1   **Neuromuscular fatigue reduces responsiveness when controlling leg external forces**
2
3   **Authors:** Pawel Kudzia[1], James M. Wakeling[2], Stephen N. Robinovitch[2], J. Maxwell Donelan[2]
4
5   **Affiliations:**
6   1- Department of Engineering Science, Simon Fraser University, Burnaby, BC V5A 1S6,
7   Canada
8   2- Department of Biomedical Physiology and Kinesiology, Simon Fraser University,
9   Burnaby, BC V5A 1S6, Canada
10
11   **Keywords:** fatigue; ground reaction forces; motor control; biomechanics; legged agility
12
13   **Corresponding author:**
14   J. Maxwell Donelan
15   mdonelan@sfu.ca
16   Department of Biomedical Physiology and Kinesiology
17   Shrum Science Centre K9625, 8888 University Drive
18   Burnaby, BC V5A 1S6, Canada

19   # Abstract

20   In legged movement, our legs push against the ground, generating external force vectors that
21   enable agile movements. Neuromuscular fatigue can reduce agility by causing physiological
22   changes, such as slowing muscle reaction time, altering proprioception, and delaying
23   neuromuscular control. Fatigue may deteriorate the nervous system's control of leg external forces,
24   contributing to reductions in agility. In this study, we investigated the effect of fatigue on the
25   performance of the nervous system in controlling the vertical component of leg external force
26   ground reaction forces. We hypothesized that increased leg fatigue would lead to declines in both
27   the responsiveness (speed) and accuracy of leg force control. To test this hypothesis, we used an
28   apparatus that allowed participants to exert controlled vertical forces with one leg against a force
29   plate while immobilizing the rest of their bodies. Participants adjusted their leg external force to
30   match step targets displayed on a screen. We induced fatigue by having participants maintain
31   submaximal leg forces, and we measured leg force control performance between fatigue trials.
32   Results showed a significant 26% reduction in mean maximum force production, leading to a
33   substantial decline in leg force control responsiveness, as evidenced by a 23% increase in rise time
34   and a 25% narrowing of bandwidth. However, fatigue did not significantly reduce leg force control
35   accuracy. Understanding the effects of fatigue on leg force control can inform the development of
36   strategies and technologies to sustain agile performance, even in the presence of fatigue.

37   # New and Noteworthy

38   We developed a method to probe the influence of neuromuscular fatigue on the control of leg
39   external forces. Our findings demonstrate that while fatigue significantly diminishes
40   responsiveness (speed), it does not compromise the accuracy of control. These insights enhance
41   our understanding of legged agility and could guide the development of strategies for optimizing
42   leg force control performance. This study paves the way for future research aimed at identifying
43   and employing effective strategies to maintain agility in the face of fatigue.

Introduction

One way that legged animals, including humans, demonstrate agility is through effective control of external leg forces. We can push against the ground with any part of our bodies, but we often do this using our legs to push our feet against the ground. The resulting reaction force from the environment, a vector quantity, accelerates our bodies. Here we consider the rapid and accurate control of the external force vector to be agility [1]. Examples of legged agility include accelerating from a standstill, jumping high and far over obstacles, and quickly changing movement direction, all of which require effective control of our leg's external forces.

Neuromuscular fatigue reduces agility. Fatigue leads to a decline in muscle force-generating capabilities [2] and reductions in maximum muscle shortening velocities [3], [4]. As mechanical power is the product of both force and shortening velocity, fatigue reduces maximum muscle power [2]. The effect of fatigue on muscle power and agility is well-documented in sports performance, particularly in rapid change-of-direction sports like soccer and basketball [5]–[7]. For example, fatigue reduces power in jumping leading to jumps of shorter distances and lower heights [8]–[12]. A second example is sprinting, in which high performance relies on fast-twitch muscle fibres. These same fibres are also the most susceptible to fatigue, leading to declines in speed in the final meters of a 100-m race [13]–[16]. Other physiological changes that may arise from fatigue include slowing of muscle reaction time [17], altering of proprioception [18], and delaying our neuromuscular control in ways that reduce the control of muscles [19]. The physiological changes described are some of the mechanisms that may explain reductions in agility and deteriorate the nervous system's control of the leg's external forces. In support of this idea, soccer players show a reduced ability to complete legged balancing tasks on unstable surfaces when fatigued [20].

The aim of our study was to characterize the effect of fatigue on the nervous system's ability to rapidly and accurately control vertical external leg forces. We hypothesized that increased leg fatigue would deteriorate the leg's control of submaximal vertical external forces, as characterized by both reduced responsiveness and accuracy. We refer to responsiveness as to how quickly a person can control the magnitude of leg vertical external force when presented with a target force level while we refer to accuracy as how close and variable their controlled force is to and around

75   an intended target value. To test this hypothesis, we built a custom apparatus that constrained

76   participants' bodies from moving, allowing their legs to maintain a static posture while controlling

77   the external vertical force magnitude below their feet. We fatigued participants by having them

78   hold submaximal vertical leg forces equal to 25% of their maximum voluntary external force and

79   measured the leg's force control performance between fatigue trials in matching commanded

80   changes in force. We quantified fatigue as reductions in vertical force during maximal voluntary

81   leg contractions, increases in force variability, and a shift to lower mean frequencies in leg muscle

82   activity. To quantify force control performance, we instructed participants to best match visually

83   displayed target step changes in vertical force magnitude by pushing more or less against a ground-

84   mounted force plate. We evaluated control performance based on how responsive and accurate

85   participants were in matching their leg's external force vertical magnitude to the commanded target

86   changes in vertical force.

Methods

87

Participants

88

89   We recruited 18 participants for the study (identifying as female: n = 11, identifying as male =7;

90   age: 26.5±3.8y; body mass:74±16 kg; height: 171±12 cm; shoe size: 9+2 US sizing; mean±std).

91   The Office of Research Ethics at Simon Fraser University approved the study. Participants

92   provided us with verbal and written informed consent before participating.

Experimental Design

93

94   To characterize human leg force control, we tested the step response of participants as they

95   selectively controlled external leg force. We used a custom apparatus (Figure 1) that we had

96   previously built [1]. The apparatus consisted of a ground-embedded force plate (Bertec

97   Corporation, Ohio, USA) that participants stood on, constrained in both the vertical and horizontal

98   directions. The force plate was connected to a computer through a data acquisition unit (USB-

99   6229, National Instruments Corporation, Texas, USA), which sampled data at 1000 Hz.

100 Participants were able to exert a variable but controlled external force vector onto the ground by

101 selectively pushing down with their leg. Our device has rigid supports that constrain participants

102 at the shoulders and forearms preventing movement vertical and horizontal motion of their upper

103   body. Although control of force-position in the medial-lateral and anterior-posterior directions
104   (i.e., center of pressure control) and control of all three orthogonal force magnitude components
105   of the external force vector is important, our work here focused only on the control of vertical
106   force magnitude. In our prior work, we characterized the control of different step sizes of medial-
107   lateral and anterior-posterior force positions, as well as the control of a range of sub-maximal
108   vertical force magnitudes and found negligible differences in control characteristics for these
109   different components of the external force vector [1]. By focusing on only the vertical component
110   of force, we believe our findings will represent the range of control characteristics for all aspects
111   of controlling the external force vector at submaximal forces and any control changes resulting
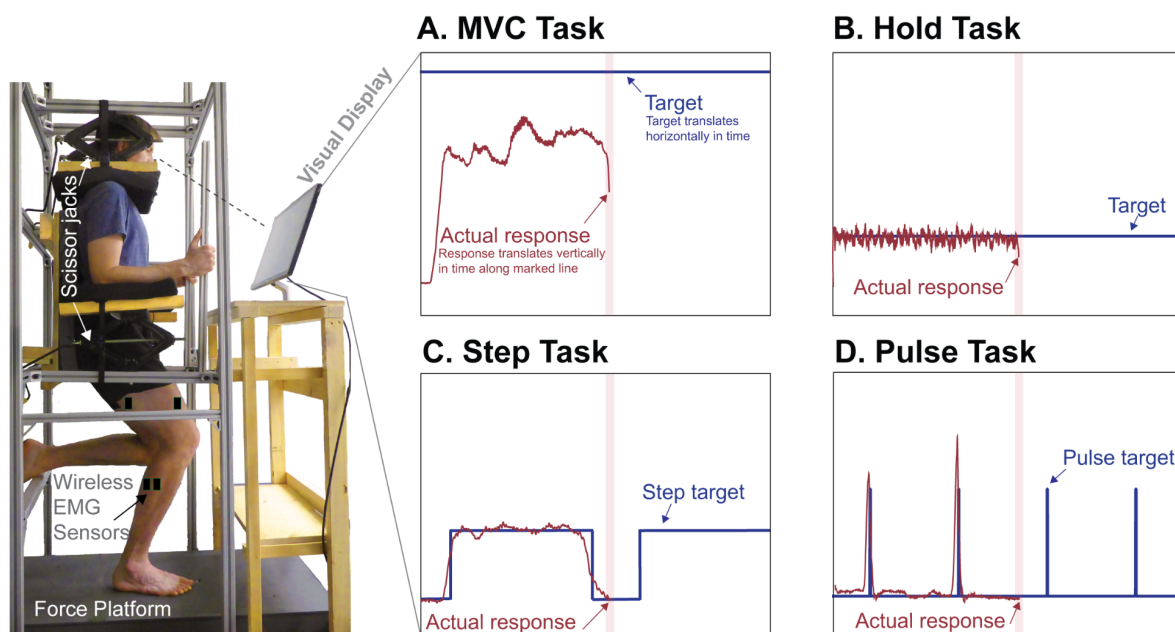112   from fatigue.

