

Differences in Motor Unit Recruitment Patterns and Low Frequency Oscillation of Discharge Rates between Unilateral and Bilateral Isometric Muscle Contractions.

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Abstract

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Introduction: Distinct cortical activities contribute to unilateral and bilateral motor control. However, it remains largely unknown whether the behavior of motor neurons differs between unilateral and bilateral isometric force generation. Here, we first investigated motor units (MUs) recruitment patterns during unilateral and bilateral force generation. Considering that the force control is primarily regulated by low-frequency synaptic inputs to motor neurons, we also examined the relation between MU discharge rate and force output during unilateral and bilateral muscle contractions. *Methods:* Using advanced electromyography (EMG) sensor arrays and spike-triggered averaging techniques, we examined a large population of MUs in the right first dorsal interosseous (FDI) muscle during unilateral and bilateral force tracking tasks. Using the principal component analysis, we analyzed the first common component (FCC) of MU discharge rate to describe the force fluctuations during unilateral and bilateral contractions. *Results:* We found that MU discharge rate decreased during bilateral compared with unilateral contractions. MU recruitment threshold increased, while the amplitude and duration of MU action potential (MUAP) remained unchanged during bilateral compared with unilateral contractions. We found that the coefficients of variation (CV) for the force and FCC signal increased during bilateral compared with unilateral contractions. Notably, the FCC signal captured a great amount of MU discharge variability, and its CV correlated with the CV of the force signal. *Conclusion:* Our findings suggest that MU recruitment patterns are altered during bilateral compared with unilateral isometric force generation, likely related to changes at the low-frequency portion of the synaptic drive.

61

Introduction

62 Fundamental differences in cortical activities exist between unilateral and bilateral motor
63 control^{1,2}. For example, electrophysiological studies in non-human primates showed that cells in
64 cortical motor areas modulate their activities during unimanual and bimanual tasks³⁻⁶, and the
65 excitatory callosal inputs undergo suppression during bimanual tasks⁷. Primate lesion studies
66 demonstrated that unilateral lesion in the supplementary motor area (SMA) does not affect the
67 animal's general motor behavior, but produces long-lasting deficits in bimanual coordination^{8,9}.
68 In humans, neurophysiological studies showed changes in corticospinal excitability and cortico-
69 cortical interactions during bilateral compared with unilateral force generation¹⁰⁻¹³.
70 Neuroimaging studies revealed that bilateral movements involve unique neural activation
71 patterns in the cortical motor network compared with unilateral movements¹⁴⁻¹⁷. Despite the
72 intensive investigation into the control of unilateral and bilateral movements at the cortical level,
73 the behavior of motor neurons in humans during unilateral and bilateral force control remains
74 poorly understood.

75 The combination of advanced electromyography (EMG) sensor arrays and signal
76 processing techniques has provided a means to examine the activity of a large population of
77 motor units (MUs) obtained from the innervated muscles non-invasively¹⁸⁻²¹. In this study, we
78 systematically assessed MU discharge rate, MU recruitment threshold, and the amplitude and
79 duration of MU action potential (MUAP) in the first dorsal interosseous (FDI) muscle during low-
80 force unilateral and bilateral contractions. Evidence has shown that MUs can be recruited in a
81 task-dependent manner²²⁻²⁴. For example, animal studies showed that separate groups of MUs
82 are selectively recruited for different movement conditions²⁵⁻²⁷. In humans, the recruitment of

83 MUs can be altered by external stimulations^{28,29}, and the brain can selectively stimulate the MUs
84 regardless of the size principle criterion²². Specifically, MUs in the FDI muscle are differentially
85 recruited for different hand movements^{20,23,24}. Notably, common drive to MUs is reduced during
86 bilateral compared with unilateral FDI muscle contractions³⁰. Moreover, a single limb during a
87 maximal bilateral contraction produces a lower force^{31,32}, and a lesser activation of slow- and
88 fast-twitch MUs³³⁻³⁵ compared with a maximal unilateral contraction. Based on the information,
89 we hypothesized that MU recruitment patterns differed between unilateral and bilateral
90 voluntary contractions.

91 The force production is accomplished by the transmission of synaptic inputs to motor
92 neurons. The pool of motor neurons receives both common and independent synaptic inputs
93 from supraspinal and spinal circuits³⁶⁻³⁹, and the force control is primarily regulated by low-
94 frequency common inputs to motor neurons^{40,41}. In this study, we also investigated the low-
95 frequency oscillations of the MU discharge rate using the principal component analysis and
96 examined its relationship with the force signal during unilateral and bilateral contractions.
97 Evidence showed that the variability of the force output increases during bilateral compared with
98 unilateral force generation^{42,43}, and the variability of low-frequency components of MU discharge
99 rate contribute to the variability of the force output^{41,44}. Therefore, we also expected that low-
100 frequency synaptic inputs contribute to the force control during unilateral and bilateral
101 contractions.

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Materials and Methods

104 *Subjects.* Thirteen right-handed healthy volunteers (28.5 ± 7.8 years old, 7 females) participated
105 in the study. All subjects reported no history of neuromuscular disorders and were naïve to the
106 paradigm and the purpose of the study. All experimental protocols were approved by the
107 Institutional Review Board of Texas A&M University. All subjects gave written informed consent
108 prior to participation, which was approved by the local ethics committee at Texas A&M University
109 in accordance with the Declaration of Helsinki.

110 *Electromyographic (EMG) recordings.* EMG was recorded from the right FDI muscle through a
111 Trigno Galileo surface sensor array (Delsys, Inc., Natick, MA) secured to the skin over the belly of
112 each muscle. The array consists of four (2 x 2) cylindrical probes (0.5 mm diameter) and pairwise
113 differentiation of the four electrodes yields four channels of the EMG signals. The amplified
114 signals were converted to digital data with a sampling rate of 2222 Hz and stored in a computer
115 for offline analysis.

