



HAL
open science

Muscles from the same muscle group do not necessarily share common drive: evidence from the human triceps surae

François Hug, Alessandro del Vecchio, Simon Avrillon, Dario Farina, Kylie Tucker

► To cite this version:

François Hug, Alessandro del Vecchio, Simon Avrillon, Dario Farina, Kylie Tucker. Muscles from the same muscle group do not necessarily share common drive: evidence from the human triceps surae. *Journal of Applied Physiology*, 2021, 130 (2), pp.342-354. 10.1152/jappphysiol.00635.2020 . hal-03298614v1

HAL Id: hal-03298614

<https://nantes-universite.hal.science/hal-03298614v1>

Submitted on 31 May 2022 (v1), last revised 4 Apr 2023 (v2)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Muscles from the same muscle group do not necessarily share common**
2 **drive: evidence from the human triceps surae**

3
4 François HUG^{1,2,3}, Alessandro DEL VECCHIO^{4,5}, Simon AVRILLON^{2,6,7},
5 Dario FARINA⁴, Kylie TUCKER²
6

7 ¹ Nantes University, Laboratory “Movement, Interactions, Performance” (EA 4334), Nantes,
8 France

9 ² The University of Queensland, School of Biomedical Sciences, Brisbane, Australia

10 ³ Institut Universitaire de France (IUF), Paris, France

11 ⁴ Neuromechanics & Rehabilitation Technology Group, Department of Bioengineering,
12 Faculty of Engineering, Imperial College London, UK

13 ⁵ Neuromuscular Physiology and Neural Interfacing Group, Department of Artificial
14 Intelligence in Biomedical Engineering, Faculty of Engineering, Friedrich-Alexander
15 University, Erlangen-Nuremberg, 91052, Erlangen, Germany

16 ⁶ Legs + Walking AbilityLab, Shirley Ryan AbilityLab, Chicago, IL, USA

17 ⁷ Department of Physical Medicine and Rehabilitation, Northwestern University, Chicago, IL,
18 USA
19
20
21

22 **Correspondence and reprints:**

Prof. François Hug
University of Nantes
Laboratory « Movement, Interactions, Performance » (EA 4334)
25 bis boulevard Guy Mollet
44300 Nantes (France)
e-mail: francois.hug@univ-nantes.fr

23
24 **Running title:** Independent control of synergist muscles
25

26 **Keywords:** Muscle synergies, gastrocnemius, common drive, electromyography, motor units,
27 coherence
28

29 **Acknowledgements:** François Hug is supported by a fellowship from the *Institut*
30 *Universitaire de France* (IUF) and a travel grant from the *Société de Biomécanique*. Support
31 was received from the French national research agency (ANR-19-CE17-002-01, COMMODE
32 project; to FH) and from the European Research Council Synergy Grant NaturalBionicS
33 (contract #810346; to DF).
34

35 All the authors in this paper have no financial or other relationships that might lead to a
36 conflict of interest.
37

38 **Dataset** availability: <https://doi.org/10.6084/m9.figshare.12126627>

39 **Abstract (250 words)**

40

41 It has been proposed that movements are produced through groups of muscles, or motor
42 modules, activated by common neural commands. However, the neural origin of motor
43 modules is still debated. Here, we used complementary approaches to determine: i) whether
44 three muscles of the same muscle group (soleus, gastrocnemius medialis [GM] and lateralis
45 [GL]) are activated by a common neural drive ; and ii) whether the neural drive to GM and
46 GL could be differentially modified by altering the mechanical requirements of the task.
47 Eighteen human participants performed an isometric standing heel raise and submaximal
48 isometric plantarflexions (10%, 30%, 50% of maximal effort). High-density surface
49 electromyography recordings were decomposed into motor unit action potentials and
50 coherence analysis was applied on the motor units spike trains. We identified strong common
51 drive to each muscle, but minimal common drive between the muscles. Further, large
52 between-muscle differences were observed during the isometric plantarflexions, such as a
53 delayed recruitment time of GL compared to GM and soleus motor units and opposite time-
54 dependent changes in the estimates of neural drive to muscles during the torque plateau.
55 Finally, the feet position adopted during the heel raise task (neutral vs internally rotated)
56 affected only the GL neural drive with no change for GM. These results provide conclusive
57 evidence that not all anatomically defined synergist muscles are controlled by strong common
58 neural drive. Independent drive to some muscles from the same muscle group may allow for
59 more flexible control to comply with secondary goals such as joint stabilization.

60

61 **New and Noteworthy**

62 In this study, we demonstrated that the three muscles composing the human triceps surae
63 share minimal common drive during isometric contractions. Our results suggest that reducing
64 the number of effectively controlled degrees of freedom may not always be the strategy

65 employed by the central nervous system to control movements. Independent control of some,
66 but not all, synergist muscles may allow for more flexible control to comply with secondary
67 goals (e.g. joint stabilization).

68

69

70 **Introduction**

71 How the central nervous system controls the large number of degrees of freedom of the
72 musculoskeletal system to produce movements remains unclear. It has been proposed that
73 muscles are controlled through motor modules, which represent groups of muscles, activated
74 by a single neural command (9, 20, 47). Evidence for the existence of motor modules, which
75 reduce the dimensionality in the control of movement, comes from animal models where
76 cortical (45) or spinal micro-stimulation (46) led to complex multi-joint forces. However, the
77 neural origin of motor modules is still debated (8, 36).

78

79 In support of the modular control of movements, there is evidence that some muscles are
80 controlled primarily by shared neural drive (11, 25, 35, 37), and that the intensity of this
81 shared drive is stronger between muscles that are anatomically and functionally closely
82 related (25, 35). Considering the behavior of a population of motor units identified from high-
83 density surface electromyography (HDsEMG), Laine et al. (37) demonstrated that the lateral
84 [vastus lateralis (VL)] and medial [vastus medialis (VM)] head of the quadriceps share most
85 of their synaptic input during isometric knee extension. Given the important role of VL and
86 VM in the control of the patellofemoral joint (40), this shared common input might achieve
87 two important goals: i) simplify the control of the task, and ii) regulate internal joint stresses.
88 While shared drive may be an optimal control strategy for the VL and VM muscles, it might
89 not be optimal for muscles that require more flexible control.

90

91 The *triceps surae* consists of the soleus (SOL), gastrocnemius medialis (GM) and lateralis
92 (GL). As GM and GL share the same two main functions (plantarflexion and knee flexion),
93 and both insert into the Achilles tendon, they are very often regarded as the same muscle (52).
94 In addition, using factorization of multiple bipolar EMG signals, these muscles are

95 consistently reported as part of the same module [e.g., gait (49), pedaling (33)]. However,
96 there is some indirect evidence that GM and GL may produce different ankle torques in the
97 frontal plane (39, 50). As such, flexibility in their control with minimal common drive, i.e. the
98 ability to activate the muscles independently, might be crucial for maintaining balance or
99 producing force in different directions. For example, Héroux et al. (27) observed a difference
100 in GM and GL motor unit discharge behavior during standing balance, with a relative absence
101 of GL motor unit activity. Taken together, these results suggest that the activation of the GM
102 and GL muscles may be partly independent, with a small amount of common drive, to allow
103 for flexible control of the ankle joint.

104

105 In this study we used multiple, complementary approaches to characterize the behavior of
106 populations of motor neurons innervating the three heads of the *triceps surae*, with specific
107 consideration of GM and GL. Our primary aim was to determine whether GL and GM share a
108 common neural drive during plantarflexion. We first estimated the within- and between-
109 muscle common neural drive using correlation techniques in the frequency domain (i.e.,
110 coherence(22, 24) applied to motor units spike trains identified from an isometric heel raise
111 task. Then, we assessed motor unit discharge characteristics during isometric plantarflexions
112 performed on an ergometer. Our secondary aim was to determine whether the neural drive to
113 GM and GL could be differentially modified by altering the mechanical requirements of the
114 task. For this purpose, we compared the motor unit discharge rate between two heel raise
115 tasks performed with different feet positions. We hypothesized that the GM and GL muscles
116 share minimal common drive, and therefore, that the neural drive to the GM and GL can be
117 independently altered. If supported, this would provide strong evidence that some
118 anatomically derived synergist muscles can be controlled by independent neural drive, and
119 force a reconsideration of our understanding of the modular control of movement.