113

Figure 1: Apparatus used to characterize external force control and fatigue participants. The setup consisted of adjustable scissor jacks that constrained the vertical and horizontal motion of the participants' torso, pressing down on their shoulders and against their forearms, and a stiff 80/20 aluminum frame securely mounted to the ground. Each participant stood on their right leg in a posture resembling the mid-stance phase of a run and applied a vertical force to the ground by pushing down with their foot onto a force platform. The real-time feedback displayed to the participants showed the vertical force they were applying to the ground, as well as the target they were trying to match. There were four different tasks with four distinct visual targets: A. the MVC Task, which involved pushing down maximally for 10 seconds while trying to reach a motivating but unattainable target (5.0 BW); B. the Hold Task, which required participants to match a target equivalent to 1.4 times their body weight (1.4 BW) for 73 seconds; C. the Step Task, which involved rapidly and accurately controlling vertical force to match 10 upcoming step targets in 73 seconds; and D. the Pulse Task, which required participants to rapidly match 10 upcoming step targets in 73 seconds by changing their vertical force to match a target force that approximated a pulse. Participant shown in figure is author and has given consent for his picture to be used in this publication.

127

128 To objectively quantify fatigue, we recorded electromyography (EMG) from the leg muscles of
129 each participant. We placed wireless EMG sensors (Delsys, Natick, USA) on the middle of the
130 muscle belly on the vastus medialis, vastus lateralis, rectus femoris, bicep femoris, gastrocnemius
131 medialis, and gastrocnemius lateralis of the right leg muscles of each participant. Prior to placing
132 the sensors, we prepared the location by removing any excess hair using a razor and rubbing it
133 down with an alcohol swab, following standard procedures. We synchronized our EMG system
134 with our force plate using a custom code, which triggered the collection of both force plate and
135 EMG data. We used an EMG sampling rate of 2000 Hz.

136

137 After placing the EMG sensors, we fitted participants into the experimental apparatus. When fitting
138 participants, we adjusted the apparatus such that participants maintained an approximately 15-
139 degree knee flexion angle in their right leg, a posture similar to that assumed by a runner at the
140 start of the stance phase [1], [21]. In this fitting process, we moved components of the apparatus
141 to push down on the participant's shoulders and up on their arms by manually rotating four scissor
142 jacks (Figure 1). Our goal here was to ensure that participants were fixed tightly within the
143 apparatus and unable to move side-to-side or vertically.

144

145 To assess the effects of leg fatigue on the control of leg external force, we commanded four types
146 of force control tasks. In all tasks, participants stood on their right leg, unless otherwise instructed.
147 We used visual feedback to allow participants to compare their actual vertical force magnitude to
148 a target that we instructed them to match. We provided real-time visual feedback using a monitor,
149 where our custom-developed software displayed both the real-time feedback of the vertical force
150 magnitude signal that the participant's foot exerted onto the force plate and the target that the
151 participant tried to rapidly and accurately match. For visual display, we normalized the real-time
152 signal to each participant's body weight and filtered the raw force signal using a low-pass fourth-
153 order Butterworth filter with a cut-off frequency of 10 Hz. We programmed the real-time signal to
154 display at the center of the screen and constrained it to only move up and down as the participant
155 pushed more or less against the force plate. We programmed the target to slide past the real-time
156 signal, giving participants time to view any upcoming changes in the target before they occurred.

157

158   In the first force control task, referred to as the Maximum Voluntary Contraction Task (MVC
159   Task), we evaluated the maximum effort of voluntary force that the leg could exert on the ground.
160   To collect the MVC Task, we asked participants to push down against the ground as hard as
161   possible and try to reach an unattainable target of 5 times their body weight (5.0 BW) displayed
162   on the screen. From pilot experiments, we found that providing participants with a target to reach,
163   even if it was not attainable, motivated them to push harder to try and reach it. Each MVC Task
164   lasted 10 seconds as participants pushed down with their foot against the ground as hard as they
165   could.

166

167   We designed the second force control task, referred to as the Hold Task, to fatigue each
168   participant's right leg. In the Hold Task, we asked participants to match and hold a target equal to
169   their body weight plus 25% of their pre-fatigue maximum voluntary contraction, as determined in
170   the MVC Task before the onset of any leg fatigue [22]. This type of sustained voluntary contraction
171   progressively recruits more motor units and leads to muscle fatigue in the active muscles [22],
172   [23]. For each Hold Task, we asked participants to hold their force level to the best of their ability
173   to match the target for a total duration of 73 seconds, the same duration as the third leg force
174   control task.

175

176   In the third leg force control task, referred to as the Step Task, we probed force control
177   characteristics by commanding target step changes in leg vertical force magnitude. Because both
178   initial speed to the new target and steady-state accuracy around the new target are objectives, we
179   anticipate that the nervous system will depend on feedback control to accomplish this task. In a
180   single Step Task, the target step function consisted of a square wave of ten matching size target
181   steps, each 4 seconds in duration, with 3 seconds between steps (totaling 73 seconds per task). The
182   lower value of the step target was 1.0 BW and the upper value (i.e., the size of the target) was 1.4
183   BW. We selected the target step size based on a previous experiment where we studied step
184   responses by commanding a range of target step sizes, both smaller and larger than the magnitude
185   chosen here [1]. We observed minor changes in control characteristics between targets of varying
186   step sizes, so we chose an intermediate step size for this experiment.

187

188   In the fourth force control task, which we referred to as the Pulse Task, we aimed to probe rapid
189   force control by asking participants to respond as rapidly as possible to changes in the target.
190   Because this task emphasizes the initial speed of response over steady-state accuracy, we anticipate
191   that the nervous system will emphasize feedforward control over feedback control when
192   accomplishing this task [24]. The target in this task resembled a pulse, changing momentarily for
193   0.05s from 1.0 BW to the target step size of 1.4 BW (the same step size as in the Step Task). In a
194   single Pulse Task, we programmed the target pulse to go from body weight to the target step size
195   ten times over the duration of 73 seconds.