116 *Experimental paradigm.* Subjects were seated in a custom chair with both arms flexed at the
117 elbow by 90° with the forearm pronated. The left and right index fingers were attached to two
118 load cells, which measured the forces exerted by the subjects. At the beginning of the
119 experiment, subjects performed two or three isometric maximal voluntary contractions (MVCs)
120 for 3-5 s with right and left index finger into abduction, separated by 60 s of rest. During maximal
121 contractions, subjects were verbally encouraged to perform maximally, and visual feedback was
122 provided. The maximal forces were used to set targets for subsequent submaximal contractions.
123 During testing, subjects were requested to perform a series of isometric voluntary contractions
124 with the right hand, while the left hand remained at rest or performed isometric voluntary

125 contractions. Subjects were instructed to perform unilateral or bilateral contractions by following
126 a trapezoidal target force trajectory, which consisted of a linearly up-ramp from rest to the
127 prescribed %MVC in 10 s, a constant force of prescribed %MVC for 10 s, and a linearly down-
128 ramp to rest in 10 s (Fig. 1A). Two constant force levels (10% and 30% of MVC) were tested.
129 Custom software written by the MotionMonitor xGen (Innovative Sports Training, Inc. Chicago,
130 IL) was used to acquire force signals from the load cell and to display visual feedback
131 corresponding to the right and left FDI muscle force in real time (Innovative Sports Training, Inc.,
132 Chicago, USA). One or two cursors were used to indicate the current force generated by the right
133 or left FDI muscle, and the subjects were asked to maintain the target force as accurately as
134 possible (Fig. 1A). Familiarization trials were completed at the beginning of the experiment to
135 ensure that subjects were able to trace the trapezoid trajectory closely. Subjects performed two
136 trials of unilateral and bilateral contractions for each force level. The order of the contractions
137 was randomized for each subject. A 30 s rest period between the contractions was provided to
138 minimize fatigue. Note that the unilateral contractions were performed with the right hand, and
139 force output and EMG signals were recorded from the right FDI. The root mean squared error
140 (RMSE) was calculated to assess the force accuracy, which measured the deviation of the force
141 signal from the target force trajectory⁴². The coefficient of variation (CV) was calculated to assess
142 the variability of the force signal relative to the mean force output⁴².

143 *EMG signal decomposition.* The recorded EMG signals were decomposed into discriminable
144 motor units (MUs) using the decomposition algorithm introduced by De Luca^{18,21,45}. For each
145 identified MU, the algorithm output consisted of MU discharge times and MUAP templates (Fig.
146 1B and C). MU waveforms (amplitude and shape) recorded from the surface electrodes were

147 obtained by applying spike-triggered averaging (STA) on the raw surface EMG signals. Specifically,
148 the discharge times of each MU identified from the decomposition system were used as triggers
149 for the STA calculation. To ensure the reliability of the STA estimate^{20,46}, two tests were
150 performed: (1) the estimation the CV of the MUAP amplitude, and (2) the maximum linear
151 correlation coefficient between the STA estimate and the decomposition-estimated templates.
152 The MUs with a correlation coefficient > 0.7 and CV of MUAP amplitude < 0.3 were retained, and
153 a total of 715 MUs were included for further analysis. For each retained MU, the MUAP amplitude
154 of the STA template was used as an estimate for the amplitude of MU, measured as the voltage
155 difference from minimum and maximum peaks. The MUAP duration was estimated as the time
156 between the zero crossings before the first positive peak of MU and the zeros crossing after the
157 last positive peak. The recruitment threshold of the selected MU was measured from the
158 averaged isometric force data over the interval -50 to 150 ms relative to the instance of the first
159 discharge event. The peak discharge rate was calculated from the 4-s averaging window in which
160 the force was relatively constant at a steady state when the discharge rate was stable, while the
161 average discharge rate was calculated from the entire contraction duration. The inter-pulse
162 interval (IPI) was measured as the time interval between adjacent pulses.

163 *Principal component analysis of the MU discharge rate.* It has been demonstrated that the
164 effective neural drive to muscles is controlled by low-frequency synaptic inputs to motor
165 neurons⁴⁷⁻⁴⁹. To investigate the relationship between the MU discharge rate and force output
166 during unilateral and bilateral contractions, we analyzed the FCC of MU discharge rate using the
167 principal component analysis. It has been shown that the FCC signal captures a great amount of
168 variability in the smoothed MU discharge rate and explains a large part of fluctuation in the

169 muscle force during contractions^{41,44}. In this study, the smoothed and detrended MU discharge
170 rate were arranged in a matrix (time sequence × MU). The FCC of MU discharge rate was
171 computed by using the eigenvalue decomposition of the covariance matrix⁴¹, and the maximum
172 eigenvalue of the covariance matrix is used to quantify the FCC signal⁴⁴. In addition, the CVs for
173 the FCC and force signal were computed as the ratio (%) between standard deviation and the
174 mean values after removing the linear trends from the signals^{41,44}.

175 *Statistical analysis.* The mean values of the threshold force, amplitude, duration, discharge rate,
176 and inter-pulse interval of the MUs were calculated during unilateral and bilateral contractions
177 for each subject. Regression analyses with a generalized linear model were conducted to examine
178 the relation between the amplitude and threshold force, as well as the relation between the
179 discharge rate and threshold force. In addition, an inverse power function was used to examine
180 the relation between the discharge rate and amplitude: $\text{discharge rate} = b \times (\text{amplitude})^a$, where
181 b is the scale factor and a is the rate of decay. The fit slopes of the amplitude vs. threshold force,
182 the discharge rate vs. threshold force, and the discharge rate vs. P-P amplitude were calculated
183 at each contraction for each subject. Repeated repeated-measures ANOVAs were performed to
184 determine the effect of TASK (unilateral, bilateral) and FORCE (10% and 30% of MVC) on MU
185 threshold force, amplitude, duration, discharge rate, inter-pulse interval, and fit slope. The same
186 analysis was used to determine the effect of TASK and FORCE on the CV for the force and FCC
187 signal. Further, linear regression analysis was used to determine the relationship between the CV
188 for the FCC signal and the CV for the force signal. For all variables, normal distribution was tested
189 by the Shapiro-Wilk's test and homogeneity of variances by the Levene's test of equality and
190 Mauchly's test of sphericity. When normal distribution could not be assumed, data were log

191 transformed. When sphericity could not be assumed, the Greenhouse-Geisser correction statistic
192 was used. Significance was set at $p < 0.05$. Group data are presented as the mean \pm SD in the text.

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194

Results

195 *MU Discharge Rate*

196 EMG signal decomposition identified a total of 715 motor units (MUs). The average
197 number of MUs obtained from the right FDI muscle per subject was 55.0 ± 16.2 (unilateral = 26.8
198 ± 8.2 ; bilateral = 28.2 ± 9.9 , $p=0.6$). Figure 2A illustrates the instantaneous MU discharge rate as
199 a function of time for the three representative MUs recorded during the unilateral (black) and
200 bilateral (grey) FDI muscle contractions at 10% (Fig. 2A, left) and 30% (Fig. 2A, right) of MVC. Note
201 that MU discharge rate in the right FDI muscle was suppressed during bilateral compared with
202 unilateral contractions.