120 **Methods**

121 **1. Participants**

122 Eighteen physically active males participated in this study (mean±standard deviation; age:
123 29.4±7.9 yr, height: 180±7 cm, body mass: 76±8 kg; body mass index: 23.6±2.7 kg.m⁻²). Of
124 note, we were not avoiding recruiting females; but for unknown reasons we failed to identify
125 enough motor units on females during our pilot testing, especially on GL. Participants had no
126 history of lower leg pain that had limited function that required time off work or sport, or a
127 consultation with a health practitioner in the previous six months. The institutional research
128 ethics committee of the University of Queensland approved this study (n°2013001448), and
129 all procedures adhered to the Declaration of Helsinki. Participants provided informed written
130 consent.

131

132 **2. Experimental design**

133 The experimental session consisted of a series of isometric and postural tasks. The
134 myoelectrical activity of the three heads of the *triceps surae* of the dominant leg (right/left;
135 16/2) was measured using HDsEMG.

136 First, participants laid prone on a custom-made dynamometer equipped with a torque sensor
137 (TRE-50K, Dacell, Korea; Fig. 1). Their knee was fully extended, and their ankle angle was
138 set to 10° of plantarflexion (0° being the foot perpendicular to the shank). The experiment
139 began with a warm-up, which included a series of submaximal contractions. Then,
140 participants performed three maximal isometric contractions for 3 to 5 s with 120-s rest in
141 between. The maximal value obtained from a moving average window of 250-ms was
142 considered as the peak torque (MVC). Then, participants performed three contractions at each
143 of the following intensities: 10%, 30%, and 50% of their MVC. The order of the intensities
144 was randomized. These contractions involved a 5-s ramp-up, a 15-s (50% of MVC) or 20-s

145 plateau (10% and 30% of MVC) and a 5-s ramp down phase. The contractions were separated
146 by either 60-s (10% of MVC) or 120-s (30% and 50% of MVC) of rest. Feedback of the target
147 and torque output was displayed on a monitor.

148 Second, participants stood barefoot on a force plate (Model 4060, Bertec, UK) and performed
149 a series of six tasks in a randomized order, including balance and heel-raise tasks. The balance
150 tasks were performed for another purpose. For the purpose of this study only the two
151 isometric heel-raise tasks were analyzed. These tasks consisted of holding the heel at a
152 standard height of 6 cm, with both feet in a neutral position (Toes neutral) or internally
153 rotated (Toes in) (Fig. 1). To provide feedback of the height, a 6-cm thick piece of high-
154 density foam was placed under the heels of the participants. The participants were instructed
155 to lightly touch the top of the foam with their heels and once the correct height was achieved
156 (in typically less than 5s), the piece of foam was removed, and data collection began. For the
157 Toes neutral condition, the participants adopted a comfortable stance width with their feet
158 pointing anteriorly. For the Toes in condition, the participants pointed their toes inward by
159 internally rotating their lower limbs, such that their feet formed an angle of 90°. About 1/4 of
160 the participants could not reach this angle in which case they were instructed to rotate their
161 lower limbs as far as possible. Each of these conditions was repeated two times for 30 to 35s
162 with 15-20 s of rest in between.

163 For both the plantarflexion tasks performed on the ergometer and the heel raise tasks, the
164 mechanical signals (torque and force) were digitized at 2048 Hz using the same acquisition
165 system as that used for HDsEMG (EMG-Quattrocento; 400-channel EMG amplifier, OT
166 Bioelettronica, Italy).

167 Note that additional measurements were performed on the VL and VM muscles for two
168 participants (#5 and #10). These participants performed an isometric body-weight squat (knee
169 angle=30°; 0°=knee fully extended) for 3×30s.

170

171 **3. High-density surface EMG recordings**

172 HDsEMG signals were recorded from the GL, GM, and SOL muscles. Two-dimensional
173 adhesive grids of 64 electrodes (13×5 electrodes with one electrode absent on a corner, gold-
174 coated, inter-electrode distance: 8 mm; [ELSCH064NM2, SpesMedica, Battipaglia, Italy])
175 were placed over both the GM and the GL muscle (Fig. 1). The grids were aligned with the
176 main fascicle direction as determined using B-mode ultrasound (Aixplorer, Supersonic
177 Imagine, France). A two-dimensional adhesive grid of 32 electrodes (8×4 electrodes, gold-
178 coated, inter-electrode distance: 10 mm; [GR10MM0804, SpesMedica, Battipaglia, Italy])
179 was placed on the medial part of the SOL, below the myotendinous junction of the GM
180 muscle (Fig. 1). This electrode was aligned with the supposed line of action of the muscle.
181 Before electrode application, the skin was shaved, and then cleaned with an abrasive pad and
182 alcohol. The adhesive grids were held on the skin using semi-disposable bi-adhesive foam
183 layers (SpesMedica, Battipaglia, Italy). The skin-electrode contact was made by filling the
184 cavities of the adhesive layers with conductive paste (SpesMedica, Battipaglia, Italy). A 8-cm
185 wide elastic band was placed over the three electrodes with a slight tension to ensure that all
186 the electrodes remained in contact with the skin throughout the experiment. Strap electrodes
187 dampened with water were placed around the contralateral (ground electrode) and ipsilateral
188 ankle (reference electrode). The EMG signals were recorded in monopolar mode, bandpass
189 filtered (10-900 Hz) and digitized at a sampling rate of 2048 Hz using a multichannel
190 acquisition system (EMG-Quattrocento; 400-channel EMG amplifier, OT Bioelettronica,
191 Italy).

192

193 **4. Data analysis**

194 In this study, we considered the neural drive as the ensemble of motor neuron discharges, and
195 this drive was estimated using the cumulative spike train (CST, sum of the motor unit
196 discharge times) of a subset of motor neurons identified by decomposition. Common drive
197 was considered as the component of the neural drive that is shared between motor neurons,
198 i.e. the common (correlated) fluctuations of motor unit discharge timings.

199

200 *Global EMG*

201 EMG signals were band-pass filtered (20-500 Hz), differentiated, and full-wave rectified. For
202 the MVC trials, the EMG amplitude was calculated over a moving time window of 500 ms.
203 The resulting highest value over the three contractions and over all the channels of the grid
204 was considered as the maximal EMG amplitude value. For the submaximal tasks, the EMG
205 amplitude was calculated over the whole contraction, averaged across all channels, and
206 normalized to that determined during the maximal isometric contractions.

207

208 *HDsEMG decomposition*

209 First, the monopolar EMG signals were bandpass filtered between 20-750 Hz with a second-
210 order Butterworth filter. The HDsEMG signals were decomposed with the convolutive blind
211 source separation method (31) implemented in the DEMUSE tool software (v4.9; The
212 University of Maribor, Slovenia). This decomposition procedure can identify motor unit
213 discharge times over a wide range of contraction intensities and has been extensively
214 validated using experimental and simulated signals (29, 30). After the automatic identification
215 of the motor units, all the motor unit spike trains were visually inspected (17, 18). As
216 classically done, only the motor units, which exhibited a pulse-to-noise ratio > 30 dB were
217 retained for further analysis (19, 37). This threshold ensured a sensitivity higher than 90% and
218 a false-alarm rate lower than 2% (30).