196   **Experimental Protocol**

197   We conducted the experiment in a single session. The session included five conditions: Training,
198   Pre-Fatigue, Fatigue-1, Fatigue-2, and Fatigue-3 (Figure 2). We started the study with the Training
199   condition to familiarize participants with the experiment. In this condition, we explained and
200   demonstrated how the visual feedback and force plate pushing worked. Then, we asked each
201   participant to perform two repetitions of the MVC Task followed by three repetitions of the Step
202   Task. From our previous work, we believe this is enough training in the apparatus to eliminate any
203   learning effects. After the Training condition, we gave participants a 1-minute break to stand freely
204   on both feet in the apparatus. Next, in the Pre-Fatigue condition, we had participants perform two
205   repetitions of the MVC Task followed by a 1-minute break, then three Step Tasks followed by a
206   1-minute break, and then two Pulse Tasks. We then gave participants a 1-minute break to rest
207   before the next condition. Next, we started the sequence of three fatigue conditions. Each Fatigue
208   condition consisted of a Hold Task followed by an MVC Task, which was repeated three times
209   within each Fatigue condition. After the third and final MVC Task in each Fatigue condition, we
210   immediately had each participant perform three repetitions of the Step Task to probe force control.
211   For each Fatigue condition, we repeated this same sequence of tasks. On the third Fatigue condition
212   and after the final Step Task, participants performed two Pulse Tasks. We gave participants a 1-
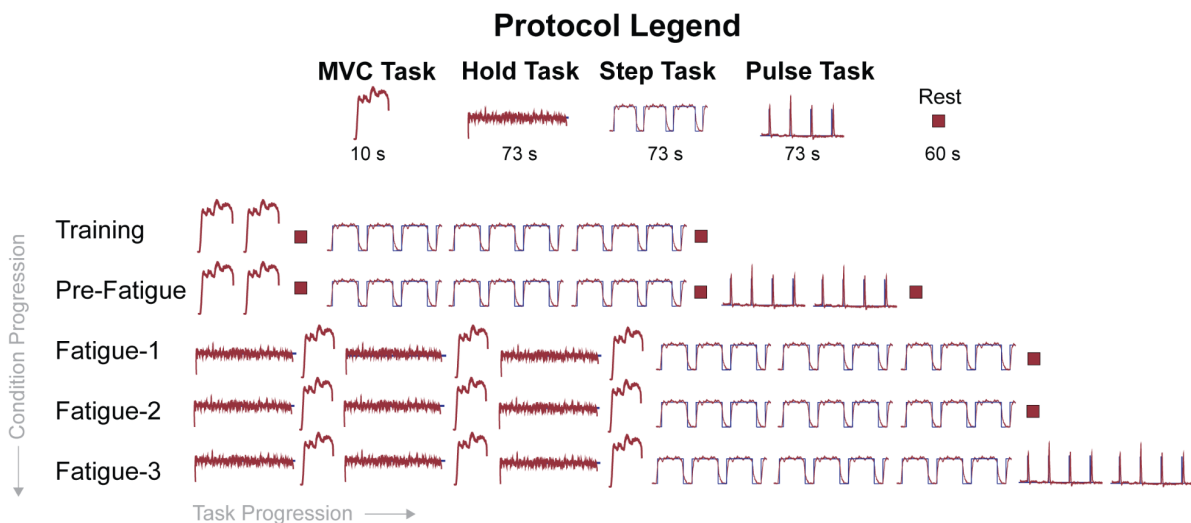213   minute break between Fatigue conditions.
214

Figure 2: A schematic of the experimental protocol which consisted of 5 conditions: Training, Pre-Fatigue, First Fatigue, Middle Fatigue, and Final Fatigue Each condition was composed of a combination of our force control tasks: Maximum Voluntary Contraction MVC Task, Hold Task, Step Task, and Pulse Task. The progression within each condition is shown as going from left to right and the progression of conditions goes from top to bottom starting from Training and finishing with Final Fatigue.

Data Analysis

For each MVC Task, we evaluated the mean vertical force output as one objective measure of fatigue (Figure 3-A). We quantified the mean vertical force output by taking the average of the signal during the midway point of the MVC Task between the 4-8 second time interval.

For each Hold Task, we evaluated the force variability of the response (Figure 3-B). We segmented each Hold Task data into one-second segments to quantity changes over time. We omitted any further analysis from the first 5 seconds of this signal as participants adjusted their vertical force to match the target during this time frame. For each 1-second segment, we then quantified force variability by calculating the standard deviation of the signal during each 1-second segment, dividing this by the mean of the signal during that time frame and multiplying this value by 100. This expresses variability as a percentage of the force magnitude.

For each step response, within each Step Task, we evaluated the responsiveness in controlling leg external force (Figure 3-C). To accomplish this, we took step data from each Step Task and segmented it into ten individual step responses such that each segmentation consisted of a six-second single-step response, with one second before the step-up and one second after the step-

238   down. For each step response, we evaluated the rise time (in units of milliseconds) as the time for

239   the signal to go from 10% to 90% of the target step size value [1]. We calculated bandwidth (in

240   units of Hz) by dividing 0.35 by the rise time [25]. The bandwidth measures the maximum

241   frequency at which a target signal can change and still be accurately tracked by the controller. We

242   remind readers that as we calculate bandwidth using rise time, bandwidth is not an independent

243   measure of responsiveness but rather depends on any changes in rise time. We restricted our

244   evaluation of the rise time and bandwidth of the response to the time interval of 0.5 seconds before

245   the step target stepped up to its high value and up to one second after the step-up occurred. Finally,

246   we quantified fall time (in units of milliseconds) as the time for the signal to go from 90% to 10%

247   of the target step size value. We evaluated the fall time between four to six seconds when the step

248   signal stepped down from the target step size to 1 BW. In this paper, we use the term

249   responsiveness to refer to rise time, bandwidth, and fall time. In robotic systems, and how we think

250   of responsiveness in this paper, a responsive system that is capable of high-fidelity tracking of a

251   target possesses a short rise time, a wide bandwidth, and a short fall time [26].

252

253   For each step response, within each Step Task, we evaluated the accuracy of controlling leg

254   external force (Figure 3-C). We quantified overshoot by taking the peak value reached by the

255   signal, subtracting the value of the target step, dividing this by the size of the step, and multiplying

256   by 100. We expressed overshoot as the percentage that the signal exceeds the target step size value.

257   A large overshoot can indicate under-damping in the controller—it can take longer for the system

258   to settle into a steady state, but it may be faster to reach its target step size [1]. We restricted our

259   evaluation of the overshoot of the response to the time interval of 0.5 seconds before the step target

260   stepped up and to one second after the step-up occurred. Next, we quantified steady-state error by

261   calculating the mean value of the signal between 2-4 seconds, subtracting the value of the target

262   step size, and taking the absolute value. We divided this by the value of the target step size and

263   multiplied it by 100 to express the steady-state error as a percentage of the target value. The steady-

264   state error informs us how much error the control system has once it has reached the target size

265   value and settled in its new state. A large error can be indicative of poor control as the system is

266   not able to well match the target value. We quantified steady-state variability by calculating the

267   standard deviation of the signal between 2-4 seconds, dividing this by the steady-state mean and

268   multiplying this value by 100. The steady-state variability, expressed as a percentage of the steady-

269   state mean, informs us how variable the system is once it has reached and settled on its new state.

270   From pilot studies, we found that using the 2-4 second interval to measure steady-state error and

271   steady-state variability was a sound assumption as participants had at this point reached a steady

272   state. In this paper, we use the term accuracy to refer to overshoot, steady-state error, and steady-

273   state variability—an accurate system has small overshoot, small steady-state error, and small

274   steady-state variability. We collectively refer to the rise time, bandwidth, overshoot, steady-state

275   error, steady-state variability, and fall time as the step response characteristics.

276

277   For each Pulse Task, we evaluated the responsiveness of the response (Figure 3-D). To accomplish

278   this, we took the data from each Pulse Task and segmented it into ten individual step responses

279   such that each segmentation consisted of a 3-second single-step response, with 1.5 seconds before

280   the step-up and 1.5 seconds after the step-down. Following the same definitions of responsiveness

281   as for the Step Task, we quantified the rise time, bandwidth, and fall time for each step in every
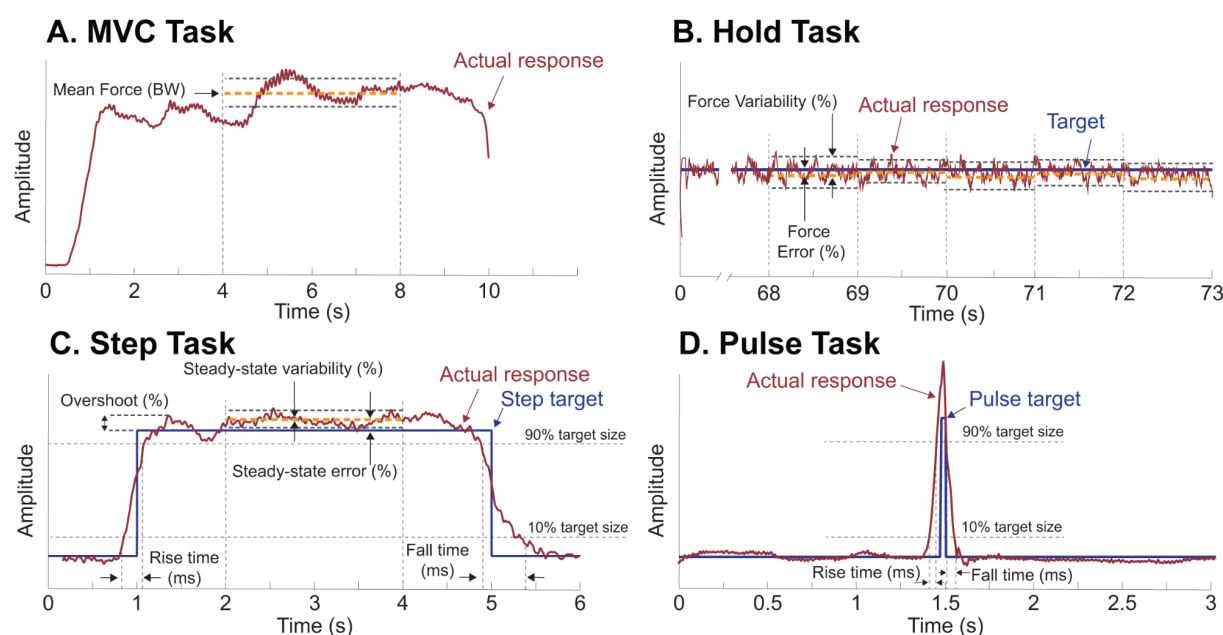
282   Pulse Task.