203 Repeated-measures ANOVA showed an effect of TASK ($F_{(1,12)} = 15.9$, $p = 0.002$) and FORCE
204 ($F_{(1,12)} = 198.2$, $p < 0.001$), but not in their interaction ($F_{(1,12)} = 0.3$, $p = 0.6$) on the peak MU
205 discharge rate. *Post hoc* analysis revealed that the peak discharge rate of the identified MUs
206 decreased significantly during bilateral (10% of MVC = 12.9 ± 2.3 pulses per second (pps); 30% of
207 MVC = 18.8 ± 3.0 pps) compared with unilateral (10% of MVC = 13.9 ± 2.2 pps; 30% of MVC = 20.0
208 ± 2.9 pps) contractions at 10% ($p = 0.002$) and 30% ($p = 0.004$) of MVC (Fig. 2C). Another repeated-
209 measures ANOVA revealed an effect of TASK ($F_{(1,12)} = 11.1$, $p = 0.006$) and FORCE ($F_{(1,12)} = 129.3$,
210 $p < 0.001$), but not in their interaction ($F_{(1,12)} = 0.007$, $p = 0.9$) on the average MU discharge rate.
211 The average discharge rate showed a decline during bilateral (10% of MVC = 4.7 ± 1.1 pps; 30%
212 of MVC = 6.5 ± 1.0 pps) compared with unilateral (10% of MVC = 5.2 ± 1.0 pps; 30% of MVC = 7.0

213 ± 1.2 pps) contractions at 10% ($p = 0.002$) and 30% ($p = 0.01$) of MVC (Fig. 2D). Repeated-
214 measures ANOVA also showed an effect of TASK ($F_{(1,12)} = 8.5$, $p = 0.01$) and FORCE ($F_{(1,12)} = 49.5$,
215 $p < 0.001$), but not in their interaction ($F_{(1,12)} = 2.1$, $p = 0.2$) on the inter-pulse interval (IPI). The
216 IPI was significantly higher during bilateral (10% of MVC = 175.6 ± 44.1 ms; 30% of MVC = 118.6
217 ± 17.3 ms) compared with unilateral (10% of MVC = 150.8 ± 30.0 ms; 30% of MVC = 107.6 ± 19.6
218 ms) contractions at 10% ($p = 0.01$) and 30% ($p = 0.02$) of MVC (Fig. 2E).

219 *MU Recruitment Threshold and MUAP Amplitude and Duration*

220 Repeated-measures ANOVA revealed an effect of TASK ($F_{(1,12)} = 11.1$, $p = 0.006$) and
221 FORCE ($F_{(1,12)} = 99.0$, $p < 0.001$), but not in their interaction ($F_{(1,12)} = 0.5$, $p = 0.5$) on the MU
222 recruitment threshold force. *Post hoc* analysis revealed that the MU recruitment threshold force
223 was higher during bilateral compared with unilateral contractions at 10% (bilateral = 1.5 ± 0.9 %
224 MVC; unilateral = 1.1 ± 0.5 % MVC; $p = 0.02$) and 30% (bilateral = 5.5 ± 1.7 % MVC; unilateral =
225 4.7 ± 1.4 % MVC; $p = 0.03$; Fig. 3A) of MVC. Repeated-measures ANOVAs showed no effect of
226 TASK on the duration ($F_{(1,12)} = 0.04$, $p = 0.9$) and amplitude ($F_{(1,12)} = 0.5$, $p = 0.5$) of the MUAP.
227 These results indicate that distinct MU recruitment patterns may be employed during unilateral
228 and bilateral muscle contractions. No changes were observed in the duration of the MUAP during
229 unilateral (10% of MVC = 10.43 ± 0.96 ms; 30% of MVC = 9.56 ± 0.89 ms) and bilateral (10% of
230 MVC = 10.62 ± 1.20 mV; 30% of MVC = 9.61 ± 1.02 mV) contractions at 10% ($p = 0.6$) and 30% (p
231 = 0.8) of MVC (Fig. 3B). The amplitude of the identified MUs was not significantly different
232 between unilateral (10% of MVC = 0.104 ± 0.06 mV; 30% of MVC = 0.226 ± 0.12 mV) and bilateral
233 (10% of MVC = 0.101 ± 0.04 mV; 30% of MVC = 0.229 ± 0.17 mV) contractions at 10% ($p = 0.4$)
234 and 30% ($p = 0.4$) of MVC (Fig. 3C).

235 *Size Principle*

236 Figure 4A illustrates MU recruitment threshold force as a function of MU amplitude
237 during unilateral and bilateral contractions at 10% (Fig. 4A, left) and 30% (Fig. 4A, right) of MVC
238 in a representative subject. The fit lines for each contraction are plotted. Note that there was a
239 linear relationship between the threshold force and MU amplitude during unilateral (black) and
240 bilateral (grey) contractions. Figure 4B shows the discharge rate in relation to MU amplitude.
241 There was an inverse power relationship between the discharge rate and MU amplitude. Figure
242 4C illustrates the threshold force as a function of the discharge rate, with regression lines
243 superimposed on the motor units. An inverse linear relation was found between the discharge
244 rate and threshold force. No differences were observed in the fit slope for threshold force vs. MU
245 amplitude (10% of MVC: unilateral = 0.044 ± 0.032 , bilateral = 0.040 ± 0.033 , $p = 0.4$; 30% of MVC:
246 unilateral = 0.024 ± 0.008 , bilateral = 0.026 ± 0.017 , $p = 0.3$), MU amplitude vs. discharge rate
247 (10% of MVC: unilateral = -0.81 ± 0.14 , bilateral = -0.84 ± 0.13 , $p = 0.4$; 30% of MVC: unilateral =
248 -0.45 ± 0.13 , bilateral = -0.48 ± 0.12 , $p = 0.2$), and threshold force vs. discharge rate (10% of MVC:
249 unilateral = -2.26 ± 1.17 , bilateral = -2.09 ± 1.33 , $p = 0.7$; 30% of MVC: unilateral = -1.32 ± 0.54 ,
250 bilateral = -1.35 ± 0.61 , $p = 0.5$) between unilateral and bilateral contractions. Together, these
251 data demonstrate that there was orderly recruitment of MUs based on MU size across a
252 population of concurrently active MUs, regardless of unilateral or bilateral contractions.

253
254 *Low-frequency oscillation of the MU discharge rate*

255 The low-frequency oscillations of MU discharge rate were examined by computing the
256 FCC of MU spike trains^{41,44}. Figure 5A and B illustrate the FCC signal of MU discharge rate (black)
257 and the force signal (grey) during unilateral and bilateral contractions in a representative subject.