219

220 *Assessment of cross-talk*

221 Before assessing the neural connectivity between the different populations of motor neurons
222 of the *triceps surae*, we used the discharge timings extracted by decomposition to assess the
223 uniqueness of the motor unit action potentials. This was done to guarantee that each motor
224 unit that was used for subsequent analysis originated from the target muscles on which the
225 high-density EMG grid was placed and was not a result of cross-talk from a neighboring
226 muscle. For this purpose, the discharge timings of each motor unit extracted by
227 decomposition were used to trigger all of the HDsEMG signals (64 [GM] +64 [GL] +32
228 [SOL] channels). The motor unit action potentials extracted by spike trigger averaging were
229 then compared between muscles. Specifically, we calculated the average amplitude of the
230 motor unit action potential, for each HDsEMG grid, by averaging the peak-to-peak amplitude
231 across all channels of each HDsEMG grid. We then compared this average peak-to-peak
232 amplitude between grids to identify motor units that originated from crosstalk. This analysis
233 assumes that the action potential representation of a motor unit will be largest when recorded
234 from the electrodes placed on the muscle of origin. Conversely, motor units that are identified
235 from a neighboring muscle will have a smaller peak-to-peak amplitude due to a greater
236 distance between the electrodes and the muscle unit (18). As such, if the average peak-to-peak
237 amplitude of a motor unit was higher in one of the muscles from where this units was not
238 originally identified, this unit was visually inspected and then omitted from the analysis.-

239

240 *Within- and between-muscle coherence*

241 We used a coherence analysis to assess the neural connectivity between motor units from the
242 same (within-muscle coherence) or from different muscles (between-muscle coherence) (3).
243 Note that coherence calculated at a given frequency represents the correlation between the

244 two signals at that frequency, with 0 indicating non correlation and 1 indicating perfect
245 correlation. Coherence within the delta band (0-5Hz) reflects the presence of common drive
246 (16, 18, 37).

247 Because the GL motor units were recruited late during the plateau of the isometric
248 plantarflexion tasks performed on the ergometer (see *Results*), the number of discharges was
249 too low to conduct coherence analysis on these tasks. In other words, too few motor units
250 were recruited during enough time to run a meaningful coherence analysis. Thus, the
251 coherence analysis was only performed on the isometric heel raise task, with Toes neutral, as
252 this was the condition during which the greatest number of motor units were identified for
253 both GM and GL.

254 Prior to this coherence analysis, the discharge times of each motor unit were visually
255 inspected. Even if it was not frequently observed, pauses in the recruitment of some motor
256 units occasionally occurred. Such pauses can affect the calculation of the coherence.
257 Therefore, if one motor unit exhibited a pause in discharges for $> 2s$, this portion of the signal
258 was discarded for all motor units. If for a given unit these pauses occurred too often, that
259 motor unit was not considered such that the analysis could still be performed on all other
260 units. On average the coherence analysis was performed on 54 ± 16 s and 47 ± 13 s, for within-
261 muscle and between-muscle coherence, respectively.

262 For the within-muscle coherence, we calculated the magnitude-squared coherence using the
263 Welch's periodogram with non-overlapping windows of 1-s (Fig 2). This analysis was
264 performed on two equally sized groups of CST. The number of motor units in each of the two
265 groups varied from 1 to the maximum number (half of the total number of identified units)
266 and 100 random permutations of the identified units were performed for each iteration. Then,
267 we estimated the proportion of common synaptic input to motor neurons using the method
268 described by Negro et al. (44). For this analysis we focused on the low frequency bandwidth

269 (0-5 Hz), as it has been shown to be the main determinant of the force output (22). The
270 relationship between the average values of coherence in the bandwidth 0-5 Hz and the number
271 of motor units was fitted by least-squares using a non-linear equation described in Negro et al.
272 (44). The rate of change (the slope) was considered as the proportion of common input with
273 respect to the total input received by the motor neuron pool (Fig. 2) [PCI; (44)]. This method
274 was validated in numerical simulations, which were based on a model of populations of motor
275 neurons that received common and independent inputs (44). The advantage of this method is
276 to provide a quantitative estimate of the relative strength of the common synaptic input,
277 independent of the number of identified units, allowing us to make direct comparisons
278 between muscles.

279 The between-muscle coherence was assessed in a similar way as the within-muscle coherence.
280 Specifically, the total number of identified motor units was used to generate the CST. Then,
281 we applied the coherence function between the CST for each muscle pair (GM-GL, GM-SOL,
282 GL-SOL). Coherence was considered significant when it was higher than the maximum value
283 of coherence for frequencies > 100 Hz, where no coherence is expected (4). In addition, we
284 considered the presence of substantial common neural drive if the coherence values reached
285 this significance threshold over the entire bandwidth 0-5 Hz.

286

287 *Motor unit discharge characteristics*

288 To compare the neural drive received by the three muscles during the isometric
289 plantarflexions performed on the ergometer, we calculated three indexes (Fig. 3). First, the
290 time of recruitment of each motor unit was determined for each contraction as the time when
291 the first action potential was observed (Fig. 3). As these tasks involved a 5-s ramp-up phase
292 before the torque plateau, a value higher than 5 s indicated that the motor unit was recruited
293 during the plateau. As expected, most of GM and SOL motor units were recruited during the

294 ramp-up phase, but surprisingly, most of the GL motor units were recruited during the plateau
295 (Fig. 3). Therefore, we were unable to consider the joint torque associated with recruitment
296 (i.e, the recruitment threshold), as classically done. Second, we determined the delta discharge
297 rate (expressed in pps.s⁻¹) to provide an estimate of the synaptic inputs received by the motor
298 neuron pools (42). This was calculated as the rate of change in discharge rate within the first 2
299 s of recruitment (Fig. 3). Because variability in instantaneous discharge rate may occur at
300 recruitment, we considered the discharge rate at recruitment as the mean of the first three
301 discharges (21). Finally, we estimated the discharge rate of each motor unit during the
302 plateau. However, as shown in Fig. 3, time-dependent changes in discharge rate were
303 observed during the plateau, with most of the GM motor units exhibiting a decrease in their
304 discharge rate. Consequently, we used a sixth-order polynomial to smooth the instantaneous
305 discharge rates (26) and then we considered the peak discharge rate from this polynomial fit.
306 We further assessed the difference in neural drive received by the three muscles by comparing
307 their time-dependent changes in neural drive during the torque plateau. To this end, we
308 estimated the neural drive through the calculation of the cumulative spike train (CST) of the
309 identified motor units (19, 43). To generate the CST of each muscle, the individual motor unit
310 discharge timings were summed and then smoothed with a Hanning window of 400-ms
311 duration (15). After down-sampling the data by 100, we calculated the slope of the linear
312 regression between CST and time to determine whether the CST decreased (negative slope
313 different to 0), increased (positive slope different to 0) or remained stable during the torque
314 plateau.

315 To determine whether the feet configuration (Toes neutral and Toes in) adopted during the
316 heel raise tasks could differentially affect GM and GL recruitment, we calculated the mean
317 motor unit discharge rate. Values of discharge rate < 4 pps were removed from this
318 calculation, as such discharge rates likely indicate inconsistent firings of the motor units (42).

319 Note that SOL motor units were not considered in this part of the experiment, as it is already
320 well known that the SOL and gastrocnemii muscles can be differentially activated by
321 modifying the knee angle (34, 38), as is expected given their different function around the
322 knee.

323

324

325

326

327 **5. Statistical analysis**

328 A Shapiro-Wilk test was used to test for a normal distribution. The discharge rate data
329 measured during the heel raise task (Toes in and Toes neutral conditions) did not pass the
330 normality test. Therefore, these data were transformed [$1/\sqrt{x}$]. The distributions of
331 the time at recruitment and delta discharge rate values did not pass the normality test either.
332 However, because no transformation was able to provide a normal distribution, we performed
333 non-parametric tests on these data. All data are reported as mean \pm standard deviation and the
334 level of significance was set at $p \leq 0.05$.

