig. 3A), there was a significant effect of "muscle" on the pooled CoV-ISI (test of moderators; $P < 0.001$). Tibialis anterior motor units had significantly lower CoV-ISI values compared with other muscles ($P < 0.02$ for all), except for the vastii ($P > 0.890$ for both) and biceps brachii ($P = 0.791$). In addition, vastii motor units

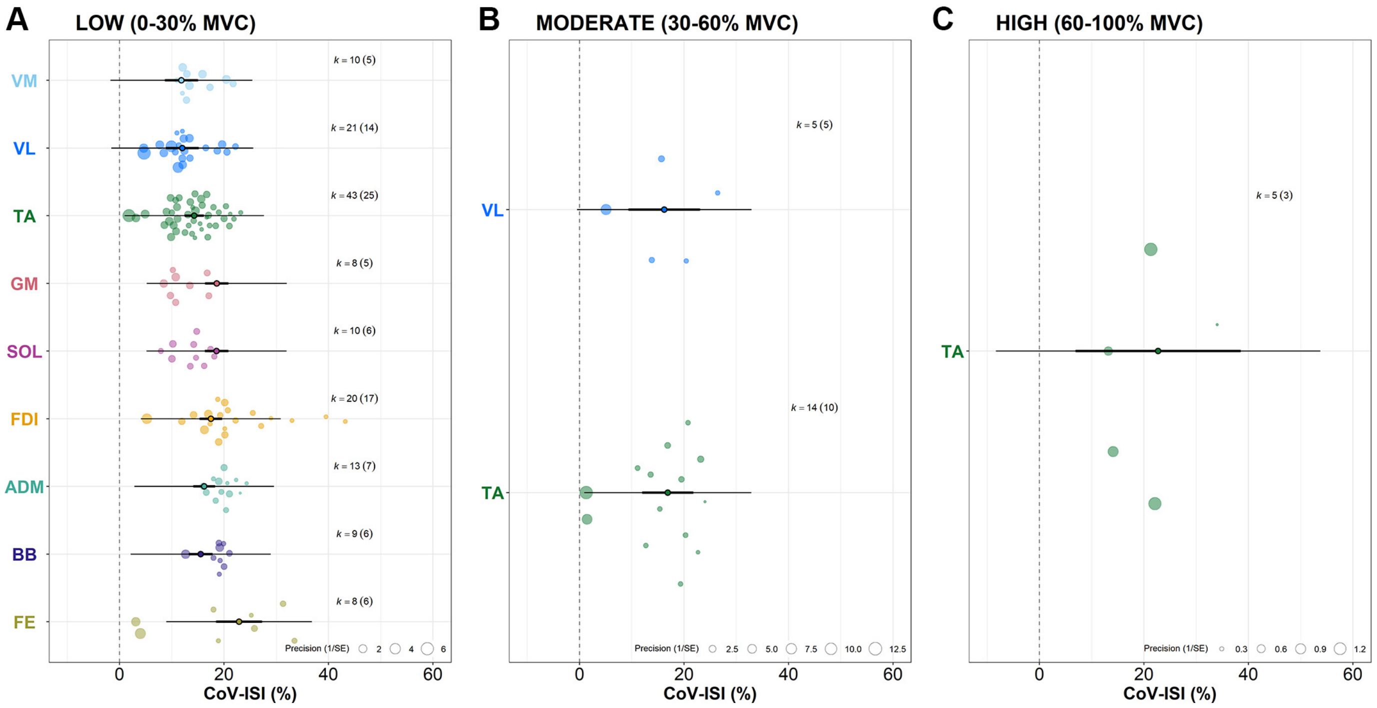

Figure 3. Orchard plots displaying the meta-analysis of means for the coefficient of variation of the interspike interval (CoV-ISI) across different human muscles (*y*-axis), separated by low (*A*), moderate (*B*), and high (*C*) force ranges. Each circle represents individual estimates. The central circle (trunk), ticker horizontal line (branch), and thinner horizontal line (twig) represent the meta-mean estimate, 95% confidence level interval, and prediction interval, respectively. For each muscle, k indicates the total number of estimates with the total number of studies in brackets. Muscle abbreviations: ADM, abductor digiti minimi; BB, biceps brachii; FDI, first dorsal interosseous; FE, forearm extensors; GM, gastrocnemius medialis; SOL, soleus; TA, tibialis anterior; VL, vastus lateralis; VM, vastus medialis.