258 Note that the fluctuation of the force signal is greater during bilateral compared with unilateral
259 contractions and the force and FCC signals have similar low-frequency oscillations. The FCC signal
260 explained a great amount of the total variability of MU discharge rate during unilateral (10% of
261 MVC = $43.2 \pm 12.1\%$; 30% of MVC = $39.5 \pm 11.3\%$) and bilateral (10% of MVC = $43.4 \pm 9.3\%$; 30%
262 of MVC = $44.1 \pm 11.2\%$) contractions. The FCC signal accounted for the most variability of MU
263 discharge rate was similar between unilateral and bilateral contractions at 10% ($p = 0.5$) and 30%
264 ($p = 0.2$) of MVC. Repeated-measures ANOVA showed an effect of TASK ($F_{(1,12)} = 10.2$, $p = 0.008$)
265 and FORCE ($F_{(1,12)} = 0.4$, $p = 0.5$), but not in their interaction ($F_{(1,12)} = 0.2$, $p = 0.6$) on the CV of the
266 FCC signal. *Post hoc* analysis showed that FCC signal quantified with the CV was greater in the
267 bilateral contractions (10% of MVC = $4.59 \pm 1.38\%$; 30% of MVC = $4.92 \pm 1.69\%$) than in the
268 unilateral contractions (10% of MVC = $4.06 \pm 1.28\%$; 30% of MVC = $4.17 \pm 1.08\%$) at 10% ($p =$
269 0.03) and 30% ($p = 0.02$) of MVC (Fig. 5C). Similarly, repeated-measures ANOVAs revealed an
270 effect of TASK ($F_{(1,12)} = 14.8$, $p = 0.02$) on the CV of the force signal. *Post hoc* analysis showed that
271 the CV of the force signal was greater during bilateral (10% of MVC = $3.52 \pm 1.14\%$; 30% of MVC
272 = $2.85 \pm 1.33\%$) compared with unilateral (10% of MVC = $2.72 \pm 0.74\%$; 30% of MVC = $2.28 \pm$
273 0.72%) contractions at 10% ($p = 0.008$) and 30% ($p = 0.04$) of MVC (Fig. 5D). Notably, we found a
274 correlation between the CVs for the force and FCC signal ($r = 0.43$, $p = 0.002$; Fig. 6). This result
275 indicates that individuals with more force fluctuation were the ones with larger variability in low-
276 frequency oscillations of MU discharge rate.

277

278

Discussion

279 Our novel findings suggest that the nervous system changes the MU recruitment patterns
280 and low-frequency common presynaptic inputs to motor neurons during bilateral and unilateral
281 force control. Specifically, we found that MU discharge rate decreased, while MU recruitment
282 threshold increased, during bilateral compared with unilateral contractions. Motor neurons
283 receive low-frequency common presynaptic inputs during the force control. Therefore, we also
284 examined low-frequency components of the neural signal (FCC), reflecting the effective
285 primary/principal neural drive to the muscle. We found that the variability of the force and FCC
286 signal increased during bilateral compared with unilateral contraction. Notably, the FCC signal
287 explained most of MU discharge rate variability, and its CV was significantly correlated with the
288 CV of the force signal. Taken together, we propose that changes at the low-frequency portion of
289 the synaptic drive may contribute to alternations in MU recruitment patterns during bilateral
290 muscle contractions.

291 *Motor Unit Recruitment Patterns during Unilateral and Bilateral Muscle Contractions*

292 Extensive evidence in animals and humans showed that distinct cortical activities
293 contribute to unilateral and bilateral force control^{3-7,10-13,16,17}. For example, bilateral motor tasks
294 result in higher neural activation in the primary sensorimotor cortex and supplementary motor
295 area compared with unilateral motor tasks¹⁶. M1 neurons are selectively fired during unilateral
296 and bilateral movements^{50,51}. In this study, we reported that the nervous system might also
297 employ distinct MU recruitment strategies during bilateral compared with unilateral
298 contractions. We suggest that two mechanisms potentially contribute to altered behavior of
299 motor neurons during unilateral and bilateral contractions: (1) changes in the recruitment order

300 of MUs, and (2) changes in the population of MUs recruited during unilateral and bilateral
301 contractions.

302 It is commonly assumed that the “size principle” rule, orderly recruitment of MUs based
303 on MU size, governs the sequences of MUs for voluntary muscle contractions⁵²⁻⁵⁶. However, some
304 evidence has shown that the orderly recruitment of MUs can be altered based on the context of
305 the movement tasks^{29,57}. For example, human studies showed that the nervous system can learn
306 to control individual MUs regardless of their size^{22,58}, indicating that the recruitment order of
307 MUs can be flexible. MUs can change their recruitment order when voluntary contractions are
308 performed in different directions^{23,59}, positions^{60,61}, and velocity levels⁵⁷. Further, animal studies
309 showed that rapid locomotor movements can result in non-orderly recruitment of MUs⁶²⁻⁶⁴. The
310 existence of orderly recruitment enables fatigue-resistant muscle contractions, but poses a
311 mechanical paradox. In contrast, a random recruitment order of MUs would be mechanically
312 effective because it can deploy the specific MUs to satisfy the mechanical demands of the motor
313 tasks in an efficient way. Our results showed orderly recruitment of MUs, with the discharge rate
314 of earlier-recruited MUs being greater than those later-recruited MUs, during both unilateral and
315 bilateral contractions, suggesting that the “size principle” rule can provide a general description
316 of MU recruitment patterns, regardless of unilateral or bilateral contractions for this task.

317 An alternative mechanism is that two different populations of MUs in the FDI muscle may
318 be recruited during unilateral and bilateral contractions. Evidence has shown that the nervous
319 system can select distinct MU populations for different movements. For example, in walking cats,
320 separate groups of MUs are selectively recruited for different movement conditions²⁵⁻²⁷.

321 Electrophysiological studies in humans revealed that different populations of lower limb MUs are
322 recruited in a task-dependent manner during locomotion⁶⁵. In the FDI muscle, MUs can also be
323 differentially recruited for different hand movements^{20,23,24}. Thus, it is possible that the
324 population of MUs recruited during bilateral contractions is modified. Indeed, our findings
325 showed that MU discharge rate decreased during bilateral compared with unilateral
326 contractions. This aligns with the previous findings showing that the activation of slow- and fast-
327 twitch MUs decreases during bilateral compared with unilateral maximal contractions³³⁻³⁵. To
328 maintain the designated force output during bilateral contractions, the reduced discharge rate
329 can be offset by the recruitment of new MUs. This agrees with evidence showing that changes in
330 MU populations can compensate for reduced MU discharge rate to maintain force⁶⁶. Further, we
331 showed that the MU recruitment threshold increased during bilateral compared with unilateral
332 contractions. Since the recruitment threshold varies for different motor units in which larger MUs
333 are typically recruited at higher threshold force while smaller MUs are recruited at lower
334 threshold force, this result may also suggest that the recruited MUs during bilateral contractions
335 are not the same MUs recruited during unilateral contractions. Thus, we suggest that separate
336 populations of MUs in the FDI may be selectively activated to produce a given force during
337 unilateral and bilateral contractions, and distinct MUs may contribute differently to the force
338 output during these two contraction conditions.