335 Statistical analyses were performed in Statistica v7.0 (Statsoft, Tulsa, OK, USA). The within-
336 muscle coherence analysis was only performed when ≥ 4 motor units were identified.
337 Consequently, the number of participants considered for this analysis differed between
338 muscles. For this reason, we used a one-way ANOVA for independent samples to compare
339 the PCI between muscles [between-subject factor: muscle (GM, GL, SOL)].

340 It is likely that different populations of motor units, with different intrinsic properties, were
341 identified during the plantarflexion tasks performed at the different intensities (10%, 20%,
342 and 50%). For this reason, we did not directly compare the time at recruitment and the *delta*
343 discharge rate between intensities, and these values were only compared between muscles
344 using a Kruskal-Wallis test for main effect [between-subject factor: muscle (GM, GL, SOL)].

345 When appropriate, *post hoc* analyses were performed using multiple comparisons of mean

346 ranks.

347 The peak motor unit discharge rate estimated from the polynomial fit during the isometric
348 plantarflexions was compared between muscles and contraction intensities using a 2-way
349 ANOVA [between-subject factor: muscle (GM, GL, SOL) and intensity (10%, 20%, and
350 50%)]. A similar two-way ANOVA was performed to test the effect of the feet position on the
351 discharge rate of GL and GM [between-subject factor: muscle (GM, GL, SOL) and condition
352 (Toes Neutral and Toes In)]. When appropriate, *post hoc* analyses were performed using the
353 Bonferroni test.

354

355 **Results**

356 The entire dataset (raw and processed data) is available at
357 <https://doi.org/10.6084/m9.figshare.12126627>

358

359 *Motor unit decomposition*

360 First, the spike-triggered averaging technique was used to identify decomposed motor units,
361 which might originate from crosstalk of one of the two other muscles. To achieve this aim, we
362 compared the amplitude of the ensemble-averaged motor unit action potentials. At this stage,
363 17 motor units that were identified from the array placed above the GL ($\approx 4\%$ of the total
364 number of GL motor units) were suspected to originate from GM. After exclusion of these
365 motor units, the number of decomposed units over each of the five motor tasks ranged from
366 173 to 335 for GM, 10 to 120 for GL, and 65 to 94 for SOL (Table 1). Note that only 10
367 motor units were decomposed for GL from the isometric plantarflexion performed at 10% of
368 MVC, which is consistent with the low global GL EMG amplitude measured at this
369 contraction intensity, i.e. $7.1 \pm 2.4\%$ of the maximal EMG amplitude measured during MVC.

370 The pulse-to-noise ratio averaged over the three muscles and the five tasks (i.e. a total of 2096
371 motor units) was 36.2 ± 4.5 (range: 30.0-53.6).

372 We used a coherence analysis to provide insight into the common neural drive received by the
373 motor neurons. Because the number of GL motor unit discharges identified during the
374 isometric plantarflexion tasks was too low (see *Methods*), the coherence analysis was only
375 performed on the isometric heel raise task performed with toes in neutral position (Toes
376 neutral). Of note, the normalized global EMG amplitude of GM and GL (GM: $24.1 \pm 6.0\%$,
377 GL: $12.1 \pm 6.9\%$, and SOL: $24.8 \pm 10.7\%$ of maximal EMG amplitude) during the Toes neutral
378 condition was close to that measured during the isometric plantarflexion at 30% of MVC
379 (GM: $28.7 \pm 6.8\%$, GL: $14.9 \pm 4.7\%$, and SOL: $18.4 \pm 11.5\%$ of maximal EMG amplitude).

380

381 *Within-muscle coherence*

382 After discarding the motor units that were recruited intermittently and the data from
383 participants with less than four consistently firing motor units, the within-muscle coherence
384 analysis was performed on 243 motor units from 17 participants for GM, 83 motor units from
385 11 participants for GL, and 63 motor units from 10 participants for SOL.

386 The proportion of common synaptic input (PCI) with respect to the total input received by the
387 motor neuron pool was estimated from the relationship between the average values of
388 coherence in the bandwidth 0-5 Hz and the number of motor units used in the calculation (see
389 *Methods*; Fig. 2). As the number of participants differed between the three muscles, we ran a
390 one-way ANOVA for independent samples. There was a significant main effect of *muscle* (F
391 $[2, 35] = 14.2$ $p < 0.001$) on the PCI values, with the PCI being lower in SOL (0.58 ± 0.06) than
392 in both GM (0.67 ± 0.06 ; $p = 0.004$) and GL (0.73 ± 0.07 , $p < 0.001$) (Fig. 4). PCI was not
393 different between GM and GL ($p = 0.063$). Note that we also ran a repeated measures ANOVA
394 on the seven participants who had enough active motor units discriminated from all the three

395 muscles. This test confirmed the existence of a significant main effect of *muscle* ($F [2, 12] =$
396 $26.9, p < 0.001$), with the PCI being lower in SOL than in both GM ($p = 0.001$) and GL
397 ($p < 0.001$), with no difference between GM and GL ($p = 0.082$).

398 The proportion of common input to motor neurons within the VL and VM, assessed on two
399 participants who performed an isometric body-weight squat (additional experiments), was in
400 the lower range of that calculated for the *triceps surae* muscles, i.e. VL: 0.50 and 0.57; VM
401 0.49 and 0.54.

402

403 *Between-muscles coherence*

404 When considering data from all participants, there was no significant correlation between the
405 coherence in the bandwidth 0-5 Hz [common drive (16)] and the minimal number of motor
406 units over the two muscles being tested ($r = 0.03, -0.15, \text{ and } -0.08$ for the GM-GL, GL-SOL,
407 and GM-SOL pair, respectively). This provides evidence that the number of motor units
408 considered in the analysis did not influence the level of coherence that is reported.
409 Consequently, after discarding the motor units that were recruited intermittently, we retained
410 all the participants with at least one motor unit per muscle. Using this criterion, the coherence
411 analysis was performed on 13 participants for GM-GL [193 (GM) and 87 (GL) motor units],
412 and 11 participants for both GM-SOL [168 (GM) and 56 (SOL) motor units] and GL-SOL [62
413 (GL) and 52 (SOL) motor units].

414 Overall, minimal between-muscle coherence was observed, regardless of the bandwidth, i.e.
415 delta (0-5 Hz), alpha (5-15 Hz), and beta (15-35 Hz) bands. For example, when considering
416 the GM-GL muscle pair, only 2/13 participants exhibited significant coherence over the entire
417 bandwidth 0-5 Hz (Fig. 5 and Fig. 6). While 5/13 participants exhibited coherence at some
418 (but not all) frequencies within the 0-5 Hz bandwidth, 6/13 participants exhibited no
419 significant coherence over this bandwidth. Note that participant #5, who exhibited the highest

420 coherence over the whole population (Fig. 5), was retested two months after the initial testing,
421 and the results confirmed the presence of significant coherence. When considering the GM-
422 SOL and GL-SOL muscle pairs, none of the participants exhibited significant coherence over
423 the entire bandwidth 0-5 Hz (Fig. 5 and Fig 6).

424 Note that the two participants who performed an isometric body-weight squat (additional
425 experiments) exhibited significant coherence between VL and VM motor units, over the entire
426 bandwidth 0-5 Hz (peak values: 0.34 and 0.81). It confirms previous results showing a strong
427 common drive between these muscles during isometric knee extension tasks (37).

428

429

430

431 *Motor unit discharge characteristics during the isometric plantarflexion tasks*

432 As indicated above, only 10 motor units were decomposed from the GL muscle during the
433 plantarflexion at 10% of MVC. As the comparison between GL and GM was the main
434 purpose of this study, no further analysis was completed on the contractions at 10% of MVC.