283

284

285   **Figure 3:** A visual analysis of the four leg force control tasks evaluated during the experiment. A. In the MVC Task,
286   we evaluated the mean force of the signal between 4-8 seconds. B. In the Hold Task, we omitted any analysis during
287   the first 5 seconds but calculated force variability for each 1-second interval for the duration of the task. C. We
288   evaluated the responsiveness (rise time, fall time, bandwidth) and accuracy (overshoot, steady-state error, steady-state
289   variability) for each step response in the Step Task. D. For each Pulse target in the Pulse Task we evaluated the
290   responsiveness.

291

292 We analyzed the EMG data to quantify changes in muscle frequency, one objective measure of
293 fatigue. We first bandpass filtered the raw EMG signals from 30 to 400 Hz using a fourth-order
294 zero-lag Butterworth filter and bandstop filtered the signal from 57–63 Hz to remove any residual
295 60 Hz noise [29]. We calculated the EMG median frequencies, a common measure of local muscle
296 fatigue [27]. To do this, we transformed the signal from the time domain into the frequency domain
297 by employing a fast-Fourier analysis to calculate the power spectrum. Next, we calculated median
298 power [28], [29]. A shift to lower median frequencies over time is viewed as evidence of local
299 muscle fatigue [28], [30].

300

301 For the Step Tasks and Pulse Task, we used exclusion criteria to remove responses that may poorly
302 describe the measured response. For the Step Task, we used the following criteria: (1) the response
303 steps up 0.5s before the target step function steps up, (2) the response does not step up within 0.5s
304 after the target step function steps up, (3) the response is already greater than 10% of the target
305 step size value during the 0.5s leading up to the step-up (4) the response steps down 1s or more
306 before the target step function steps down. For the Pulse Task, we used the following criteria: (1)
307 the response rises up 0.25s before the pulse target steps up, and (2) the response does not fall down
308 until greater than 0.25s after the pulse target steps down. We removed the step responses that meet
309 these exclusion criteria from all subsequent analyses.

Statistical Analysis

311 To determine the effects of our protocol on fatigue, we evaluated several objective measures. The
312 first measure we evaluated was changes in mean force magnitude during the maximum voluntary
313 contraction (MVC) task. A decrease in maximum vertical force is one indicator of fatigue [23]. To
314 calculate this measure, we compared the mean force values from the final MVC tasks completed
315 in each condition for each participant. Our second measure was force variability during each of
316 the consecutive Hold Tasks in each fatigue condition. Increased force variability as fatigue
317 progressed is an indicator of local muscle fatigue [31], [32]. To calculate this measure, we
318 compared the mean force variability for the final ten seconds of each Hold Task repeated in each
319 fatigue condition for each participant. To estimate force variability before the onset of fatigue
320 (referred to as "Pre-Fatigue"), we also calculated the mean force variability for the first ten seconds
321 of the Hold Task in the first Fatigue-1 condition. Our third measure was reductions in median

322   EMG frequency. As with force variability, we compared the mean of the median EMG frequencies

323   determined for the first ten seconds before the onset of fatigue and the final ten seconds of each

324   fatigue condition. To evaluate the effects of our protocol on leg external force control, we next

325   determined step response characteristics. For all conditions, we took the mean value of each step

326   response characteristic for the first five Step Task responses for each participant immediately

327   following the final MVC task. We used the same approach to characterize step response

328   characteristics for the Step Task and the Pulse Task. To determine if there were differences in

329   mean values between conditions, we performed a repeated-measures analysis of variance. If a

330   significant difference was found, we conducted post hoc pairwise comparisons between the group

331   means to identify which conditions produced similar mean values. We adjusted p-values for

332   multiple comparisons using Bonferroni corrections. In all cases, we used MATLAB's statistical

333   analysis toolbox and accepted $p<0.05$ as statistically significant. Unless otherwise stated we

334   present all data in the text as mean± standard deviation

Results

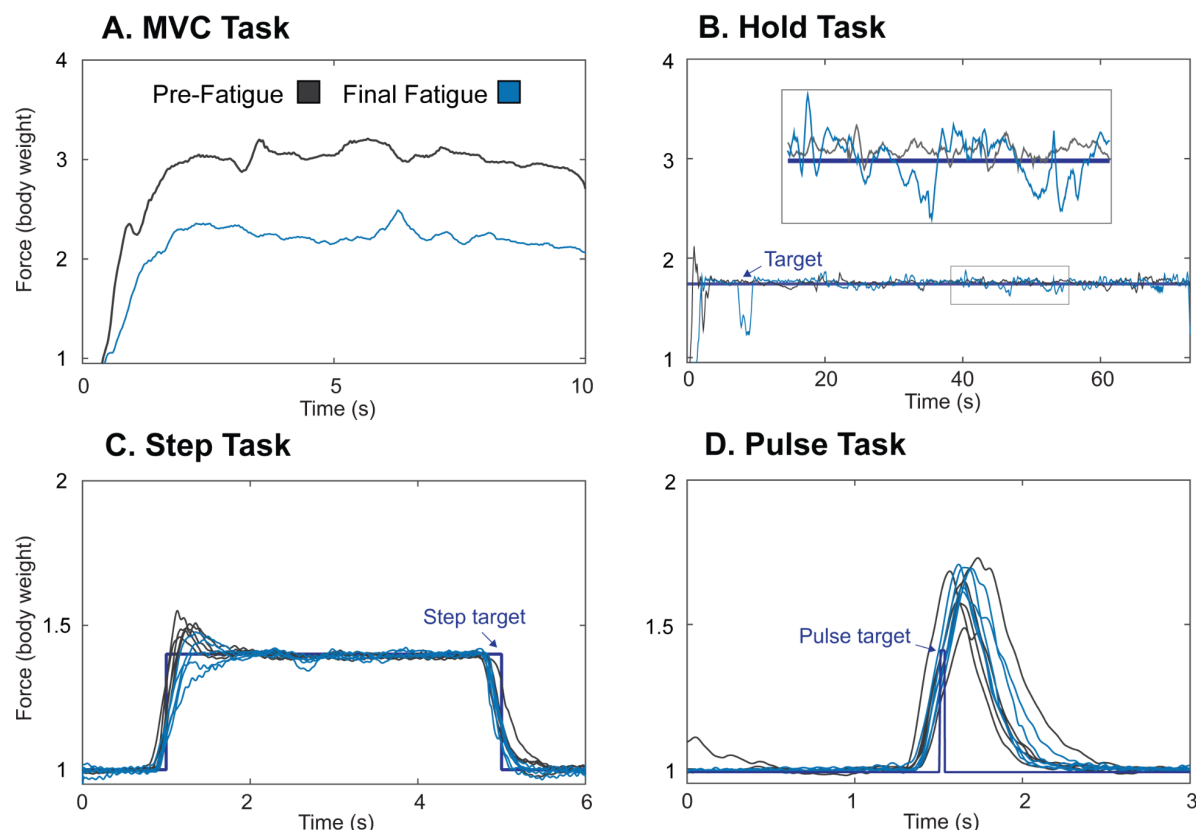## Participants fatigued during the protocol

Figure 4: Representative data for one participant comparing the Pre-Fatigue (grey) and Final Fatigue (blue) conditions for the A. MVC Task, B. Hold Task, C. Step Task, and D. Pulse Task. For C. and D. the first five responses immediately following the final MVC Task in each condition are shown. As the participant progressed through the protocol, they exhibited fatigue as indicated by a reduction in force for the MVC task and an increase in force variability during the Hold Task.