339 *Low-frequency oscillation of MU discharge rate*

340 The motoneuron pool receives common and independent presynaptic inputs from
341 supraspinal and spinal circuitries³⁶⁻³⁹, and low-frequency common synaptic inputs determine the
342 force control^{40,67}. The next question is to address if common inputs to motor neurons, during

343 bilateral contractions, were different from those present during unilateral contractions. Here,
344 the principal component analysis of the smoothed MU spike trains (the FCC signal) was used to
345 provide insights into the low-frequency oscillation of the neural drive to the FDI muscle. Indeed,
346 we found that low-frequency oscillations of MU discharge rate were well represented by the FCC
347 signal extracted by principal component analysis during (10% of MVC = $43.2 \pm 12.1\%$; 30% of MVC
348 = $39.5 \pm 11.3\%$) and bilateral (10% of MVC = $43.4 \pm 9.3\%$; 30% of MVC = $44.1 \pm 11.2\%$)
349 contractions. The FCC signal likely reflects the effective drive to the muscle because it captures
350 low-frequency oscillations of the force signal^{40,41,44}. Here, we reported an increased variability
351 (CV) of the force signal during bilateral compared with unilateral contractions, demonstrating a
352 poorer force control during the bilateral tasks. Our findings are consistent with previous
353 behavioral studies showing that the bimanual force output was more variable with respect to
354 unilateral conditions^{42,43}. In addition, our results showed that the variability of the FCC signal was
355 greater in the bilateral contractions than in the unilateral contractions, indicating an increased
356 variability in the smoothed discharge rate during bilateral contractions. It was previously shown
357 that the low-frequency oscillations of MU discharge rate regulate force steadiness and the FCC
358 signal captures most of the force fluctuation^{41,44}. Thus, the increased variability in the FCC signal
359 may be related to the reduced ability of the nervous system to produce a stable neural drive to
360 the muscle during bilateral contractions. This is in agreement with previous studies showing that
361 the effective neural drive to muscles was reduced during a maximal bilateral contraction^{33-35,68}.
362 This is also supported by the high correlation found between the CV for the FCC signal and the
363 CV for the force signal, in which we found that participants with more variability of the FCC signal
364 also showed larger force fluctuation. This result further confirms that the low-frequency

365 oscillatory component of the MU discharge rate has a great influence on force fluctuation.
366 Together, our results indicate that the differences in force variability during unilateral and
367 bilateral contractions could be attributed to changes at the low-frequency components of
368 synaptic inputs to motor neurons.

369 *Conclusion*

370 In conclusion, we analyzed the behavior of motor neurons and low-frequency common
371 synaptic inputs to motor neurons during unilateral and bilateral contractions. Understanding the
372 bilateral control properties regulating motor neuron behavior and common synaptic inputs is
373 important for understanding the mechanisms underlying motor abnormality. Thus, our results
374 are particularly relevant for individuals with neurological disorders, such as stroke⁶⁹⁻⁷¹ and spinal
375 cord injury^{72,73}, since bilateral training is a common motor rehabilitation strategy for those
376 patients. Therefore, our findings can provide the background information for developing
377 rehabilitation strategies for patients with stroke and spinal cord injury.

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581 **Figure legends**

582 **Figure 1. A**, diagram showing the visual display presented to all subjects during testing of
583 unilateral and bilateral contractions. Subjects were instructed to remain at rest with the left hand
584 while the right hand was at rest or performed 10 or 30% of maximal voluntary contraction (MVC)
585 during index finger abduction. The trapezoids represent the trajectories that subjects needed to
586 keep the cursor in. The trapezoid width (geometry height of the trapezoid) represents the
587 magnitude of force required to accomplish each task, normalized to the maximal index finger
588 abduction determined in each subject. **B**, Motor unit recruitment threshold and discharge rate
589 during an isometric contraction of the first dorsal interosseous (FDI) muscle (plateau 10% of MVC)
590 in a representative subject. The arrows highlight the recruitment of identified motor units. The
591 black line represents the net force output. **C**, The smoothed discharge rate of six representative
592 motor units.

593 **Figure 2. A**, The instantaneous motor unit discharge rate as a function of time for the three
594 representative motor units during unilateral (black) and bilateral (grey) contractions. **B**, Group
595 data (n=13) showing peak discharge rate during unilateral and bilateral contractions. Data from
596 individual subjects are shown. **C**, Group data (n=13) showing average discharge rate during
597 unilateral and bilateral contractions. Data from individual subjects are shown. **D**, Group data
598 (n=13) showing inter pulse interval during unilateral and bilateral contractions. Data from
599 individual subjects are shown. Error bars indicate SEs. *P<0.05, comparison between unilateral
600 and bilateral contractions.

601 **Figure 3. A**, Motor unit recorded from the FDI muscle. The amplitude and duration of motor unit
602 action potential (MUAP) were measured as shown by the arrows. **B**, Group data (n=13) showing
603 MUAP amplitude during unilateral and bilateral contractions. **C**, Group data (n=13) showing
604 MUAP duration during unilateral and bilateral contractions. **D**, Group data (n=13) showing MU
605 recruitment threshold during unilateral and bilateral contractions. Error bars indicate SEs.
606 *P<0.05, comparison between unilateral and bilateral contractions.

607 **Figure 4. A**, MUAP amplitude as a function of the threshold force at each contraction in a
608 representative subject. Linear regression lines are drawn through the data at each contraction.
609 **B**, MU discharge rate as a function of MUAP amplitude at each contraction in a representative
610 subject. An individual power function is fit to the data at each contraction. **C**, MU discharge rate
611 as a function of the threshold force at each contraction with regression lines superimposed on
612 motor units in a representative subject. Each data point represents 1 MU. Group data (n=13)
613 showing the fitted slopes are also shown.