435 At 30% of MVC, most of the identified motor units discharged during the three contractions
436 (93% for GM, 69% for GL, and 68% for SOL). There was a significant main effect of *muscle*
437 on the time at recruitment ($H = 68.7$, $df = 2$, $p < 0.001$), with the GL motor units being
438 recruited much later ($11.5 \pm 5.9s$) than both GM ($4.4 \pm 3.3s$, $p < 0.001$) and SOL motor units
439 ($5.2 \pm 4.2s$, $p < 0.001$). No difference of time at recruitment was observed between GM and
440 SOL ($p = 0.20$). As the time at recruitment was calculated from the start of the 5-s ramp-up
441 period (see *Methods*), this result indicates that most of the motor units from GL started to be
442 recruited during the torque plateau (Fig. 7). There was a significant main effect of *muscle* on
443 the *delta* discharge rate measured during the first 2s after recruitment ($H = 17.2$, $df = 2$,
444 $p = 0.002$). The *delta* discharge rate was significantly lower for SOL (1.4 ± 0.9 pps. s^{-1}) than for

445 both GL (1.8 ± 1.5 pps. s^{-1} , $p=0.012$) and GM (2.0 ± 1.3 pps. s^{-1} , $p<0.001$). No difference between
446 GL and GM was observed ($p=1$).

447 Similar results were observed for the contractions performed at 50% of MVC, with a
448 significant main effect of *muscle* on the time at recruitment ($H = 80.7$, $df = 2$, $p<0.001$). As
449 observed at 30% of MVC, GL motor units were recruited much later ($9.5 \pm 4.2s$) than both GM
450 ($3.7 \pm 2.6s$, $p<0.001$) and SOL motor units ($4.4 \pm 2.7s$, $p=0.018$) (Fig. 7). At this intensity, SOL
451 motor units were also recruited later than GM motor units ($p<0.001$). There was also a main
452 effect of *muscle* on the delta discharge rate ($H = 26.9$, $df = 2$, $p<0.001$). The *delta* discharge
453 rate was significantly lower for both SOL (1.5 ± 1.2 pps. s^{-1} , $p<0.001$) and GL (1.6 ± 1.9 pps. s^{-1} ,
454 $p<0.001$) when compared to GM (2.6 ± 1.6 pps. s^{-1}). There was no difference between GM and
455 SOL ($p=0.961$).

456 There was a significant main effect of *muscle* ($F [2, 766] = 83.4$, $p<0.001$), a significant main
457 effect of *intensity* ($F [1, 766] = 68.9$, $p<0.001$), and a significant *muscle* \times *intensity* interaction
458 ($F [2, 766] = 8.7$, $p=0.002$) on the peak motor unit discharge rate estimated from the
459 polynomial fit (Fig. 7). Regardless the contraction intensity, the discharge rate was lower for
460 SOL than for both GM and GL (all p values <0.037). While there was no difference in
461 discharge rate between GM and GL at 30% of MVC ($P=1$), the discharge rate was
462 significantly higher for GM (14.0 ± 3.0 pps) than GL (12.2 ± 2.6 pps; $p<0.001$) at 50% of MVC.
463 This result is mainly explained by the absence of an increase in discharge rate of the GL
464 motor units between the two intensities ($P=1$).

465 We estimated the change in neural drive of each muscle during the plateau of the force-
466 matched contractions through the assessment of the change in their cumulative spike trains
467 (CST). When considering all the participants and the three contractions at 30% of MVC, we
468 observed a significant decrease in the GM CST for most of the contractions (48% decrease,
469 vs. 42% increase and 10% no change). Conversely, a significant increase in the CST was

470 observed in 92% of the contractions for GL and 54 % of the contractions for SOL. Opposite
471 change in CST was observed in 64%, 65% and 44% of the contractions when considering
472 GM-GL, GM-SOL, and GL-SOL pair, which provides strong evidence for opposing changes
473 in neural drive to these muscle pairs.

474 When considering the contractions at 50% of MVC, we observed a significant decrease in the
475 GM and SOL CST for most of the contractions (69% and 71% for GM and SOL,
476 respectively). Conversely, a significant increase in the GL CST was observed in 100% of the
477 contractions. Opposite change in CST was observed in 66%, 36% and 67% of the contractions
478 when considering GM-GL, GM-SOL, and GL-SOL pairs.

479
480
481
482

483 *Effect of toe position on motor units discharge rate during isometric heel raise*

484
485 We compared the discharge rate of all identified motor units during the heel raise tasks
486 between Toes neutral (335 and 120 motor units for GM and GL, respectively) and Toes in
487 (312 and 85 motor units for GM and GL, respectively) (Fig. 8). There was a significant main
488 effect of *condition* ($F [1, 848] = 7.4, p=0.006$), a significant main effect of *muscle* ($F [1, 848]$
489 $= 12.7, p<0.001$), and a significant *muscle* \times *condition* on the discharge rate ($F [1, 848] =$
490 $10.5, p=0.001$). While no change in motor units discharge rate was observed for GM between
491 the two conditions ($p=1$), there was a significant increase in the discharge rate of GL motor
492 units, from 10.2 ± 1.2 pps for Toes neutral to 10.8 ± 1.5 pps for Toes in ($p=0.002$).

493

494 **Discussion**

495 We identified strong common neural drive to the motor neuron pools innervating each
496 muscle, but minimal common drive between pools innervating different muscles. Together
497 with differences in motor unit behaviors, our results provide evidence for minimal common

498 drive between the muscle heads of the triceps surae, which contrasts with observations from
499 other anatomically derived synergist muscles. This important result has implications for our
500 current understanding of the modular control of muscle coordination.

501

502 *Strong common synaptic input to motor neurons within each muscle*

503 We assessed the PCI received by the motor neuron pools of the three muscles of the *triceps*
504 *surae*. PCI values reported here were similar to those reported in the *abductor digiti minimi*,
505 *tibialis anterior*, and *vastus medialis* (44). This suggests that motor neurons of a single muscle
506 receive most of their input from a common source. Unlike the previous observations made by
507 Negro, Yavuz and Farina (44), but in line with other data obtained from the first dorsal
508 interosseous and the biceps brachii (21), we observed a significant difference between
509 muscles, with GL (PCI=0.73) and SOL (PCI=0.58) having the highest and lowest PCI values,
510 respectively. These between-muscle differences may be interpreted as differences in the
511 effective neural drive that is converted to force, presumably underlying differences in the
512 control of these muscles.

513

514 *Minimal level of common drive between the heads of the triceps surae*

515 We determined that the three heads of the *triceps surae* receive minimal common drive during
516 isometric heel raise tasks (Toes neutral). To reach this conclusion, we performed a coherence
517 analysis between the CST of each muscle (15, 18, 37). To the best of our knowledge, this is
518 the first report minimal (or an absence of) coherence in all the frequency bands reflecting
519 cortical and spinal inputs (24) between muscles that share the same main function(s) and that
520 belong to the same muscle group. As such, it was important to rule out the possibility that our
521 approach failed to identify existing coherence. First, the coherence analysis requires that the
522 CST is calculated from several motor units such that the synaptic input is represented over a

523 broad frequency range (23). Our analysis was performed on a relatively large number of units
524 (Table 1) with, for example, 14.8 ± 7.3 (GM) and 6.7 ± 3.2 (GL) motor units when considering
525 the coherence between GM and GL. It is important to note that some of the participants who
526 exhibited no significant GM-GL coherence in the bandwidth 0-5 Hz (Fig. 5) were among the
527 participants whose data allowed the largest number of motor units to be discriminated (e.g. 21
528 [GM] and 8 [GL] units for participant #12, 16 [GM] and 9 [GL] units for participant #18).
529 Second, we tested our analysis procedure on the VL and VM muscles of two participants. In
530 line with the strong common input shared by these muscles (37), we observed a significant
531 coherence in the bandwidth 0-5 Hz for both participants. Given the above considerations, we
532 believe that our dataset and analysis methods were appropriate to show coherence if it did
533 exist between the muscles of the *triceps surae*.