Table 2. *Meta-estimates of coefficient of variation of the interspike interval (%)*

	Low (<30% MVC)			Moderate (30%–60% MVC)			High (>60% MVC)		
Muscle	**Meta-mean**	**95% LCI**	**95% UCI**	**Meta-mean**	**95% LCI**	**95% UCI**	**Meta-mean**	**95% LCI**	**95% UCI**
Forearm extensors	22.87	18.45	27.3						
Abductor digiti minimi	16.19	14.11	18.27						
Biceps brachii	15.52	13.25	17.79						
First dorsal interosseous	17.48	15.32	19.63						
Gastrocnemius medialis	18.6	16.37	20.83						
Soleus	18.57	16.33	20.81						
Tibialis anterior	14.3	12.44	16.16	16.91	12.01	21.81	22.71	6.9	38.52
Vastus lateralis	12.01	8.86	15.17	16.22	9.36	23.07			
Vastus medialis	11.83	8.65	15.02						

LCI, lower confidence interval; MVC, maximal voluntary contraction; UCI, upper confidence interval.

exhibited lower CoV-ISI values compared with the forearm extensors ($P < 0.003$ for both), gastrocnemius medialis ($P < 0.020$ for both), and soleus ($P < 0.020$ for both). No other significant differences were found between muscles. Detailed contrasts, including estimated mean differences in CoV-ISI between muscles and corresponding P values, are provided in Supplemental File S5.

At the moderate force range (30%–60% MVC; Fig. 3*B*), the tibialis anterior and the vastus lateralis were the only muscles with at least five estimates. No significant differences were found in the CoV-ISI between these muscles ($P = 0.864$).

To assess whether the experimental method (surface vs. intramuscular electromyography) influenced motor unit discharge behavior, we conducted a moderator analysis using estimates from the low force range (0%–30% MVC). No significant differences were found between methods for mean discharge rate (test of moderators; $P < 0.985$) or CoV-ISI (test of moderators; $P < 0.329$).

Effect of contraction intensity on motor unit discharge behavior.

To investigate whether the slope of the relationship between contraction intensity and motor unit discharge behavior varied across muscle groups, we performed linear meta-regressions including all muscles with at least 10 estimates. For the mean discharge rate meta-regressions, the slopes were significant for all muscles analyzed ($P < 0.001$ for all), indicating that higher contraction intensities were consistently associated with increased mean discharge rates (Figs. 4 and 5). However, the slopes differed significantly between muscles (test of moderators; $P < 0.001$), ranging from 0.069 for the soleus to 0.199 for the forearm extensors. Detailed statistical results, including estimated slopes for each muscle, are provided in Supplemental File S6.

The soleus exhibited the lowest slope compared with the other muscles ($P < 0.022$ for all). Excluding the comparison between the vastus medialis and gastrocnemius