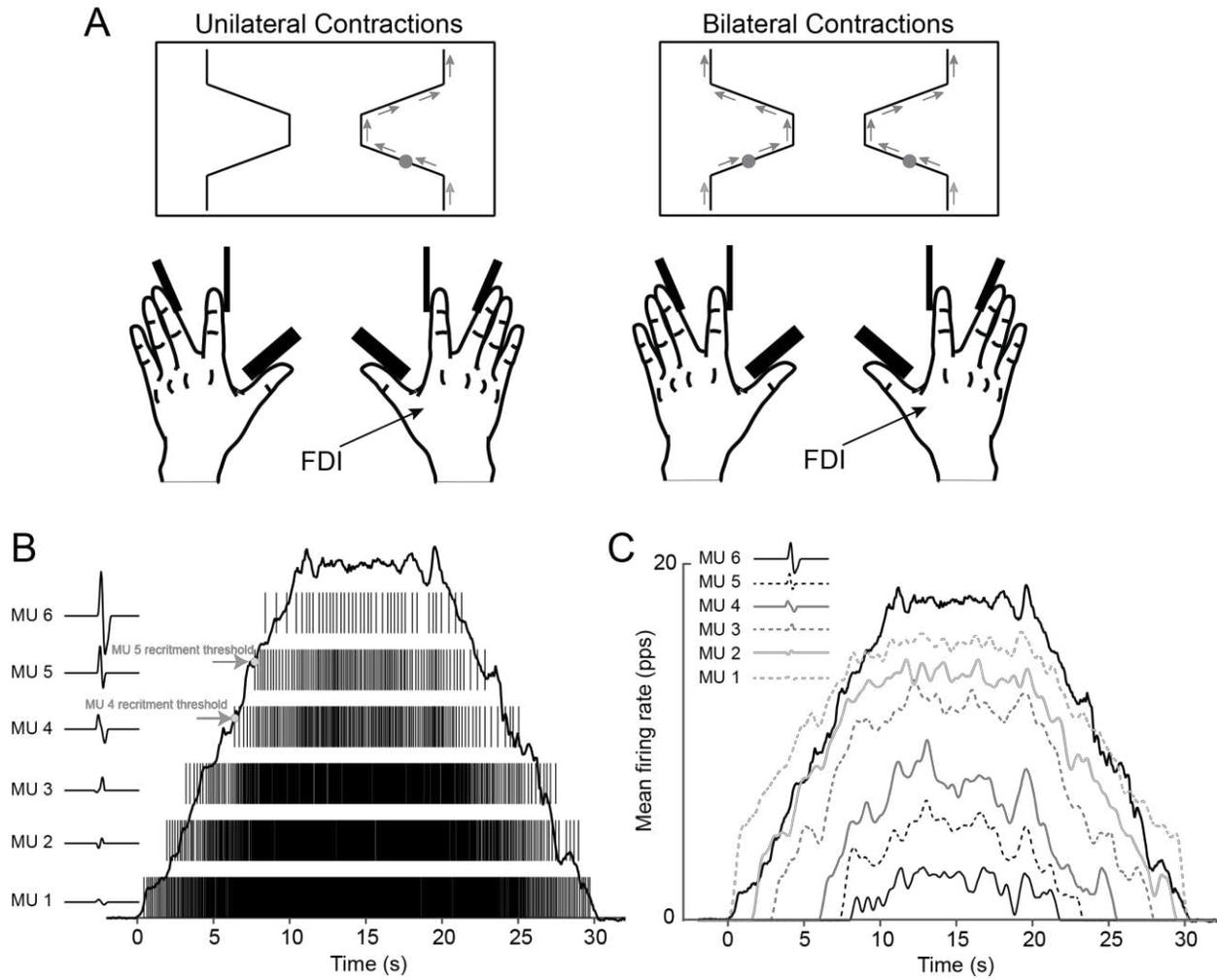
614 **Figure 5. A**, First common component (FCC) and force. Comparison between the FCC and the
615 force signal during unilateral and bilateral contractions in a representative subject. **B**, graph
616 showing correlation between the CVs for the force and FCC signal. Note that individuals with
617 more force fluctuation were the ones with larger variability in low-frequency oscillations of MU
618 discharge rate.

619 **Figure 6.** Graph showing correlation between the CVs for the force and FCC signal. Note that
620 individuals with more force fluctuation were the ones with larger variability in low-frequency
621 oscillations of MU discharge rate.

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Figure 1

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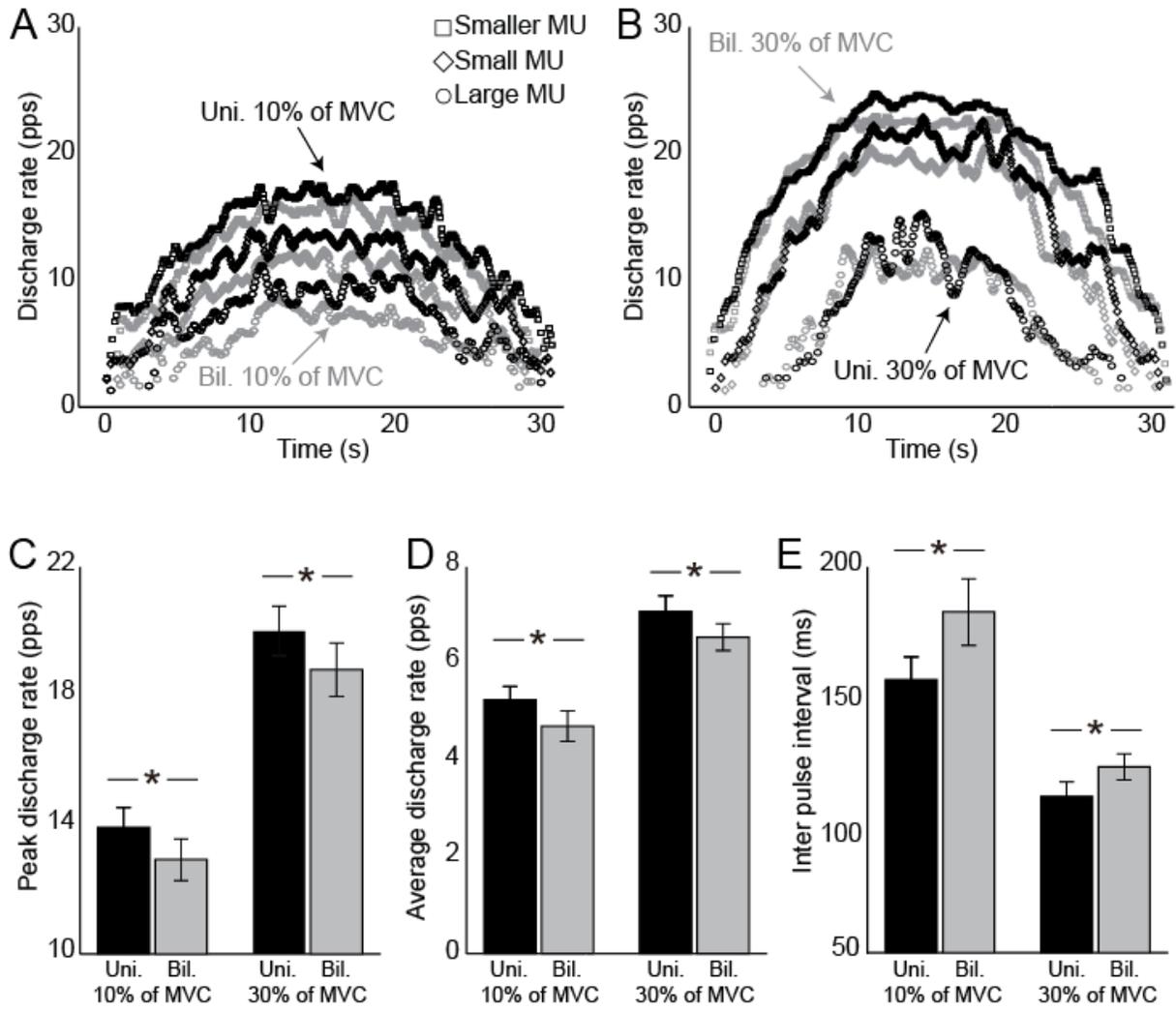
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Figure 3