534 Our conclusion that the three heads of the *triceps surae* share minimal common drive is
535 further strengthened by two complementary approaches. First, the motor unit discharge
536 characteristics observed during the isometric plantarflexion tasks performed on the ergometer
537 revealed obvious differences among muscles. GL motor units were recruited much later than
538 either SOL or GM motor units at both contraction intensities (Fig. 3 and 6). Even though this
539 difference in recruitment time might be explained by different intrinsic motor neuron
540 properties rather than different neural drive, the fact that opposite changes in CST were
541 observed in most of the contractions provides evidence that the three muscles receive different
542 neural drive (Fig. 3). Our proposition provides an explanation for the absence of active GL
543 motor units observed during standing balance (27). Second, the differential change in the
544 discharge rate of GL and GM observed between the heel raise tasks performed with Toes in
545 and Toes neutral provide definitive evidence that these muscles are not controlled primarily
546 by shared neural drive, as it is the case for other synergist muscles.

547

548 *GM and GL are “non-identical twins”*

549 Even though SOL and Gastrocnemii are consistently reported as part of the same synergy
550 during walking (van den Hoorn et al., 2015), the observation that the SOL muscle does not
551 share a common drive with the two gastrocnemius muscles is not surprising given their
552 different functions and previous observations of dissociated motor unit behavior of GM and
553 SOL in humans (34, 38) and animals (28). However, considering that muscles that share the
554 same function(s) are thought to share neural drive (25, 37), the minimal coherence between
555 GM and GL, despite attaching to the same distal tendon, is somewhat surprising. Our findings
556 do not support the long-held belief that GM and GL are the “same muscle” such that they are
557 named the “twin” muscles in some languages, e.g. “jumeaux” in French and “gemelos” in
558 Spanish.

559 The minimal common drive between GL and GM may be related to the complexity of ankle
560 joint control. Control at the ankle is important in maintaining balance during a wide variety of
561 tasks, such as quiet stance, walking, running and maintaining balance when responding to
562 perturbations. Therefore, relative independent control of these muscles may allow for flexible
563 control of the ankle joint to comply with secondary goals (e.g. joint stabilization, distribution
564 of tendon strain). This is supported by indirect neurophysiological and biomechanical
565 measures of human GL and GM, that suggest different actions in the frontal plane (12, 39,
566 50). Also, these muscles are architecturally different, with GL exhibiting a smaller volume
567 and longer fascicles than GM (13). This means that these two muscles have different
568 contractile dynamics (6). Therefore, an independent control of GM and GL might be an
569 optimal way for the nervous system to tune the activation to the mechanical requirements of
570 the task (32). Overall, the minimal common drive observed between GM and GL suggests
571 that reducing the number of effectively controlled degrees of freedom may not always be the
572 strategy used by the central nervous system to control movements, even when this strategy

573 would be functionally viable. This is in agreement with recent results showing that the central
574 nervous system compromises between restoration of task performance and optimization of
575 joint load after VL denervation in rats (2). Of note, we cannot rule out an alternative
576 interpretation that the lack of common drive between GM and GL is a suboptimal strategy
577 resulting from the late, and perhaps incomplete, evolution of the Achilles tendon and
578 plantarflexors for human locomotion (1).

579

580 *Modular organization of muscle coordination*

581 It has been proposed that the central nervous system produces movements through the
582 combination of motor modules; each module being composed of muscles activated by shared
583 inputs to their motor neurons (5, 14, 47). However, the neural origin of motor modules is
584 debated, with some studies suggesting that they reflect biomechanical constraints of the task
585 rather than a neural control strategy (36, 48). Using a similar approach to that used in our
586 study, shared neural drive was found between two thigh muscles for which control is
587 biomechanically constrained [VL and VM; (37)] as well as between two hands muscles for
588 which control is not biomechanically constrained [first dorsal interosseous and thenar
589 muscles; (18)]. Here, we observed little, if any, coherence in the bandwidth corresponding to
590 both the spinal and cortical drive, suggesting that GM and GL are controlled mostly
591 independently. Taken together, it provides evidence against a pure association between
592 biomechanical constraints and modular muscle control. Indeed, GM and GL are both
593 anatomically and biomechanically associated during plantarflexion, as performed in our
594 study. However, these constraints did not determine modular control of their activation, even
595 though control with reduced dimensionality would have been viable for these specific
596 plantarflexion tasks. This and previous studies thus point to the possibility that neural
597 connectivity may be partly dissociated from biomechanical connectivity.

598 It is important to note that classical non-invasive approaches, based on factorization of
599 multiple bipolar EMG signals, consistently report GM and GL as part of the same module(s)
600 (33, 49). Together with our results, this suggests that separate EMG signals can be correlated,
601 but in a way that does not reflect a common synaptic input (42). The non-invasive approach
602 with EMG decomposition used in the present study could be extended to other muscles to
603 provide a comprehensive description of neural muscle modules that could be distinguished
604 from “biomechanical” modules.

605

606 *Limitations*

607 This experiment requires consideration of several methodological aspects. First, the level of
608 common synaptic input to the motor neuron pools of GM, GL and SOL has been estimated
609 only indirectly from the recorded motor neuron outputs. Moreover, in most cases, it was
610 assumed that the transmission at the motor neuron population level was linear, as it has been
611 proposed in previous work (23), although it cannot be excluded that transmission to the motor
612 neuron output included some non-linear components (7, 51). The coherence between the
613 cumulative discharge times calculated over a group of motor neurons reflects the common
614 components of the synaptic input, although the frequency bands of these components may not
615 be the same between input and output when accounting for non-linear transmission. Similarly,
616 the model we used to estimate the PCI does not specifically account for persistent inward
617 currents which introduce further non-linearity in the system (7). Second, the SOL muscle is
618 composed by four compartments with different architecture (10) and different innervation
619 (41). Given the placement of our surface EMG electrodes (see Methods), it is likely that we
620 measured only one compartment, which did not represent the motor unit activity in the entire
621 muscle. It is therefore possible that neural drive was shared between GM or GL and other
622 SOL compartments. Finally, the observation of minimal common drive between the heads of

623 the triceps surae cannot be extrapolated to other motor tasks such as dynamic tasks. Whether
624 similar results would be observed during dynamic locomotor tasks remains an open question.

625

626

627 **References**

628

- 629 1. **Aerts P, D'Aout K, Thorpe S, Berillon G, and Vereecke E.** The gibbon's Achilles
630 tendon revisited: consequences for the evolution of the great apes? *Proc Biol Sci* 285:
631 2018.
- 632 2. **Alessandro C, Rellinger BA, Barroso FO, and Tresch MC.** Adaptation after vastus
633 lateralis denervation in rats demonstrates neural regulation of joint stresses and strains.
634 *Elife* 7: 2018.
- 635 3. **Baker SN, Kilner JM, Pinches EM, and Lemon RN.** The role of synchrony and
636 oscillations in the motor output. *Exp Brain Res* 128: 109-117, 1999.
- 637 4. **Baker SN, Pinches EM, and Lemon RN.** Synchronization in monkey motor cortex
638 during a precision grip task. II. effect of oscillatory activity on corticospinal output. *J*
639 *Neurophysiol* 89: 1941-1953, 2003.
- 640 5. **Berniker M, Jarc A, Bizzi E, and Tresch MC.** Simplified and effective motor control
641 based on muscle synergies to exploit musculoskeletal dynamics. *Proc Natl Acad Sci U S*
642 *A* 106: 7601-7606, 2009.
- 643 6. **Biewener AA.** Locomotion as an emergent property of muscle contractile dynamics. *J*
644 *Exp Biol* 219: 285-294, 2016.
- 645 7. **Binder MD, Powers RK, and Heckman CJ.** Nonlinear Input-Output Functions of
646 Motoneurons. *Physiology (Bethesda)* 35: 31-39, 2020.
- 647 8. **Bizzi E, and Cheung VC.** The neural origin of muscle synergies. *Front Comput*
648 *Neurosci* 7: 51, 2013.
- 649 9. **Bizzi E, Cheung VC, d'Avella A, Saltiel P, and Tresch M.** Combining modules for
650 movement. *Brain Res Rev* 57: 125-133, 2008.
- 651 10. **Bolsterlee B, Finni T, D'Souza A, Eguchi J, Clarke EC, and Herbert RD.** Three-
652 dimensional architecture of the whole human soleus muscle in vivo. *PeerJ* 6: e4610,
653 2018.
- 654 11. **Bremner FD, Baker JR, and Stephens JA.** Correlation between the discharges of motor
655 units recorded from the same and from different finger muscles in man. *J Physiol* 432:
656 355-380, 1991.
- 657 12. **Cohen JW, Gallina A, Ivanova TD, Vieira T, McAndrew DJ, and Garland SJ.**
658 Regional modulation of the ankle plantarflexor muscles associated with standing external
659 perturbations across different directions. *Exp Brain Res* 2019.
- 660 13. **Crouzier M, Lacourpaille L, Nordez A, Tucker K, and Hug F.** Neuromechanical
661 coupling within the human triceps surae and its consequence on individual force-sharing
662 strategies. *J Exp Biol* 221: 2018.
- 663 14. **d'Avella A, and Bizzi E.** Shared and specific muscle synergies in natural motor
664 behaviors. *Proc Natl Acad Sci U S A* 102: 3076-3081, 2005.
- 665 15. **De Luca CJ, LeFever RS, McCue MP, and Xenakis AP.** Behaviour of human motor
666 units in different muscles during linearly varying contractions. *J Physiol* 329: 113-128,
667 1982.