Objective measures of fatigue demonstrated that participants were fatigued during the protocol. Task data for a representative participant are shown in Figure 4. Fatigue was demonstrated by a reduction in the mean maximum MVC force (Figure 4A). As participants progressed through the protocol conditions, they exhibited significant reductions (p=1.3e-12) in the mean force magnitude during the MVC Tasks (Figure 5-A). During Pre-Fatigue, participants on average exerted a vertical mean leg force of 2.95±0.58 BW and by the final fatigue condition, participants exerted a mean force of 2.20±0.47 BW, a significant (p=4.7e-6) reduction of 26% in mean maximum force production. Next, we found significant increases in force variability (p=0.002) as participants

352   progressed through Fatigue conditions executing the Hold Tasks (Figure 5-B). During Pre-Fatigue,

353   participants had a mean force variability of 0.61± 0.31% and by the final condition, participants

354   had a mean force variability of 2.83±2.93% a significant (p=0.027) increase of 368%. Finally, we

355   found significant reductions in the mean median frequency for several muscles specifically the

356   gastrocnemius lateralis (p=0.002), gastrocnemius medialis (p=0.0019), and the bicep femoris

357   (p=0.003) (Figure 5-C). Comparing the Pre-Fatigue to the final fatigue condition, the

358   gastrocnemius lateralis medialis exhibited a significant (p=0.016) reduction of 10% in frequency

359   reducing from 126±24 Hz to 113±27 Hz; the gastrocnemius medialis exhibited a significant (p=

360   0.048) reduction of 10% reducing in frequency from 133±28Hz to 119±34Hz; and the bicep

361   femoris exhibited a reduction of 11% reducing in frequency from 90±12Hz to 79±13Hz but this

362   only approached but did not reach significance between these two conditions (p=0.074). The other

363   three muscles (vastus lateralis, vastus medialis, and rectus) did not show any significant changes
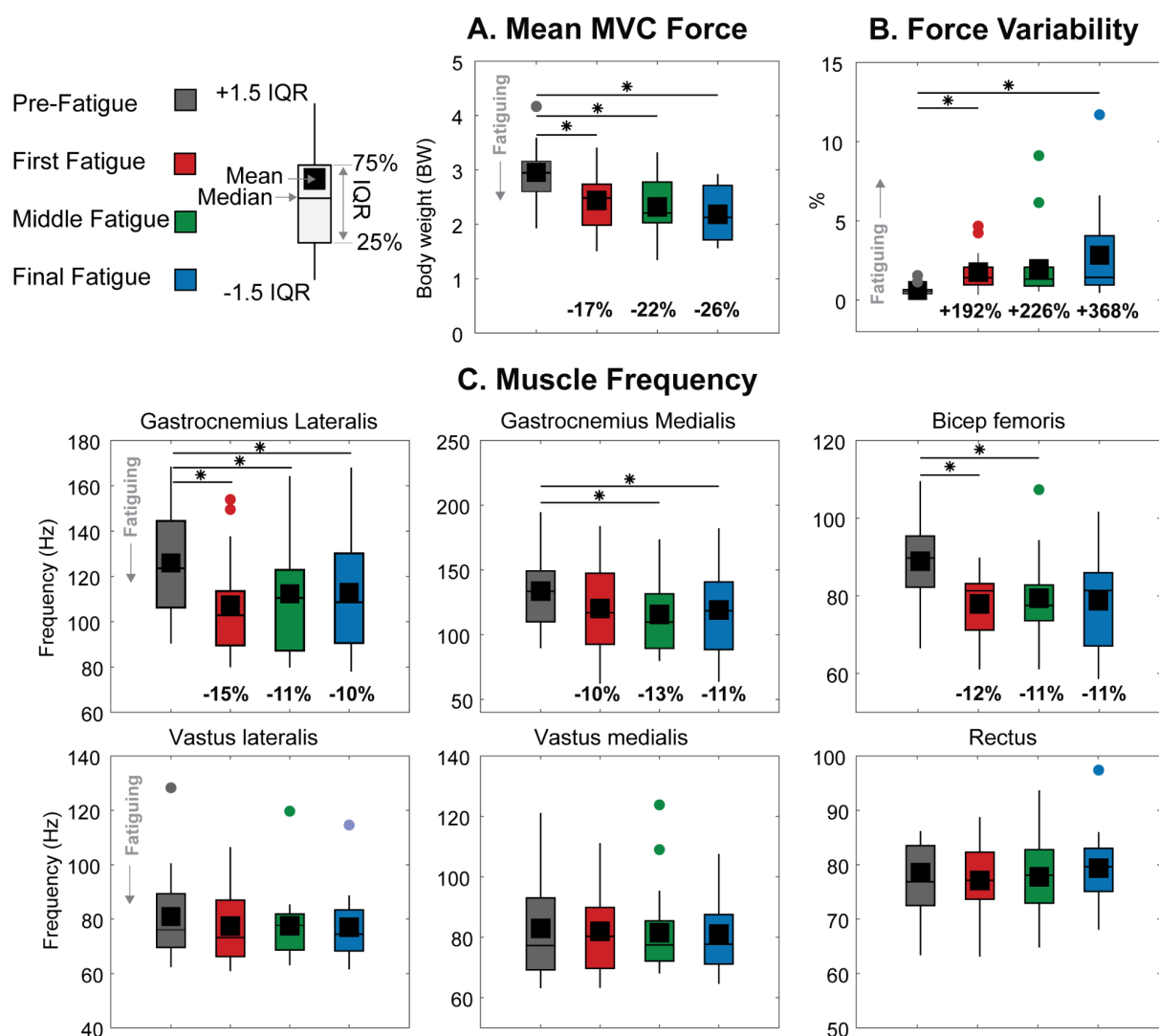
364   in EMG median frequency.

Figure 5: Objective measures of fatigue. As participants progressed through the protocol (Fatigue 1-3), they demonstrated A. A decline in Mean MVC vertical force, B. An increase in force variability, and C. A reduction in the median EMG frequency of several of the measured leg muscles. If we found the repeated measure ANOVA to be significant, we show any significant pairwise comparisons indicated with an asterisk. The legend on the top left explains the values shown in the box and whiskers plots.

Fatigue led to reductions in leg force control responsiveness

As participants grew fatigued, their responsiveness decreased, demonstrated by a significant decline in both rise time (p = 0.0011) and bandwidth (p = 0.0014). However, this decrease in responsiveness wasn't reflected in changes in fall time (p = 0.109) (Figure 6-A). Comparing the rise time of 303 ± 100 ms in the Pre-Fatigue condition to 373 ± 94 ms in the final fatigue condition, we observed a significant (p = 0.0006) increase of 23%. Simultaneously, bandwidth decreased

377 significantly (p = 0.04831) from 1.33 ± 0.6 Hz to 1.00 ± 0.25 Hz, a reduction of 25%. Despite

378 these changes, we did not observe any alteration in force control accuracy between these two
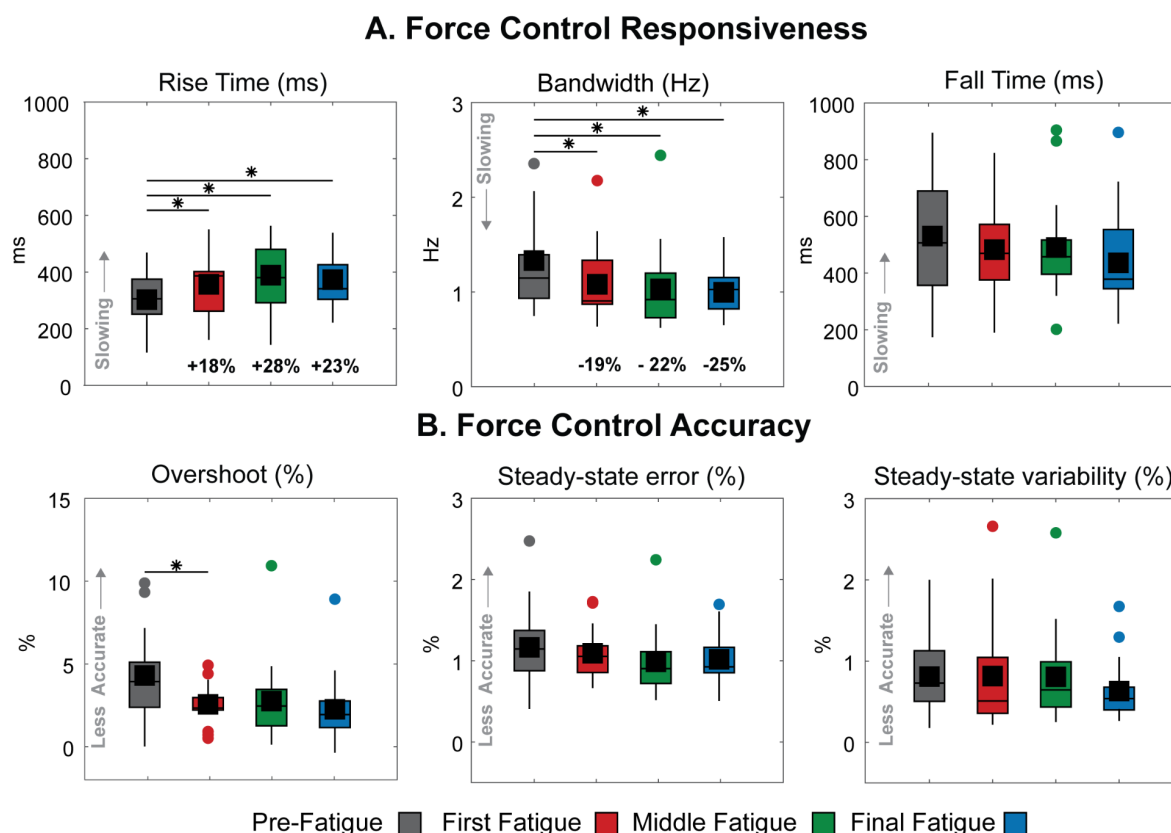
379 conditions (Figure 6-B).