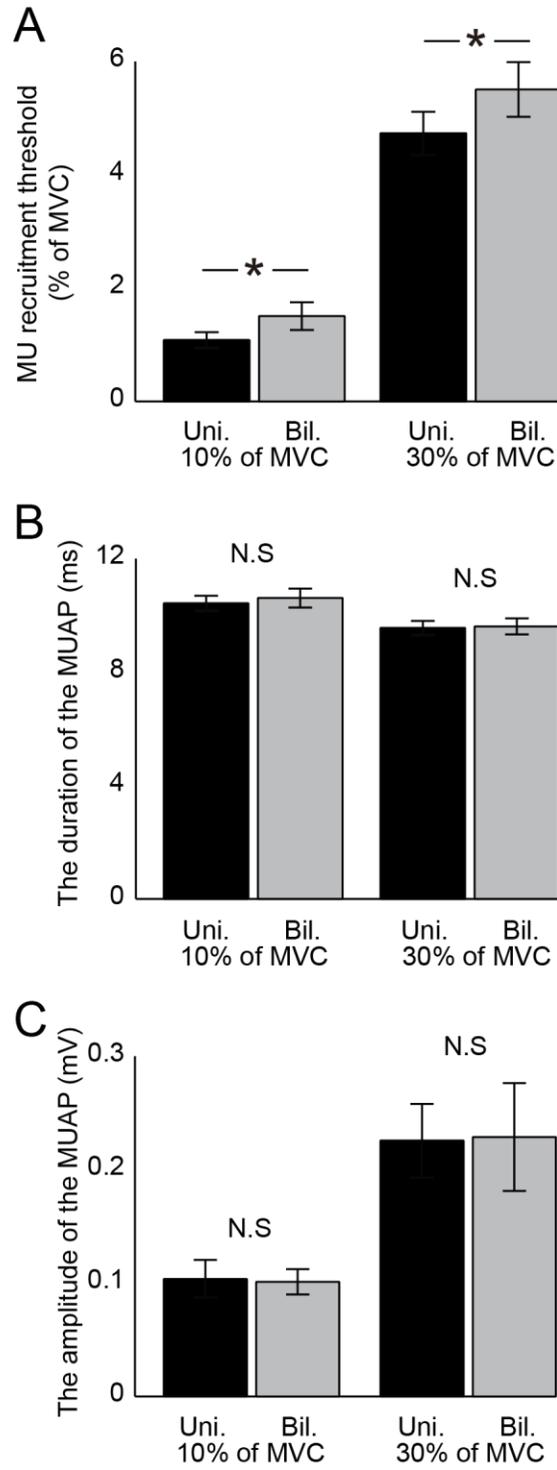
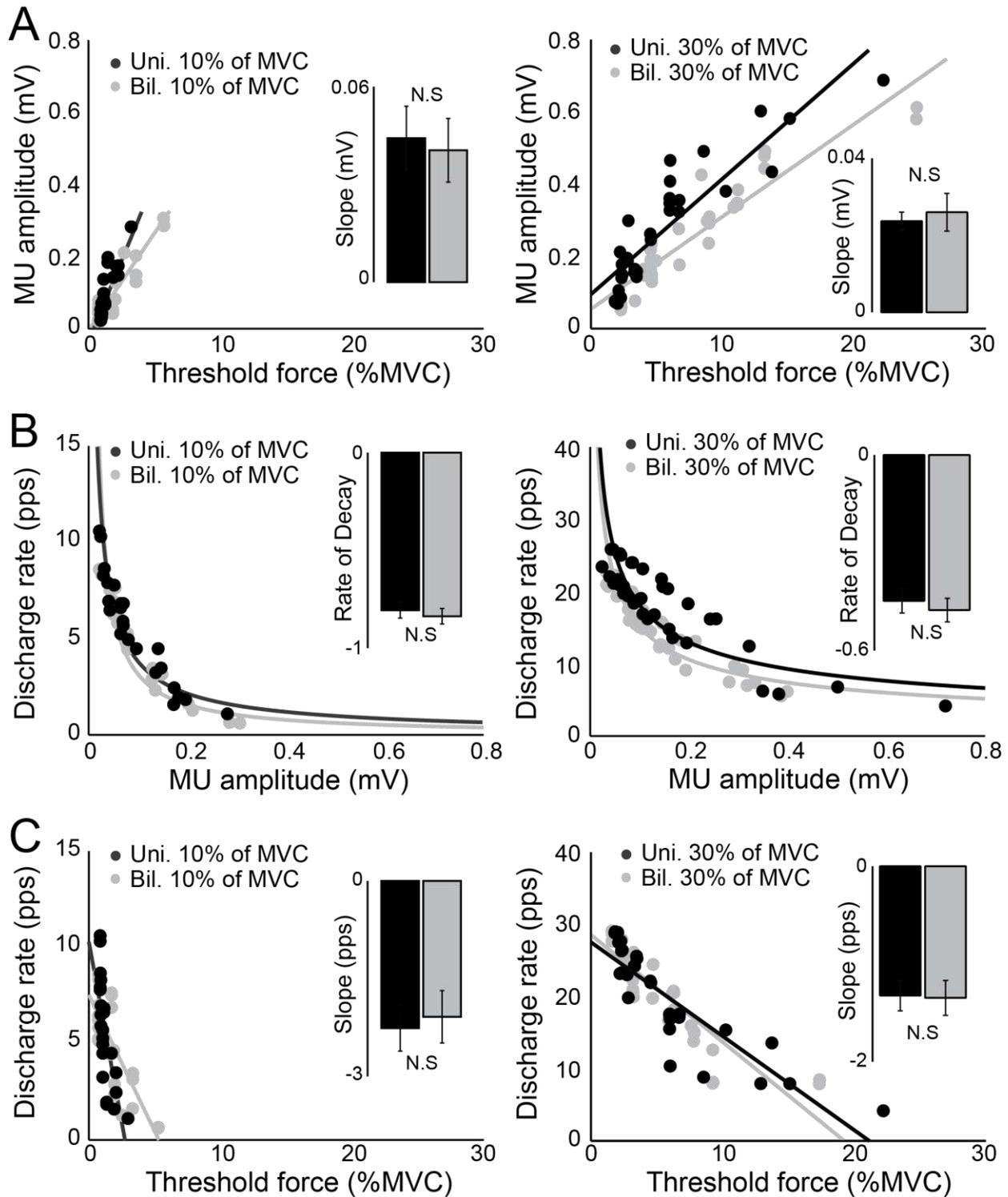


