Discharge properties of abductor hallucis before, during, and after an isometric fatigue task

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KELLY LA, RACINAS S, CRESSWELL AG. Discharge properties of abductor hallucis before, during, and after an isometric fatigue task. J Neurophysiol 110: 891–898, 2013. First published May 15, 2013; doi:10.1152/jn.00944.2012.—Abductor hallucis is the largest muscle in the arch of the human foot and comprises few motor units relative to its physiological cross-sectional area. It has been described as a postural muscle, aiding in the stabilization of the longitudinal arch during stance and gait. The purpose of this study was to describe the discharge properties of abductor hallucis motor units during ramp and hold isometric contractions, as well as its discharge characteristics during fatigue. Intramuscular electromyographic recordings from abductor hallucis were made in 5 subjects; from those recordings, 42 single motor units were decomposed. Data were recorded during isometric ramp contractions at 60% maximum voluntary contraction (MVC), performed before and after a submaximal isometric contraction to failure (mean force 41.3 ± 15.3% MVC, mean duration 233 ± 116 s). Motor unit recruitment thresholds ranged from 10.3 to 54.2% MVC. No significant difference was observed between recruitment and derecruitment thresholds or their respective discharge rates for both the initial and postfatigue ramp contractions (all P > 0.25). Recruitment threshold was positively correlated with recruitment discharge rate (r = 0.47, P < 0.03). All motor units attained similar peak discharge rates (14.0 ± 0.25 pulses/s) and were not correlated with recruitment threshold. Thirteen motor units could be followed during the isometric fatigue task, with a decline in discharge rate and increase in discharge rate variability occurring in the final 25% of the task (both P < 0.05). We have shown that abductor hallucis motor units discharge relatively slowly and are considerably resistant to fatigue. These characteristics may be effective for generating and sustaining the substantial level of force that is required to stabilize the longitudinal arch during weight bearing.

abductor hallucis; fatigue; intrinsic foot muscle; motor unit discharge properties; posture

ABDUCTOR HALLUCIS (AH) is the largest and most medially located of the plantar intrinsic foot muscles (Kura et al. 1997; Ledoux et al. 2001) and comprises a relatively low number of motor units (Johns and Fuglevand 2011). Its function is to both abduct and flex the great toe at the first metatarsophalangeal (MTP) joint. AH has been shown to be involved in postural stabilization during upright stance, with activation patterns being highly correlated with medial postural sway (Kelly et al. 2012). It has also been suggested that AH is involved in maintaining longitudinal arch (LA) height during gait (Basmajian and Stecko 1963; Mann and Inman 1964). However, little is known about the neurophysiological properties of this muscle, as well as how these properties may influence force production.

Active muscle force is regulated by the nervous system via two mechanisms; recruitment (and derecruitment) and rate coding. The utilization of recruitment and rate coding strategies varies greatly between muscles. Postural muscles, such as soleus, are active for sustained periods maintaining upright posture (Sherrington 1915) generally display relatively low peak discharge rates (10–25 Hz) (Bellemare et al. 1983; Dalton et al. 2009; Kuchinad et al. 2004; Oya et al. 2009) and are reliant on recruitment to generate and maintain force across their full range of force production (Oya et al. 2009), whereas muscles requiring precise control of movement, such as hand muscles, tend to have complete recruitment achieved at relatively low force levels (~30–50% of maximal voluntary contraction (MVC)), thereafter relying on rate coding to generate and maintain force (De Luca et al. 1982; Moritz et al. 2005; Thomas et al. 1986; Zijdewind 2002).

In addition to recruitment and rate coding strategies, the number of motor units within a particular muscle will also have a significant impact on the ability to generate and grade active force (Campbell et al. 1973; Diderikson et al. 2012). Muscles with a lower number of motor units relative to their physiological cross-sectional area (PCSA) tend to have a reduced ability to precisely control gradation of force (Enoka 1995). Interestingly, AH has been shown to possess few motor units (Johns and Fuglevand 2011) relative to its PCSA, and thus these motor units may be inherently large compared with other muscles of the foot (Campbell et al. 1973) and hand (Sica et al. 1974), which contain greater motor unit numbers relative to their PCSA (Kura et al. 1997; Linscheid et al. 1991).

During sustained submaximal (fatiguing) contractions, a decline in force-producing capacity is generally accompanied by an increase in excitatory drive to the alpha motoneuron pool (Hoffman et al. 2009; Löschler et al. 1996). If the contraction force is below the upper limit of motor unit recruitment, an increase in excitatory drive will generally incite recruitment of new motor units to help maintain the required force. Despite an increase in central drive to the motoneuron pool, motor unit discharge behavior can vary considerably during sustained submaximal contractions, with studies reporting a decrease (Dalton et al. 2010; Garland et al. 1997; Mottram 2004; Vila-Cha et al. 2010), an increase (Adam and Deluca 2005; Griffin et al. 2001; Kuchinad et al. 2004), or no change in discharge rate (Christie and Kamen 2009; Pascoe et al. 2011). It has been suggested that the reported inconsistencies between studies in discharge behavior that occur during sustained sub-
maximal contractions are due to varying interactions between cortical input and spinal motoneuron responsiveness (Kernell and Monster 2004; McNeil et al. 2011a), as well as the nature of the task (i.e., high vs. low intensity) (Kuchnad et al. 2004) and the recruitment threshold of the motor units being investigated (Riley et al. 2008a).