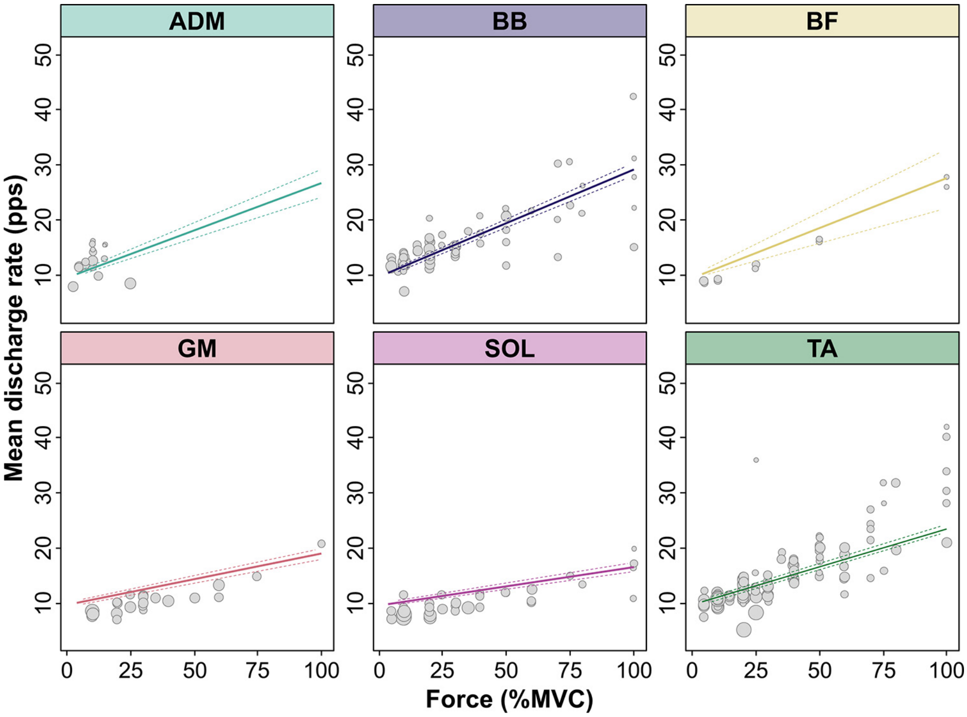

Figure 4. Bubble plots displaying the meta-regressions for the effect of force contraction intensity (% maximal voluntary contraction; MVC; *x*-axis) on motor unit discharge rates (*y*-axis) across different human muscles. Muscle abbreviations: ADM, abductor digiti minimi; BB, biceps brachii; BF, biceps femoris; GM, gastrocnemius medialis; SOL, soleus; TA, tibialis anterior.

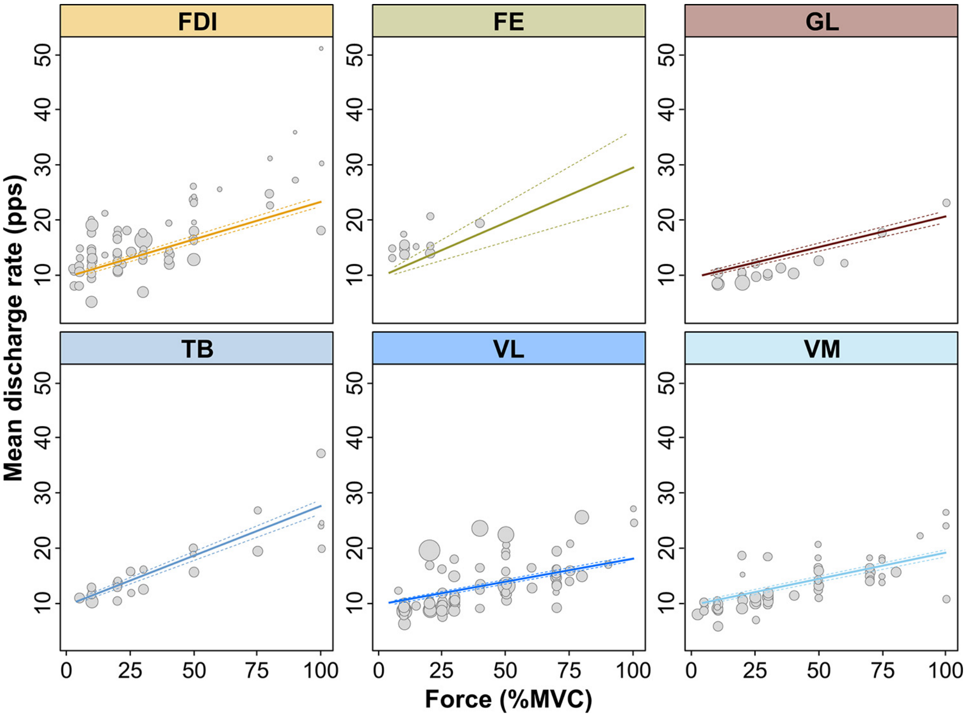

Figure 5. Bubble plots displaying the meta-regressions for the effect of force contraction intensity (% maximal voluntary contraction; MVC; *x*-axis) on motor unit discharge rates (*y*-axis) across different human muscles. Muscle abbreviations: FDI, first dorsal interosseous; FE, forearm extensors; GL, gastrocnemius lateralis; TB, triceps brachii; VL, vastus lateralis; VM, vastus medialis.

medialis ($P = 0.755$), the vastus lateralis presented significantly lower slopes than all other muscles ($P < 0.047$ for all). Similarly, the vastus medialis and gastrocnemius medialis showed lower slopes compared with most other muscles, aside from the forearm extensors ($P > 0.097$ for both) and biceps femoris ($P > 0.058$ for both), with no significant differences between them ($P = 1.000$). The gastrocnemius lateralis also displayed significantly lower slopes than most other muscles, except for the forearm extensors ($P = 0.314$), biceps femoris ($P = 0.296$), and vastus medialis ($P = 0.134$). In contrast, the biceps brachii and triceps brachii exhibited the steepest slopes across muscles ($P < 0.001$ for all), except when compared with the biceps femoris ($P = 1.000$ for both), forearm extensors ($P = 1.000$ for both), and abductor digiti minimi ($P > 0.778$ for both), with no significant differences between them ($P = 0.367$)

Regarding the CoV-ISI meta-regressions, the slopes were significant for all analyzed muscles ($P < 0.030$ for all), indicating that higher contraction intensities were consistently associated with increased CoV-ISI (Fig. 6). The slopes also differed significantly between muscles (test of moderators; $P < 0.001$), ranging from 0.013 for the tibialis anterior to 0.217 for the abductor digiti minimi (Supplementary File S6).