Figure 6: A. We assessed force control responsiveness by examining changes in rise time, bandwidth, and fall time. B. We evaluated force control accuracy through alterations in overshoot, steady-state error, and variability. In cases where we found the repeated measure ANOVA significant, we displayed significant pairwise comparisons, denoted by an asterisk.

The Pulse Task was resilient to the effects of fatigue

386 As participants grew fatigued, they did not exhibit changes in responsiveness during the Pulse

387 Task (Figure 7), evidenced by the absence of significant changes in rise time (p=0.9722),

388 bandwidth (p=0.9147), or fall time (p=0.7830). Since the primary objective of the Pulse Task was

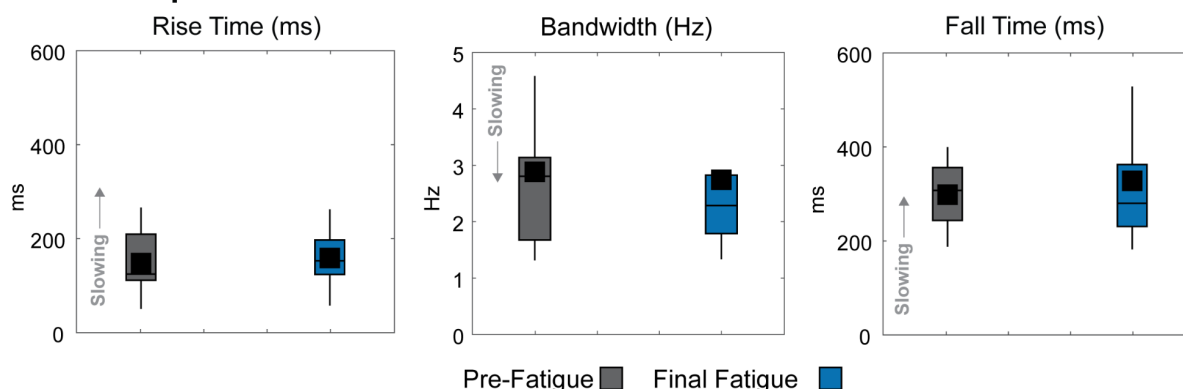389 responsiveness, we did not evaluate accuracy.

Pulse Responsiveness

Figure 7: Pulse Task responsiveness, assessed by rise time, bandwidth, and fall time, comparing the Pre-Fatigue condition to the final fatigue condition, Fatigue-3. We did not evaluate the accuracy of the Pulse Task, as its primary objective was responsiveness. When the need for accuracy was removed from the objective, participants exhibited greater responsiveness compared to the Step Task, which required both responsiveness and accuracy.

Participants exhibited higher responsiveness in the Pulse Task compared to the Step Task

We observed that participants demonstrated greater responsiveness in the Pulse Task than in the Step Task across all measures. In comparing the Pre-fatigue responsiveness of the two tasks, participants in the Pulse Task had a rise time of 148 ± 64 ms, a bandwidth of 2.88 ± 1.47 Hz, and a fall time of 299 ± 68 ms. In contrast, participants in the Step Task had a rise time of 303 ± 100 ms, a bandwidth of 1.33 ± 0.60 Hz, and a fall time of 531 ± 199 ms. During Pre-Fatigue, the Pulse Task exhibited a 51% faster rise time (p = 6.8e-6), a 116% wider bandwidth (p = 4.0e-4), and a 42% faster fall time (p = 6.0e-4) than the Step Task.

Discussion

In this study, we investigated the impact of fatigue on the ability to control the vertical component of leg external ground forces, finding that fatigue led to a decrease in force control responsiveness (speed). Our protocol successfully fatigued participants, as shown by several objective measures including a decrease in mean maximum voluntary contraction force during the MVC Task, increased force variability during the Hold Tasks, and reductions in median EMG frequency in multiple lower leg muscles. Consistent with our hypothesis, we observed that fatigued participants demonstrated a significant decline in responsiveness, marked by a 23% increase in rise time and a corresponding 25% reduction in bandwidth. However, contrary to our hypothesis, we found that fatigued participants did not exhibit significant changes in leg force control accuracy. Furthermore,

413   we found that in the Pulse Task—a task in which participants displayed overall greater
414   responsiveness when compared to the Step Task—control was resilient to the effects of fatigue.
415

416   There are several limitations to our study. One limitation is that mechanical compliance, both
417   within the participants' bodies and within the testing apparatus, may have influenced the measured
418   force. To minimize this potential issue, we used stiff materials and securely fixed the participants
419   in the apparatus, as described in [1]. Another limitation is that we only evaluated force control at
420   a single sub-maximal vertical force level. In real-life situations, leg external forces vary widely
421   depending on the task. However, previous research suggests that aspects of force control might
422   not differ significantly at different sub-maximal force levels of up to 60% of MVC when fatigued
423   [1], [33]. A third limitation is that our study results may not generalize to other populations, such
424   as older adults or individuals with chronic conditions. These groups could exhibit different control
425   characteristics even before the onset of fatigue [34]. [35], [36]. Lastly, our study used a
426   standardized fatigue protocol that might not accurately reflect real-world conditions in which
427   fatigue occurs. For example, real-world conditions can involve not only physical but also cognitive
428   demands, both of which may affect motor control and be subject to fatigue [37]. Our study targeted
429   fatigue at the neuromuscular level and did not actively investigate the separate effects of physical
430   and cognitive fatigue [38].
431

432   Fatigue can impact responsiveness through several pathways. One significant mechanism involves
433   the inhibition of feedforward connections, or neural drive, from the brain to the muscles. Neural
434   drive refers to the intensity or strength of the feedforward signals sent from the central nervous
435   system to the muscles [39]. This reduction in neural drive may be due to a decrease in the release
436   of neurotransmitters, an alteration in the firing patterns of motor neurons, or a reduction in the
437   sensitivity of muscle fibres to neurotransmitters [39]. When an individual is fatigued, the intensity
438   of these feedforward signals may be reduced, leading to a decrease in muscle force-generating
439   capabilities [40], [41]. It may also be the case that fatigue leads to a reduction in the sensory
440   feedback gains involved in the control of muscle force. In a feedback control system,
441   responsiveness is determined, in part, by the ratio between output (e.g., muscle force) and sensory
442   input (e.g., muscle length or velocity), known as feedback gains. Sensory feedback gains can be
443   adjusted dynamically to achieve task success [42]. As feedback gains decrease, the control system

444   becomes less responsive [43]. A comparison of the responsiveness results from the Step Task—

445   which relies on feedback control and was affected by fatigue—and the Pulse Task—which relies

446   more on feedforward control and was not affected by fatigue—suggests that in our experiment,

447   fatigue primarily affected sensory feedback pathways and not neural drive.