- 668 16. **De Luca CJ, LeFever RS, McCue MP, and Xenakis AP.** Control scheme governing
669 concurrently active human motor units during voluntary contractions. *J Physiol* 329: 129-
670 142, 1982.
- 671 17. **Del Vecchio A, Falla D, Felici F, and Farina D.** The relative strength of common
672 synaptic input to motor neurons is not a determinant of the maximal rate of force
673 development in humans. *J Appl Physiol (1985)* 127: 205-214, 2019.
- 674 18. **Del Vecchio A, Germer CM, Elias LA, Fu Q, Fine J, Santello M, and Farina D.** The
675 human central nervous system transmits common synaptic inputs to distinct motor neuron
676 pools during non-synergistic digit actions. *J Physiol* 2019.
- 677 19. **Del Vecchio A, Ubeda A, Sartori M, Azorin JM, Felici F, and Farina D.** Central
678 nervous system modulates the neuromechanical delay in a broad range for the control of
679 muscle force. *J Appl Physiol (1985)* 125: 1404-1410, 2018.
- 680 20. **Dominici N, Ivanenko YP, Cappellini G, d'Avella A, Mondì V, Cicchese M, Fabiano
681 A, Silei T, Di Paolo A, Giannini C, Poppele RE, and Lacquaniti F.** Locomotor
682 primitives in newborn babies and their development. *Science* 334: 997-999, 2011.
- 683 21. **Farina D, Castronovo AM, Vujaklija I, Sturma A, Salminger S, Hofer C, and
684 Aszmann O.** Common Synaptic Input to Motor Neurons and Neural Drive to Targeted
685 Reinnervated Muscles. *J Neurosci* 37: 11285-11292, 2017.
- 686 22. **Farina D, and Negro F.** Common synaptic input to motor neurons, motor unit
687 synchronization, and force control. *Exerc Sport Sci Rev* 43: 23-33, 2015.
- 688 23. **Farina D, Negro F, Muceli S, and Enoka RM.** Principles of Motor Unit Physiology
689 Evolve With Advances in Technology. *Physiology (Bethesda)* 31: 83-94, 2016.
- 690 24. **Farmer SF, Bremner FD, Halliday DM, Rosenberg JR, and Stephens JA.** The
691 frequency content of common synaptic inputs to motoneurons studied during voluntary
692 isometric contraction in man. *J Physiol* 470: 127-155, 1993.
- 693 25. **Gibbs J, Harrison LM, and Stephens JA.** Organization of inputs to motoneurone pools
694 in man. *J Physiol* 485 (Pt 1): 245-256, 1995.
- 695 26. **Gorassini M, Yang JF, Siu M, and Bennett DJ.** Intrinsic activation of human
696 motoneurons: possible contribution to motor unit excitation. *J Neurophysiol* 87: 1850-
697 1858, 2002.
- 698 27. **Heroux ME, Dakin CJ, Luu BL, Inglis JT, and Blouin JS.** Absence of lateral
699 gastrocnemius activity and differential motor unit behavior in soleus and medial
700 gastrocnemius during standing balance. *J Appl Physiol (1985)* 116: 140-148, 2014.
- 701 28. **Hodgson JA.** The relationship between soleus and gastrocnemius muscle activity in
702 conscious cats--a model for motor unit recruitment? *J Physiol* 337: 553-562, 1983.
- 703 29. **Holobar A, and Farina D.** Blind source identification from the multichannel surface
704 electromyogram. *Physiol Meas* 35: R143-165, 2014.
- 705 30. **Holobar A, Minetto MA, and Farina D.** Accurate identification of motor unit discharge
706 patterns from high-density surface EMG and validation with a novel signal-based
707 performance metric. *J Neural Eng* 11: 016008, 2014.
- 708 31. **Holobar A, and Zazula D.** Multichannel Blind Source Separation Using Convolution
709 Kernel Compensation. *IEEE Transactions on Signal Processing* 55: 4487-4496, 2007.
- 710 32. **Hudson AL, Gandevia SC, and Butler JE.** A Principle of Neuromechanical Matching
711 for Motor Unit Recruitment in Human Movement. *Exerc Sport Sci Rev* 47: 157-168,
712 2019.
- 713 33. **Hug F, Turpin NA, Couturier A, and Dorel S.** Consistency of muscle synergies during
714 pedaling across different mechanical constraints. *J Neurophysiol* 106: 91-103, 2011.
- 715 34. **Kennedy PM, and Cresswell AG.** The effect of muscle length on motor-unit recruitment
716 during isometric plantar flexion in humans. *Exp Brain Res* 137: 58-64, 2001.