Excluding comparisons with the biceps brachii ($P > 0.190$ for both), the first dorsal interosseous and abductor digiti minimi showed the steepest slopes compared with other muscles ($P < 0.016$ for all), with no significant difference between them ($P = 1.000$). In contrast, the soleus and tibialis anterior exhibited the lowest slopes relative to all other muscles, except for the biceps brachii ($P > 0.565$ for both), with no significant differences between them ($P = 0.831$).

DISCUSSION

Main Findings

This systematic review and meta-analysis aimed to estimate and compare motor unit discharge behavior across human muscles, separated into low, moderate, and high force ranges. We summarized the findings of studies published up to January 7, 2025, investigating motor unit discharge rate and discharge rate variability (CoV-ISI) during voluntary isometric contractions at various force levels. The main findings were that at low-to-moderate forces (<60% MVC) the first dorsal interosseous, biceps brachii, and forearm extensors had the highest discharge rates, whereas the soleus had the lowest. At high force levels (>60% MVC), the tibialis anterior was reported to have the highest mean discharge rate compared with all other muscles, with the soleus again showing the lowest. Regarding the CoV-ISI main findings, due to a lack of studies investigating more than the tibialis anterior and vastus lateralis at moderate-to-high force ranges, main comparisons were possible in the low force range only. The tibialis anterior had the lowest CoV-ISI compared with all other muscles, except for the biceps brachii and the vastii. In addition, the vastii had lower CoV-ISI than the forearm extensors, gastrocnemius medialis, and soleus.

We also explored whether the effect of contraction intensity on motor unit discharge behavior varied across different muscles using meta-regressions. Our main findings indicate that contraction intensity was positively associated with the mean discharge rates in all muscles investigated. The biceps brachii and triceps brachii presented the steepest slopes, whereas the soleus and vastus lateralis showed the lowest slopes. Contraction intensity was also positively associated with the CoV-ISI in all muscles investigated. The first dorsal interosseous and abductor digiti minimi exhibited the steepest