448

449   The distinction between the effects of fatigue on feedback and feedforward control is important

450   for understanding how the nervous system adapts to fatigue and could inform the development of

451   interventions to maintain or improve motor performance under fatigued conditions [44]. For

452   example, targeted interventions could focus on enhancing feedforward control through training

453   programs [45] or provide external sensory feedback to optimize performance in the presence of

454   fatigue [44]. The ability of individuals to maintain optimal performance in fatigued conditions is

455   critical, particularly for athletes. Therefore, identifying and developing effective interventions can

456   have a significant impact on their ability to perform at their best, even when fatigued.

457

458   Our observed reductions in leg force control responsiveness are large enough that they could

459   negatively impact agile performance. Agile performance relies on the ability to quickly and

460   accurately respond to changes in the environment. A decrease in responsiveness can increase the

461   time needed for the system to respond accurately to these changes, leading to a decline in

462   performance. This has been illustrated in simulation experiments using robotic legs, where

463   reductions in responsiveness, as indicated by increases in rise time and narrowing of bandwidth,

464   were observed when the controller time delay was increased [46]. And in hardware experiments

465   with legged robots— narrowing bandwidth and increasing controller time delay resulted in the

466   robot failing to land properly during a drop landing task [46]. However, the consequences of a

467   25% reduction in responsiveness, as observed in our study, on a system's or individual's agility

468   may depend on their specific abilities and the task. For instance, the MIT Cheetah, a highly agile-

469   legged robot, has a leg force responsiveness that is 100 times faster than that measured in

470   humans—a 25% reduction in responsiveness may not significantly affect its performance [47],

471   [48]. On the other hand, humans already exhibit comparatively slow rise times and narrow

472   bandwidths, suggesting that a 25% decrease in responsiveness is more likely to impair agile

473   performance. Indeed, fatigue-induced temporal changes in humans affect agile performance—

474 fatigued athletes exhibit prolonged drop landing contact times [20] and decreased running speed
475 [49].

476

477 Fatigue leads to reductions in leg force control responsiveness, potentially raising the risk of injury
478 during physical activities. To preserve performance, individuals may compensate for these
479 decreases by altering their body mechanics. For example, fatigued athletes have been observed
480 landing from jumps with more flexed knees or shifting their load from plantar flexors to knee
481 extensors [5]. Such fatigue-induced changes in body mechanics can compromise stability and
482 heighten injury risk by placing extra stress on specific joints or muscles not typically engaged or
483 active during certain movements [50], [51]. In men's collegiate soccer matches, for example,
484 players sustained approximately 50% more injuries in the second half compared to the first half
485 [52].

486

487 In our experiment we developed a method for fatiguing participants and benchmarking the impact
488 of fatigue on leg force control performance, laying groundwork for studying interventions that
489 address fatigue and enhance agility. Potential interventions, such as strength training or
490 exoskeletons, could be explored in diverse populations, including athletes, military personnel, and
491 older adults. By understanding the effects of fatigue on leg force control responsiveness and
492 accuracy, it may be possible to develop targeted strategies that not only mitigate the consequences
493 of fatigue but also optimize agility across various tasks and populations. This research will help
494 with future work focused on identifying, assessing, and implementing effective interventions that
495 cater to the unique needs of individuals relying on leg force control for optimal performance.

496

497

498

499

500
501
502

Acknowledgements

504 We would like to thank all the participants who volunteered their time for our study.

Author Contributions

506 P.K. and J.M.D. conceived and designed research; P.K. performed experiments; P.K. analyzed
507 data; P.K. J.M.W., S.N.R., and J.M.D. interpreted results of experiments; P.K. prepared figures;
508 P. K. and J.M.D. drafted the manuscript; P.K., J.M.W., S.N.R., and J.M.D. edited and revised
509 manuscript; P.K., J.M.W., S.NR, and J.M.D. approved the final version of the manuscript.

Competing interests

511 The authors declare no competing or financial interests.

Funding

Work Cited

[1] P. Kudzia, S. N. Robinovich, and J. M. Donelan, "Characterizing the performance of human leg external force control," *Sci. Rep.*, vol. 12, no. 1, p. 4935, Mar. 2022.

[2] M. Nocella, B. Colombini, G. Benelli, G. Cecchi, M. A. Bagni, and J. Bruton, "Force decline during fatigue is due to both a decrease in the force per individual cross-bridge and the number of cross-bridges," *J. Physiol.*, vol. 589, no. Pt 13, pp. 3371–3381, Jul. 2011.

[3] G. Boccia *et al.*, "Decrease of muscle fiber conduction velocity correlates with strength loss after an endurance run," *Physiol. Meas.*, vol. 38, no. 2, pp. 233–240, Feb. 2017.

[4] D. A. Jones, "Changes in the force-velocity relationship of fatigued muscle: implications for power production and possible causes," *J. Physiol.*, vol. 588, no. Pt 16, pp. 2977–2986, Aug. 2010.

[5] N. Cortes, D. Quammen, S. Lucci, E. Greska, and J. Onate, "A functional agility short-term fatigue protocol changes lower extremity mechanics," *J. Sports Sci.*, vol. 30, no. 8, pp. 797–805, Mar. 2012.

[6] J. B. Thorlund, P. Aagaard, and K. Madsen, "Rapid muscle force capacity changes after soccer match play," *Int. J. Sports Med.*, vol. 30, no. 4, pp. 273–278, Apr. 2009.

[7] T. Spiteri, R. U. Newton, M. Binetti, N. H. Hart, J. M. Sheppard, and S. Nimphius, "Mechanical Determinants of Faster Change of Direction and Agility Performance in Female Basketball Athletes," *J. Strength Cond. Res.*, vol. 29, no. 8, pp. 2205–2214, Aug. 2015.

[8] J. Oliver, N. Armstrong, and C. Williams, "Changes in jump performance and muscle activity following soccer-specific exercise," *J. Sports Sci.*, vol. 26, no. 2, pp. 141–148, Jan. 2008.

[9] M. F. Bobbert, M. M. Van Der Krogt, H. Van Doorn, and C. J. de Ruiter, "Effects of Fatigue of Plantarflexors on Control and Performance in Vertical Jumping," *Med. Sci. Sports Exercise*, vol. 43, no. 4, p. 673, Apr. 2011.

[10] A. L. Rodacki, N. E. Fowler, and S. J. Bennett, "Multi-segment coordination: fatigue effects," *Med. Sci. Sports Exerc.*, vol. 33, no. 7, pp. 1157–1167, Jul. 2001.

[11] C. N. Cooper, N. C. Dabbs, J. Davis, and N. M. Sauls, "Effects of Lower-Body Muscular Fatigue on Vertical Jump and Balance Performance," *J. Strength Cond. Res.*, vol. 34, no. 10, pp. 2903–2910, Oct. 2020.

[12] J. L. R. Jayalath, M. de Noronha, N. Weerakkody, and R. Bini, "Effects of fatigue on ankle biomechanics during jumps: A systematic review," *J. Electromyogr. Kinesiol.*, vol. 42, pp. 81–91, Oct. 2018.

[13] W. Schlicht, W. Naretz, D. Witt, and H. Rieckert, "Ammonia and lactate: differential information on monitoring training load in sprint events," *Int. J. Sports Med.*, vol. 11 Suppl 2, pp. S85–90, May 1990.

[14] A. Mero and E. Peltola, "Neural activation fatigued and non-fatigued conditions of short and long sprint running," *Biol. Sport*, vol. 6, no. 1, pp. 43–58, 1989.

[15] A. Ross, M. Leveritt, and S. Riek, "Neural influences on sprint running," *Sports Med.*, vol. 31, no. 6, pp. 409–425, 2001.

[16] T. Finni, H. Kyröläinen, J. Avela, and P. V. Komi, "Maximal but not submaximal performance is reduced by constant-speed 10-km run," *J. Sports Med. Phys. Fitness*, vol. 43, no. 4, pp. 411–417, Dec. 2003.

[17] S. Benesch, W. Pütz, D. Rosenbaum, and H. Becker, "Reliability of peroneal reaction time measurements," *Clin. Biomech.*, vol. 15, no. 1, pp. 21–28, Jan. 2000.

[18] F. Mohammadi and A. Roozdar, "Effects of fatigue due to contraction of evertor muscles on the ankle joint position sense in male soccer players," *Am. J. Sports Med.*, vol. 38, no. 4, pp. 824–828, Apr. 2010.

[19] J. C. Wilkins, T. C. Valovich McLeod, D. H. Perrin, and B. M. Gansneder, "Performance on the Balance Error Scoring System Decreases After Fatigue," *J. Athl. Train.*, vol. 39, no. 2, pp. 156–161, Jun. 2004.