- 717 35. **Kerkman JN, Daffertshofer A, Gollo LL, Breakspear M, and Boonstra TW.**
718 Network structure of the human musculoskeletal system shapes neural interactions on
719 multiple time scales. *Sci Adv* 4: eaat0497, 2018.
- 720 36. **Kutch JJ, and Valero-Cuevas FJ.** Challenges and new approaches to proving the
721 existence of muscle synergies of neural origin. *PLoS Comput Biol* 8: e1002434, 2012.
- 722 37. **Laine CM, Martinez-Valdes E, Falla D, Mayer F, and Farina D.** Motor Neuron Pools
723 of Synergistic Thigh Muscles Share Most of Their Synaptic Input. *J Neurosci* 35: 12207-
724 12216, 2015.
- 725 38. **Lauber B, Lichtwark GA, and Cresswell AG.** Reciprocal activation of gastrocnemius
726 and soleus motor units is associated with fascicle length change during knee flexion.
727 *Physiol Rep* 2: 2014.
- 728 39. **Lee SS, and Piazza SJ.** Inversion-eversion moment arms of gastrocnemius and tibialis
729 anterior measured in vivo. *J Biomech* 41: 3366-3370, 2008.
- 730 40. **Lieb FJ, and Perry J.** Quadriceps function. An anatomical and mechanical study using
731 amputated limbs. *J Bone Joint Surg Am* 50: 1535-1548, 1968.
- 732 41. **Loh EY, Agur AM, and McKee NH.** Intramuscular innervation of the human soleus
733 muscle: a 3D model. *Clin Anat* 16: 378-382, 2003.
- 734 42. **Martinez-Valdes E, Negro F, Falla D, De Nunzio AM, and Farina D.** Surface
735 electromyographic amplitude does not identify differences in neural drive to synergistic
736 muscles. *J Appl Physiol (1985)* 124: 1071-1079, 2018.
- 737 43. **Negro F, Holobar A, and Farina D.** Fluctuations in isometric muscle force can be
738 described by one linear projection of low-frequency components of motor unit discharge
739 rates. *J Physiol* 587: 5925-5938, 2009.
- 740 44. **Negro F, Yavuz US, and Farina D.** The human motor neuron pools receive a dominant
741 slow-varying common synaptic input. *J Physiol* 594: 5491-5505, 2016.
- 742 45. **Overduin SA, d'Avella A, Carmena JM, and Bizzi E.** Microstimulation activates a
743 handful of muscle synergies. *Neuron* 76: 1071-1077, 2012.
- 744 46. **Tresch MC, and Bizzi E.** Responses to spinal microstimulation in the chronically
745 spinalized rat and their relationship to spinal systems activated by low threshold
746 cutaneous stimulation. *Exp Brain Res* 129: 401-416, 1999.
- 747 47. **Tresch MC, and Jarc A.** The case for and against muscle synergies. *Curr Opin*
748 *Neurobiol* 19: 601-607, 2009.
- 749 48. **Valero-Cuevas FJ, Venkadesan M, and Todorov E.** Structured variability of muscle
750 activations supports the minimal intervention principle of motor control. *J Neurophysiol*
751 102: 59-68, 2009.
- 752 49. **van den Hoorn W, Hodges PW, van Dieen JH, and Hug F.** Effect of acute noxious
753 stimulation to the leg or back on muscle synergies during walking. *J Neurophysiol* 113:
754 244-254, 2015.
- 755 50. **Vieira TM, Windhorst U, and Merletti R.** Is the stabilization of quiet upright stance in
756 humans driven by synchronized modulations of the activity of medial and lateral
757 gastrocnemius muscles? *J Appl Physiol (1985)* 108: 85-97, 2010.
- 758 51. **Watanabe RN, and Kohn AF.** Fast Oscillatory Commands from the Motor Cortex Can
759 Be Decoded by the Spinal Cord for Force Control. *J Neurosci* 35: 13687-13697, 2015.
- 760 52. **Winter SL, and Challis JH.** Reconstruction of the human gastrocnemius force-length
761 curve in vivo: part 1-model-based validation of method. *J Appl Biomech* 24: 197-206,
762 2008.
- 763

764

765 **Figure legends**

766

767 **Figure 1. Experimental setup. Panel A** shows the placement of the high-density
768 electromyography electrodes. A two-dimensional adhesive grid of 64 electrodes was placed
769 over both the gastrocnemius medialis (GM) and the gastrocnemius lateralis (GL) muscle. A
770 two-dimensional adhesive grid of 32 electrodes was placed on the medial part of the soleus
771 (SOL), below the myotendinous junction of the GM muscle. **Panel B** shows the isometric
772 plantarflexion task performed on the ergometer (knee was fully extended and ankle angle at
773 10° of plantarflexion). **Panel C** shows the isometric heel raise task which consisted of holding
774 the heel at a standard height of 6 cm, with either the feet in neutral position (comfortable
775 stance; Toes neutral) or internally rotated (Toes in).

776

777 **Figure 2. Individual example of the assessment of the proportion of common input**
778 **(PCI). Panel A** shows the smoothed discharge rate (cut-off frequency=2 Hz) of 25 motor
779 units identified from the gastrocnemius medialis, during the isometric heel raise task
780 performed with the toes in neutral position, for participant #12. Note that only 20s of the
781 contraction are depicted here. **Panel B** shows the results of the coherence analyses performed
782 on two cumulative spike trains, with varying number of motor units in each group, i.e. from 1
783 to 12 motor units. Each estimation is the average of 100 random permutations of motor units.
784 The horizontal line indicates the threshold of significant coherence for 12 motor units per
785 group. **Panel C** represents the relationship between the mean values (\pm standard deviation) of
786 coherence in the bandwidth 0-5 Hz and the number of motor units. This relationship was
787 fitted by least-squares (red line) and the rate of change was considered as an index of the
788 proportion of common input (PCI).

789

790 **Figure 3. Individual example of the assessment of the neural drive during the isometric**
791 **plantarflexions performed on the ergometer. Panel A** represents the smoothed discharge
792 rate (cut-off frequency=2 Hz) of the motor units identified in participant #11 during the
793 contraction at 30% of MVC. **Panel B** shows three outcomes (time at recruitment, delta and
794 peak discharge rate) estimated from the instantaneous discharge rate of one motor unit of the
795 gastrocnemius medialis muscle. Note that the peak discharge rate value was estimated from a
796 sixth-order polynomial used to smooth the instantaneous discharge rates. **Panel C** shows the
797 cumulative spike train (CST; index of neural drive) of each of the three muscles. GM,
798 Gastrocnemius medialis; GL, Gastrocnemius lateralis; SOL, Soleus (medial-posterior
799 compartment); MVC, maximal voluntary contraction.

800

801 **Figure 4. Proportion of common synaptic input to motor neurons within the same**
802 **muscle, estimated during the isometric heel raise (Toes neutral).** The within-muscle
803 coherence analysis was performed on 17, 11, and 10 participants for gastrocnemius medialis
804 (GM), gastrocnemius lateralis (GL), and soleus (SOL), respectively. Each participant is
805 represented by a different color and the horizontal line indicates the mean value. \$, indicates
806 significant difference compared with SOL. There was no significant difference between GM
807 and GL.

808

809 **Figure 5. Between-muscle coherence estimated during the isometric heel raise (toes**
810 **neutral).** **Panel A** shows examples of the coherence between GM and GL for two
811 participants: Participant #18 who exhibited no coherence and participant #5 who exhibited the
812 highest coherence over the population tested. The horizontal lines represent the threshold of
813 significance defined as the highest coherence value for frequencies > 100 Hz, at which no
814 coherence is expected. The other panels show, for each participant, the frequencies at which a

815 significant coherence was observed (**Panel B** for GM-GL, **Panel C** for GM-SOL, **Panel C** for
816 GL-SOL). Some participants were discarded from this analysis as too few motor units were
817 discriminated to allow this analysis. Individual coherence data are depicted on Fig 5-1, 5-2
818 and 5-3 (extended data). GM, Gastrocnemius medialis; GL, Gastrocnemius lateralis; SOL,
819 Soleus.

820

821 **Figure 6: Individual data of coherence between the three heads of the triceps surae**
822 **estimated during the isometric heel raise (toes neutral).** The red horizontal lines represent
823 the threshold of significance defined as the highest coherence value for frequencies > 100 Hz,
824 at which no coherence is expected. Some participants were discarded from this analysis as too
825 few motor units were discriminated to allow this analysis. GM, Gastrocnemius medialis; GL,
826 Gastrocnemius lateralis; SOL, Soleus.

827

828 **Figure 7. Motor unit discharge characteristics during the isometric plantarflexion tasks**
829 **performed at 30% (Panel A) and 50% of MVC (Panel B).** Each participant is represented
830 by a different colour and the horizontal bar indicates the mean value. The dashed horizontal
831 line on the upper panels indicate the beginning of the torque plateau. *, $p < 0.05$ for
832 comparison with GM; \$, $p < 0.05$ for comparison with SOL; £, $p < 0.05$ for comparison with
833 GL. GM, Gastrocnemius medialis; GL, Gastrocnemius lateralis; SOL, Soleus; MVC, maximal
834 voluntary contractions.

835

836 **Figure 8. Discharge rate during the isometric heel raise performed with different feet**
837 **configurations.** Each participant ($n=14-17$) is represented by a different colour and the
838 horizontal bar indicates the mean value. *, $p < 0.05$ for comparison with Toes neutral. GM,
839 Gastrocnemius medialis; GL, Gastrocnemius lateralis.

840

841