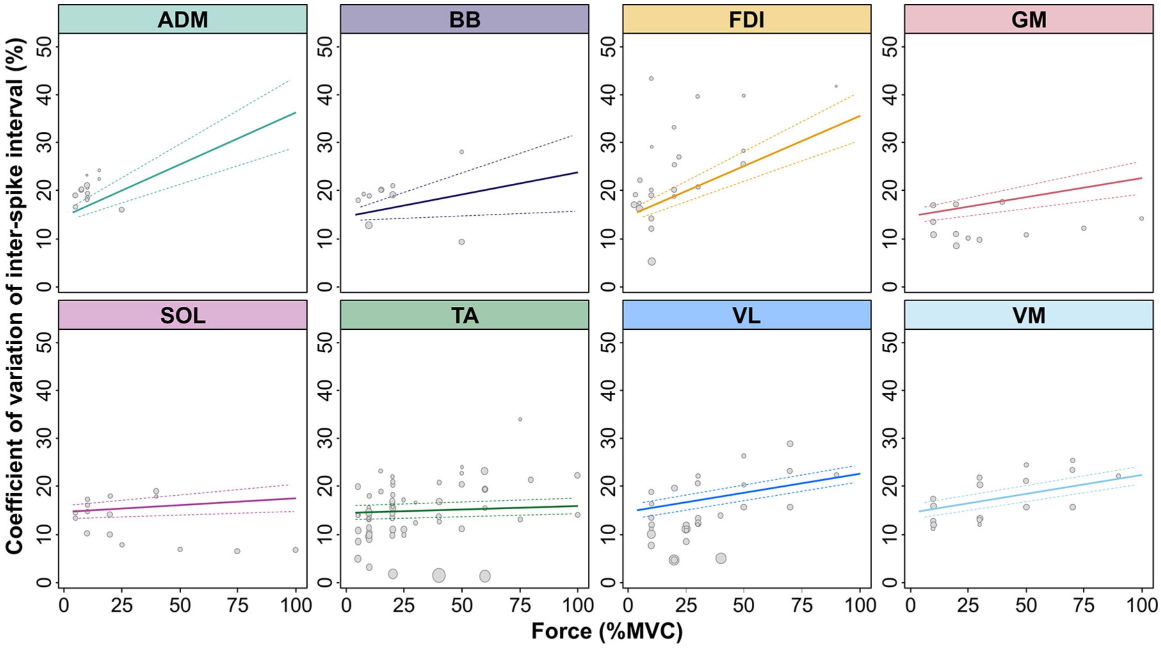

Figure 6. Bubble plots displaying the meta-regressions for the effect of force contraction intensity (% maximal voluntary contraction; MVC; *x*-axis) on the coefficient of variation of the interspike interval (CoV-ISI; *y*-axis) across different human muscles. Muscle abbreviations: ADM, abductor digiti minimi; BB, biceps brachii; FDI, first dorsal interosseous; GM, gastrocnemius medialis; SOL, soleus; TA, tibialis anterior; VL, vastus lateralis; VM, vastus medialis.

slopes, whereas the tibialis anterior and soleus presented the lowest slopes.

Motor Unit Rate Coding

Minimum discharge rates of human motor units during voluntary contractions have been reported to discharge between 5 and 7 pps (52–54), which was corroborated by the individual estimates extracted in this meta-analysis (minimum value of 5.07 pps; see Supplemental File S3). As contraction intensity increases, discharge rates progressively rise, as visually observed in the meta-means results (note the rightward shift in the *x*-axis from Fig. 2, *A–C*), indicating an overall mean discharge rate of ~12 pps, 16 pps, and 21 pps at low, moderate, and high force ranges, respectively (Table 1). In all muscles investigated, this positive association between force and mean discharge rate was statistically confirmed through meta-regressions, revealing that an increase of 1% MVC in contraction intensity was associated with an increase in the mean discharge rate ranging from 0.07 to 0.20 pps (see angular coefficients in Supplementary File S6). These increases in motor unit discharge rate throughout force gradation can be explained by the fact that, after the motor units are recruited, rate coding is required to continue increasing muscle tension to achieve maximum force (55). Consequently, this mechanism becomes responsible for generating force beyond the muscle recruitment range (56–58). Thus, differences in motor unit discharge rate slopes across force gradation between muscles could be explained by variations in the relative contribution of rate coding and recruitment to facilitate increased force demands. Muscles with steeper slopes, such as the triceps brachii, may rely on discharge rate modulation more than motor unit recruitment at lower force levels compared with the soleus and vastii muscles, which have lower slopes and subsequently require continuous recruitment to achieve higher force levels (Figs. 4 and 5). However, it is important to note that, unlike studies that investigated force gradation through ramp contractions (a progressive increase in force during a single contraction), this systematic review pooled results from studies investigating isometric contractions performed at different force levels. Therefore, the rate coding mechanisms observed here are distinct from those seen during ramp contractions, which depend on the rate of torque development and should not be directly compared with those contractions.

Modulation of the motor unit discharge rate is a complex mechanism that depends on several factors (55, 59). In fact, motor unit discharge behavior is correlated with *1*) synaptic drive (55), *2*) membrane resistance and rheobase current (60), *3*) motoneuron activation history (61), *4*) motoneuron size (59), *5*) function (62), or *6*) the characteristics of the active population of motor units (60). The observed differences in individual muscle's motor unit discharge rate behavior may, therefore, result from variations in some or all of these correlated factors. Specifically, the function, anatomy, and specific tasks performed by the muscles appear to be key determinants of the mean discharge rate (56). In this meta-analysis, upper-body muscles, such as the first dorsal interosseous and forearm extensors, presented greater discharge rates compared with the muscles of the lower-body, such as the triceps surae (Fig. 2). This difference in discharge rate likely reflects the increased need for upper-body muscles (included in this review) to produce smooth tension development, as these muscles are used more in fine motor control (58). A higher motor unit discharge rate implies a greater degree of motor unit twitch fusion (63), resulting in smoother increases in tension development. In addition, similar to other sampling processes, higher motor unit discharge rates allow synaptic inputs to be more accurately represented (64), which may be relevant for achieving precise motor control in the upper limbs. Furthermore, as elegantly demonstrated by Bigland-Ritchie et al. (65) on the force-frequency curve, even small increases (1–2 pps) in the steepest portion of the force-frequency curve can significantly increase the force output of a muscle. In contrast, muscles like the triceps surae do not require higher discharge rates as they are primarily responsible for providing long-duration ankle joint stability during stance and walking tasks (66). Previous research has shown that the discharge pattern of gastrocnemius medialis motor units is highly intermittent during standing and that this muscle relies more on recruitment than on discharge rate to stabilize posture (67). Moreover, the soleus, whose anatomical function is to maintain balance and posture, primarily requires sustained low-level contractions rather than rapid, powerful ones (68), which explains its lower discharge rate. Other factors may account for the differences observed between upper- and lower-body muscles, such as the characteristics of the descending tracts innervating these muscle groups such as differences in activation thresholds (69).