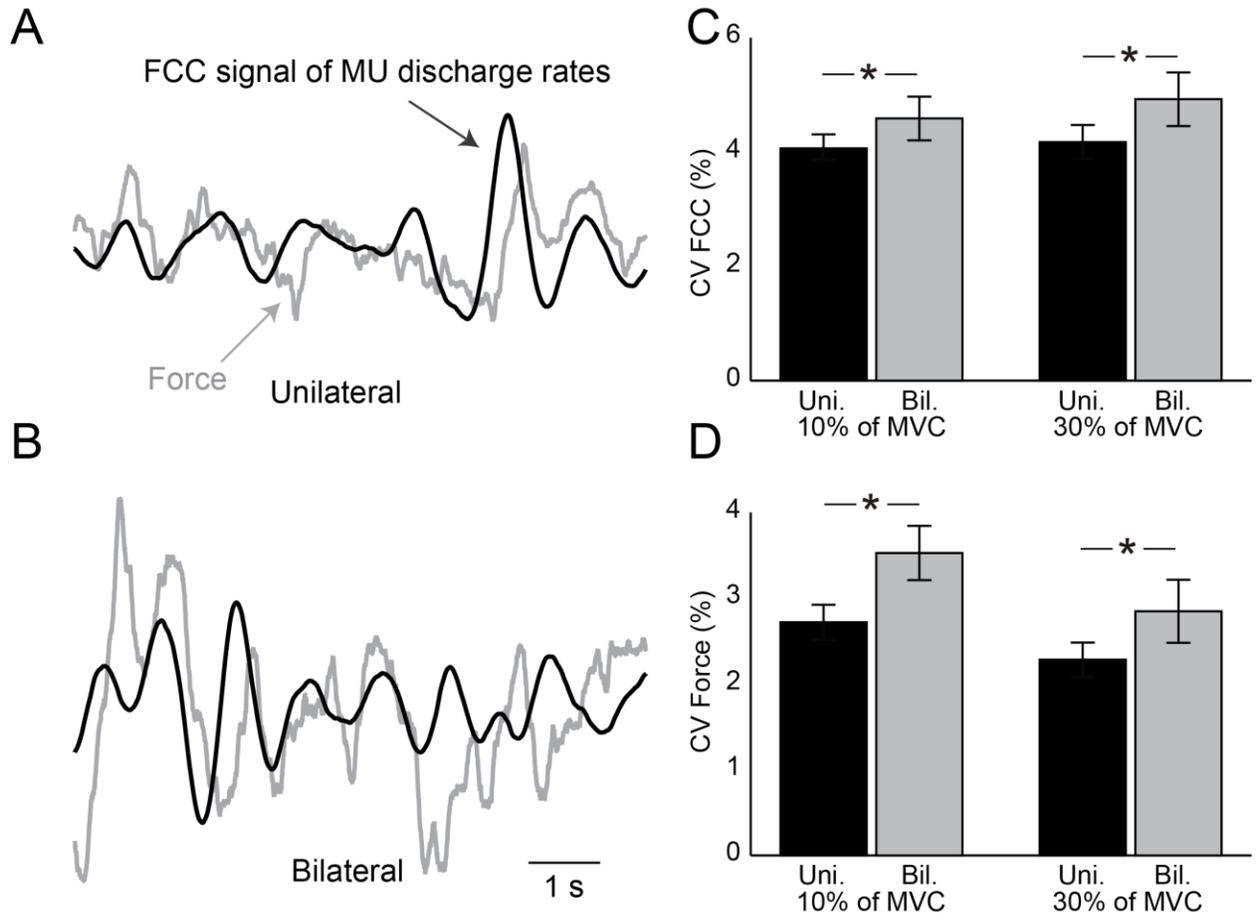
Figure 4



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Figure 5

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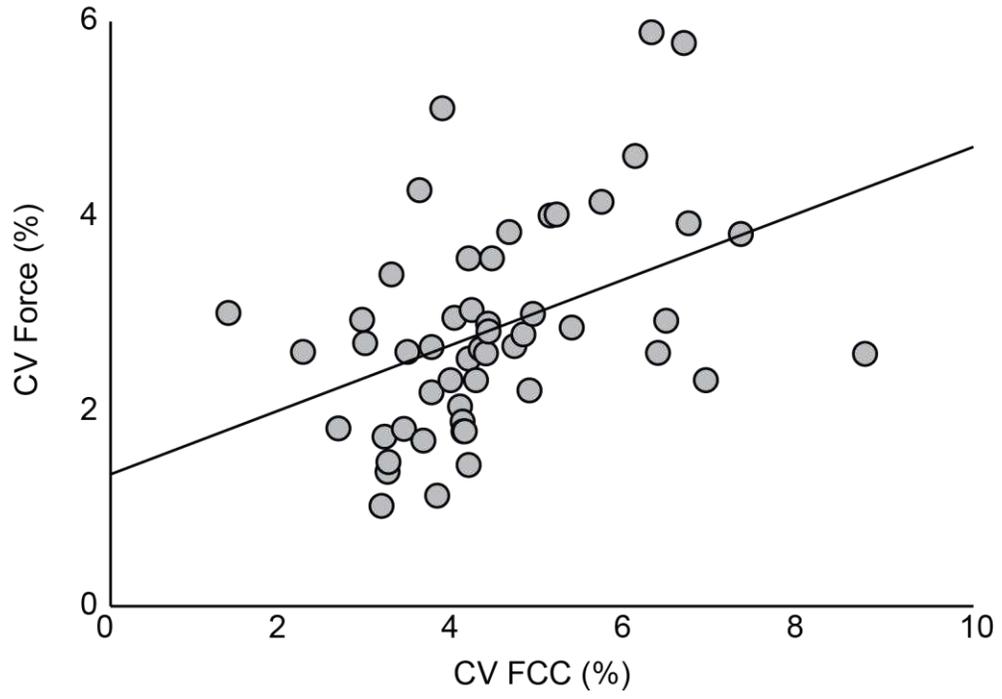
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Figure 6



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