[20] E. Zemková and D. Hamar, "The effect of soccer match induced fatigue on neuromuscular performance," *Kinesiology*, vol. 41, no. 2, 2009, [Online]. Available: https://hrcak.srce.hr/file/70903

[21] R. K. Fukuchi, C. A. Fukuchi, and M. Duarte, "A public dataset of running biomechanics and the effects of running speed on lower extremity kinematics and kinetics," *PeerJ*, vol. 5, p. e3298, May 2017.

[22] J. L. Taylor and S. C. Gandevia, "A comparison of central aspects of fatigue in submaximal and maximal voluntary contractions," *J. Appl. Physiol.*, vol. 104, no. 2, pp. 542–550, Feb. 2008.

[23] R. M. Enoka and J. Duchateau, "Muscle fatigue: what, why and how it influences muscle function," *J. Physiol.*, vol. 586, no. 1, pp. 11–23, Jan. 2008.

[24] A. D. Kuo, "The relative roles of feedforward and feedback in the control of rhythmic movements," *Motor Control*, vol. 6, no. 2, pp. 129–145, Apr. 2002.

[25] M. T. Thompson, "Review of Signal Processing Basics," in *Intuitive Analog Circuit Design*, Elsevier, 2014, pp. 15–52.

[26] A. F. Azocar, L. M. Mooney, L. J. Hargrove, and E. J. Rouse, "Design and Characterization of an Open-Source Robotic Leg Prosthesis," in *2018 7th IEEE International Conference on Biomedical Robotics and Biomechatronics (Biorob)*, Aug. 2018, pp. 111–118.

[27] A. Phinyomark, S. Thongpanja, H. Hu, P. Phukpattaranont, and C. Limsakul, "The usefulness of mean and median frequencies in electromyography analysis," *Computational intelligence in electromyography analysis-A perspective on current applications and future challenges*, vol. 81, p. 67, 2012.

[28] S. Nagata, A. B. Arsenault, D. Gagnon, G. Smyth, and P. A. Mathieu, "EMG power spectrum as a measure of muscular fatigue at different levels of contraction," *Med. Biol. Eng. Comput.*, vol. 28, no. 4, pp. 374–378, Jul. 1990.

[29] J. R. Potvin and L. R. Bent, "A validation of techniques using surface EMG signals from dynamic contractions to quantify muscle fatigue during repetitive tasks," *J. Electromyogr. Kinesiol.*, vol. 7, no. 2, pp. 131–139, Jun. 1997.

[30] F. B. Stulen and C. J. DeLuca, "Frequency parameters of the myoelectric signal as a measure of muscle conduction velocity," *IEEE Trans. Biomed. Eng.*, vol. 28, no. 7, pp. 515–523, Jul. 1981.

[31] S. E. Salomoni and T. Graven-Nielsen, "Muscle fatigue increases the amplitude of fluctuations of tangential forces during isometric contractions," *Hum. Mov. Sci.*, vol. 31, no. 4, pp. 758–771, Aug. 2012.

[32] N. B. Singh, A. Arampatzis, G. Duda, M. O. Heller, and W. R. Taylor, "Effect of fatigue on force fluctuations in knee extensors in young adults," *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, vol. 368, no. 1920, pp. 2783–2798, Jun. 2010.

[33] G. Boccia *et al.*, "Neuromuscular Fatigue Does Not Impair the Rate of Force Development in Ballistic Contractions of Submaximal Amplitudes," *Front. Physiol.*, vol. 9, p. 1503, Oct. 2018.

[34] B. L. Tracy and R. M. Enoka, "Older adults are less steady during submaximal isometric contractions with the knee extensor muscles," *J. Appl. Physiol.*, vol. 92, no. 3, pp. 1004–1012, Mar. 2002.

[35] B. C. M. Smits-Engelsman, Y. Westenberg, and J. Duysens, "Children with developmental coordination disorder are equally able to generate force but show more variability than typically developing children," *Hum. Mov. Sci.*, vol. 27, no. 2, pp. 296–309, Apr. 2008.

[36] M. A. Oliveira, A. M. Rodrigues, R. M. S. Caballero, R. D. S. Petersen, and J. K. Shim, "Strength and isometric torque control in individuals with Parkinson's disease," *Experimental Brain Research*, vol. 185, no. 3. pp. 533–533, 2008. doi: 10.1007/s00221-008-1290-3.

[37] R. M. Enoka and J. Duchateau, "Translating Fatigue to Human Performance," *Med. Sci. Sports Exerc.*, vol. 48, no. 11, pp. 2228–2238, Nov. 2016.

[38] F. Skala and E. Zemková, "Effects of Acute Fatigue on Cognitive Performance in Team Sport Players: Does It Change the Way They Perform? A Scoping Review," *NATO Adv. Sci. Inst. Ser. E Appl. Sci.*, vol. 12, no. 3, p. 1736, Feb. 2022.

[39] J. L. Taylor, M. Amann, J. Duchateau, R. Meeusen, and C. L. Rice, "Neural Contributions to Muscle Fatigue: From the Brain to the Muscle and Back Again," *Med. Sci. Sports Exerc.*, vol. 48, no. 11, pp. 2294–2306, Nov. 2016.

[40] F. Ranieri and V. Di Lazzaro, "The role of motor neuron drive in muscle fatigue," *Neuromuscul.*

627   *Disord.*, vol. 22 Suppl 3, pp. S157–61, Dec. 2012.

628 [41] B. Bigland-Ritchie, "Muscle fatigue and the influence of changing neural drive," *Clin. Chest Med.*,
629   vol. 5, no. 1, pp. 21–34, Mar. 1984.

630 [42] E. Azim and K. Seki, "Gain control in the sensorimotor system," *Curr Opin Physiol*, vol. 8, pp. 177–
631   187, Apr. 2019.

632 [43] Franklin, *Feedback Control of Dynamic Systems*. Pearson Education, 2008.

633 [44] R. Sigrist, G. Rauter, R. Riener, and P. Wolf, "Augmented visual, auditory, haptic, and multimodal
634   feedback in motor learning: a review," *Psychon. Bull. Rev.*, vol. 20, no. 1, pp. 21–53, Feb. 2013.

635 [45] P. Aagaard, "Training-induced changes in neural function," *Exerc. Sport Sci. Rev.*, vol. 31, no. 2, pp.
636   61–67, Apr. 2003.

637 [46] M. S. Ashtiani, A. Aghamaleki Sarvestani, and A. Badri-Spröwitz, "Hybrid Parallel Compliance
638   Allows Robots to Operate With Sensorimotor Delays and Low Control Frequencies," *Front Robot AI*,
639   vol. 8, p. 645748, Jun. 2021.

640 [47] P. M. Wensing, A. Wang, S. Seok, D. Otten, J. Lang, and S. Kim, "Proprioceptive Actuator Design in
641   the MIT Cheetah: Impact Mitigation and High-Bandwidth Physical Interaction for Dynamic Legged
642   Robots," *IEEE Trans. Rob.*, vol. 33, no. 3, pp. 509–522, Jun. 2017.

643 [48] B. Katz, J. D. Carlo, and S. Kim, "Mini Cheetah: A Platform for Pushing the Limits of Dynamic
644   Quadruped Control," in *2019 International Conference on Robotics and Automation (ICRA)*, May
645   2019, pp. 6295–6301.

646 [49] R. D. Johnston, T. J. Gabbett, and D. G. Jenkins, "Influence of an intensified competition on fatigue
647   and match performance in junior rugby league players," *Journal of Science and Medicine in Sport*,
648   vol. 16, no. 5. pp. 460–465, 2013. doi: 10.1016/j.jsams.2012.10.009.

649 [50] S.-H. Chen and L.-S. Chou, "Gait balance control after fatigue: Effects of age and cognitive demand,"
650   *Gait Posture*, vol. 95, pp. 129–134, Jun. 2022.

651 [51] P. C. R. D. Santos, F. A. Barbieri, I. Zijdewind, L. T. B. Gobbi, C. Lamoth, and T. Hortobágyi, "Effects
652   of experimentally induced fatigue on healthy older adults' gait: A systematic review," *PLoS One*, vol.
653   14, no. 12, p. e0226939, Dec. 2019.

654 [52] National Collegiate Athletic Association, "Men's soccer Injuries NCAA." [Online]. Available:
655   https://www.datalyscenter.org/sites/datalyscenter.org/files/NCAA_M_Soccer_Injuries_HiRes.pdf

656