Interestingly, the motor unit discharge rate of muscle groups that either work together to create torque around a joint (synergists) or stabilize the forces around a joint (agonist-antagonist relationship) can differ significantly. Synergist muscles appear to have similar discharge behaviors in human muscles at low force levels, as seen with no differences between the gastrocnemii or between the vastii muscles. However, as the force increases to moderate-to-high ranges, the vastus medialis discharges at significantly higher rates than the vastus lateralis (~15% greater). This increased discharge rate in the vastus medialis compared with the lateralis may be associated with differences in the mechanics of these muscles and their roles during knee extension (70, 71). At higher force levels, it is possible that the vastus medialis must discharge at greater frequencies to compensate for the mechanical advantage of the vastus lateralis in force production (72), otherwise, asymmetry in tension development could destabilized the knee joint, potentially leading to injury through improper patella tracking. In addition, the fibers of the vastus medialis are oriented more obliquely to the femur from the proximal to the distal region (71, 73), which may reduce its ability to transmit extension tension to the patella as part of its contribution to the medial pull during knee extension (74).

Regarding the agonist-antagonist relationship, in the low force range, the motor unit discharge behavior, based on the meta-means of the muscle groups with enough estimates, indicated that the discharge rate of the tibialis anterior was moderately higher than the triceps surae (~12%), the biceps brachii was higher compared with the triceps brachii (~10%), and the forearm extensors were higher than the forearm flexors (~32%) (see estimated mean differences and corresponding *P* values in Supplementary File S5). However, this was not the case for the vastii and biceps femoris relationship (~2%). Interestingly, when the force was increased to high levels, the significant differences between the biceps brachii and triceps brachii disappeared (~1.7%). The differences seen in the low force range may be a result of the amount of slack or pretension in the musculotendinous unit. At lower force levels, depending on the joint angle, either the agonist or antagonist muscle may have a certain amount of slack or tension in the muscle-tendon unit, which allows a lower discharge rate to efficiently transfer the tension along the tendon's line of action to produce torque about the joint (75). However, at higher forces, the amount of pretension would be greater during the steady portion of the force output, which was the focus of this meta-analysis. As a result, opposing muscles working to stabilize a joint would be similarly advantaged in maintaining joint stability, thereby not requiring significantly different discharge rates to maintain the desired force. It should be noted that these findings need to be taken with caution. The use of broad force ranges (30%–40%) may skew results, as we did not compare individual force levels of individual studies but a pooled meta-mean of the low, moderate, and high force ranges. In addition, one cannot discount the importance of task-dependent reciprocal inhibition in joint stability and the modulation of the motor unit discharge rate, even during isometric contractions. As Sherrington (76) observed, the excitatory activity of the agonist muscle requires a corresponding relaxation of the antagonist muscle for optimal function. Furthermore, if reciprocal inhibition were to collapse, as is the case in upper motoneuron disorders (77) and in aging (78, 79), this would result in excessive cocontraction of the opposing muscles, leading to little movement (77). Kagamihara and Tanaka (80) reported that reciprocal inhibition was present at low (5 and 15% MVC) but seemed to dissipate at higher forces (>30%MVC), which may be an optimization mechanism at lower forces allowing for a smoother force production without interruption of competing muscle groups. Moreover, reciprocal inhibition may be responsible for the asymmetry of motor unit discharge profiles (modulation), leading to a smoother production of forces at low levels than symmetry at higher forces, which results in greater variability in force production. The reduction in reciprocal inhibition is evident during tonic isometric contractions at higher force levels when reciprocal inhibition is saturated and greater antagonist muscle activation is seen, despite the contractions being isometric where cocontraction is lower. In addition, the decrease in reciprocal inhibition at higher forces may be due to the importance of joint stability in injury avoidance from excessive force production from one muscle group over the other (81).

Motor Unit Discharge Rate Variability (CoV-ISI)

Based on the meta-estimates results of the CoV-ISI, human motor units discharge within a narrow range of variability (i.e., relatively low CoV-ISI values), with minimal variation across muscles. As shown in Table 2, the CoV-ISI meta-means ranged from 11 to 23%. Several factors may account for this narrow operational range of variability during isometric voluntary contractions. First, the low discharge rate variability in motor units is believed to optimize force steadiness, particularly at low-to-moderate force levels (82–85). The variability in motor unit discharge rate is a result of both common synaptic inputs and synaptic noise, which accounts for ~70% of the variability (85, 86). Notably, both simulated and experimental data have consistently demonstrated that low-frequency oscillations of synaptic inputs shared across the motoneuron pool are the primary determinant of force production (83–85). Second, common synaptic inputs reduce discharge variability by coherently controlling motor unit behavior (83, 87–90), which further contributes to stable force production (91). Finally, motor unit behavior studies often set a cutoff for motor unit discharge variability, therefore including only motor units with CoV-ISI below 20%–30% (92), which would artificially compress these observed results leading to the variability falling within this range.

Interestingly, the upper-body muscles overall showed greater variability in motor unit discharge rate than the lower-body muscles. This increased variability may be related to greater synaptic noise to the muscles of the upper- compared with the lower-body (85). This hypothesis aligns with the meta-regression results of the CoV-ISI (Fig. 6), where the first dorsal interosseous and the abductor digiti minimi showed significantly larger variations in CoV-ISI throughout force gradation (i.e., steepest slopes) compared with other muscles. Furthermore, as previously discussed, greater motor unit discharge rates were reported in the upper- compared with lower-body muscles. Given that an increased number of discharges has been associated with greater synaptic noise (86, 93), it would be expected that higher motor unit discharge rates would correspond with greater CoV-ISI.

Limitations and Future Directions

Despite the relevance of the current findings, several limitations must be acknowledged. First, it must be acknowledged that the findings of the current review are restricted to sustained isometric contractions and may not necessarily be applicable to what may occur during rapid and/or dynamic contractions (e.g., concentric or eccentric actions). Second, the number of studies investigating muscles beyond the tibialis anterior, vastii, first dorsal interosseous, and biceps brachii is limited. This lack of data restricted the statistical power of some analyses in this review. For instance, in the moderate-to-high force ranges, we were only able to calculate the CoV-ISI meta-means for the tibialis anterior and vastus lateralis (Fig. 3), as these were the only muscles with at least five reported estimates. Muscles in other regions, such as the shoulder complex, remain significantly understudied. Third, the included studies in this review often focused on specific force levels, primarily isometric contractions at 10%, 20%, 30%, and 50% of MVC, limiting our understanding of motor unit discharge behavior across the full force gradation process. Fourth, it is now widely recognized that motor unit data exhibit hierarchical dependencies, as multiple motor units recorded from the same muscle within a participant are not statistically independent (94). Historically, analyses often treated each motor unit as an independent observation, which we now understand may introduce bias. Recent studies have begun addressing this issue using linear mixed models to account for within-subject clustering, and we recommend that future studies adopt these models to improve the accuracy of their analyses. Finally, several studies lacked detailed reporting of all relevant variables, often omitting numerical descriptions of results, which further limited the scope of our analyses. To strengthen future research, the literature would benefit from more investigations across a wider range of muscles, force levels, and more comprehensive reporting of results.

Of the studies identified as part of the search strategy, 132 were from HDEMG surface data. Of the 132 studies, 91 used grids with more than five electrodes, and 41 used four or five electrodes and focused on populations between the ages of 18–35 where the majority of the participants were healthy young males with a limited physiological range (38). Some limitations have been reported in these studies that used this new and evolving technology. Some of the highlighted limitations from the investigated literature suggest that the HDEMG surface grid electrode results may be influenced by *1*) a bias toward more superficial motor units, limited volume detection, cross talk and signal selectivity (95–108), *2*) the superposition of discharges leading to potential cancellation, overlap, or misidentification of unique motor units (101, 109–115), *3*) force level, with low force outputs from simple tasks (i.e., slow trapezoidal) while avoiding rapid changes in force output for favorable motor unit identification accuracy (95, 97, 100, 114, 116–124), *4*) a preference toward the identification of later recruited and larger amplitude motor units (111, 112, 122, 122, 124–130), *5*) the influence of the thickness of subcutaneous tissue on motor unit separability (100, 107, 131–135), and *6*) the ability to track changes in MU shape, particularly following interventions (i.e., muscle swelling and fatigue) (25, 97, 99, 100, 108, 114, 122, 136–138).

Although considered the gold standard, intramuscular recordings are not free of challenges. Beyond the obvious potential discomfort associated with electrode insertion and placement, limitations include the small number of motor units that can be detected due to volume conduction and difficulties in distinguishing far-field motor units (i.e., high degree of selectivity of the intramuscular electrode) (139). Accurate electrode placement can also be difficult, both in terms of positioning and depth, as it is possible to position the electrode in an area with no or low activity (e.g., due to muscle compartmentalization). Consequently, there is often the need to reposition the needle to locate an area with higher activity, potentially leading to a recording bias based on the electrode's pick-up volume (140). In addition, the movement of the needle, especially during force variations, can lead to difficulty during decomposition due to changes in the motor unit shape (92) and increased complexity of the interference pattern (139). However, HDEMG does provide a robust alternative to record the myoelectric signal, namely, by having the ability to record a greater number of motor units within the active motor unit pool (without needle relocation) and the ability to track single motor units across trials and over days (assuming no significant changes in muscle physiology or architecture) (25, 141–143).

Underrepresented populations also remain a challenge in this field. Studies on these populations are considerably fewer than those conducted on healthy individuals, and the literature would benefit from more research focused on *1*) persons with disability (109), *2*) older adults and persons following bed rest with possible muscle atrophy or low-quality muscle (i.e., fibromyalgia) or those who have potentially undergone motor unit remodeling (i.e., amyotrophic lateral sclerosis) (96, 125, 131), *3*) females (38, 144), *4*) populations with different muscle dimensions (134), or *5*) to understand planned rehabilitation for disease, injury, or athletic training (108). Future directions should prioritize technological advancements, including the development of novel, potentially population-specific, grid electrodes, and optimization of supporting decomposition algorithms. In addition, the study of motor unit discharge behavior will likely require innovative electrode configurations and a hybrid approach combining both surface and intramuscular recordings to fully capture the complexity of motor unit discharge behavior across diverse populations and force levels.

Conclusions

In this systematic review, we identified 262 studies that reported motor unit discharge behavior during isometric steady-state contractions at various force levels across a variety of human muscles and muscle groups. Overall, the motor unit discharge rate increased with the intensity of the force output regardless of muscle or muscle group, and contraction intensity was also positively associated with the variability in the motor unit discharge rate in all muscles. These findings augment the importance of motor unit discharge behavior in joint stability throughout force gradation. In addition, this review highlighted the importance of motor unit discharge rate in force production, which continues to increase in many muscles above 50 to 90% MVC to achieve maximal outputs.

The individual muscle analysis revealed that smaller muscles, such as the first dorsal interosseous and forearm extensors have greater discharge rates at lower forces compared with the triceps surae. In addition, the analysis revealed the muscles of the upper body discharge at greater frequencies than those of the lower body. As for the variability of the motor unit discharge rate, the analysis revealed that human muscles operate within a narrow range (low CoV-ISI) which may be necessary for joint stability and optimization of force stability, particularly during low to moderate force tasks. Interestingly, it was the muscles of the upper body that had greater discharge variability compared to those of the lower body. This, again, maybe task dependent on the muscles that had enough estimates to be compared, such as the tibialis anterior, soleus, and first dorsal interosseus.

These findings only reflect those of an isometric contraction and may not represent dynamic or force-varying contractions. In addition, they may not necessarily represent the neural control of force output in females as most of the motor unit data comes from young, healthy males (38). It must be emphasized that our systematic-review also revealed that there is much more work to be done to increase our understanding of the complexities of motor unit behavior, specifically in the understudied muscle groups, such as the deltoid and pectoralis. It is also important that we continue to advance the technology used to study motor unit behavior to estimate the changes in behavior through electrophysiology better. This field of study has come a long way yet remains in its infancy, with many technological and physiological advancements on the horizon that must be considered as part of future investigations.

DATA AVAILABILITY

All individual estimates extracted from each study are provided at https://doi.org/10.6084/m9.figshare.27325089.

SUPPLEMENTAL MATERIAL

Supplemental Files S0–S6: https://doi.org/10.6084/m9.figshare.27325089.

ACKNOWLEDGMENTS

The authors thank Prof. Andrew J. Fuglevand for instrumental feedback on an early version of this manuscript which was integral to the construction of the final version.

GRANTS

This study was funded by the European Research Council Consolidator Grant “INcEPTION,” Contract No. 101045605. J. Greig Inglis was supported by the Marie Skłodowska-Curie Actions Grant “MUDecomp,” Agreement No. 101151712.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

J.G.I., H.V.C., and F.N. conceived and designed research; J.G.I., H.V.C., C.C., and A.B. performed experiments; J.G.I., H.V.C., and F.N. analyzed data; J.G.I., H.V.C., and F.N. interpreted results of experiments; H.V.C. prepared figures; J.G.I., H.V.C., and F.N. drafted manuscript; J.G.I., H.V.C., C.C., A.B., and F.N. edited and revised manuscript; and J.G.I., H.V.C., C.C., A.B., and F.N. approved final version of manuscript.

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