Another factor determining the discharge behavior of a particular muscle during a fatiguing contraction is the composition of muscle fibers within that muscle, that is, the percentage of fatigue-resistant slow-twitch fibers relative to the more fatigue-sensitive fast-twitch fibers (Kernell et al. 1999; Kernell and Monster 2004). Postural muscles, which have a higher percentage of fatigue-resistant slow-twitch fibers, tend to be relatively resistant to fatigue-induced alterations in motor unit discharge behavior (Kuchnad et al. 2004; Macefield et al. 2000).

Fluctuations in resting membrane potential (due to synaptic noise) are known to lead to increased discharge variability, which also influences the ability of a muscle to maintain target force (Calvin and Stevens 1968). The coefficient of variation (CV) of interspike interval (ISI) is a relative measure of motor unit discharge variability and provides an insight into the interplay between increased central drive and spinal motoneuron inhibition that occurs during sustained contractions (Calvin and Stevens 1968). Motor unit discharge variability significantly hinders force output and steadiness (Enoka et al. 2002; Moritz et al. 2005; Tracy et al. 2005) and has been shown to increase under conditions of muscle fatigue (Christie and Kamen 2009).

The manner in which a postural muscle with a low number of motor units relative to its PCSA, such as AH, utilizes recruitment and rate coding strategies to generate and sustain force remains unclear. Given the suggestion that AH is responsible for postural support of the LA during stance, we hypothesized that motor units in AH would have relatively slow discharge rates while displaying relatively high levels of fatigue resistance. Therefore, the aims of this study were to describe the single motor unit (SMU) discharge properties of AH during controlled ramp and hold contractions as well as during an isometric submaximal constant load fatigue task.

METHODS

Participants. Five healthy males who had no history of neuromuscular disorder volunteered to participate in this study (mean ± SD for age, height, and weight were 30 ± 5 yr, 180 ± 3 cm, and 79 ± 7 kg, respectively). The procedures were approved by the local scientific ethics committee and performed according to the Declaration of Helsinki. All subjects gave their written informed consent.

Familiarization procedure. Precise control of isometric force development and relaxation is imperative when studying the recruitment and derecruitment characteristics of an SMU. However, an isolated contraction of AH (abduction and flexion of the hallux) is a novel task that can be particularly difficult to perform with accuracy. As such, all subjects attended the laboratory between two and six times to familiarize themselves with the required experimental tasks to reduce task variability. This included performing controlled isometric ramp and hold flexion/abduction (F-AB) contractions of the hallux, sustained isometric F-AB contractions at a constant submaximal force, and maximal voluntary effort isometric F-AB contractions. Participants were trained to flex and abduct their hallux at the first MTP joint, in the absence of interphalangeal joint flexion. The hallux F-AB task was designed on the basis of pilot experimental data that indicated this was an effective method to isolate contraction of the AH and reduce the risk of co-contraction of agonist hallux flexors. Force feedback was given visually via a computer monitor located at eye level directly in front of the subject. The acceptable error for force tracking was set at ±3% MVC (De Luca et al. 1996). All participants conducted several practice trials until the investigator was satisfied that the participant could adequately follow the target force templates.

Experimental setup. Participants sat comfortably with the right shank and foot secured with Velcro straps in a rigid, custom-built brace, which stabilized the leg, ankle, and midfoot, preventing changes in ankle and midfoot joint angles (Fig. 1A). The shank was positioned perpendicular to the plantar surface of the brace, and the foot was positioned in ~10° of eversion and parallel to the plantar surface of the brace. The inner lining of the boot contained an air bladder that was inflated to improve comfort and further reduce any possible change in joint angle. A compression load cell (model MB miniature beam; Interface, Scottsdale, AZ) able to detect a minimal mass of 0.0056 kg was aligned to the plantar surface of the big toe and secured with an additional Velcro strap.

Intramuscular electromyography and force measurement. Intramuscular electromyography (EMG_{IM}) recordings were collected in the right foot of each subject with the use of a quadrifilar fine-wire electrode (Micro-probes, Gaithersburg, MA), which was inserted in the largest and most proximal segment of the AH muscle (Tosovic et al. 2012) with the aid of a delivery needle (0.5-mm diameter × 50 mm; Fig. 1B). Quadrifilar electrodes consist of four insulated fine wires glued together at the tip, with reduced-area cut ends acting as the recording surfaces, making them highly selective (Adams 2005). Ultrasound guidance was used to ensure accuracy of electrode placements for all needle insertions. Two channels of EMG_{IM} were recorded from these electrodes to improve both the precision and yield of SMUs from the recordings. A reference surface electrode was placed on the medial malleolus of the right ankle.

All EMG_{IM} signals were amplified 1,000 times, recorded with an open bandwidth (Delsys Bagnoli, Boston, MA), analog-to-digital converted at a sampling rate of 20 kHz, and collected using Spike2 software (Cambridge Electronic Design, Cambridge, UK). EMG signal quality was assessed by asking the participant to conduct a brief, low-intensity isometric contraction. In the case of apparent signal contamination due to movement artifact, the position of the fine-wire electrodes was adjusted by gently pulling on the exposed wires, withdrawing them ~1 mm. The quality of the signal was subsequently reassessed and the procedure repeated until at least one SMU could be easily distinguished by visual inspection.

Fig. 1. Experimental setup for recording of intramuscular electromyography (EMG) during isometric contractions of abductor hallucis. A: the foot and shank were stabilized in a rigid, custom-built brace with a force transducer aligned to the plantar aspect of the big toe, allowing measurement of flexion-abduction force. B: a medial approach was used to insert the quadrifilar fine-wire electrodes, under ultrasound guidance, into the abductor hallucis muscle, which is located along the medial longitudinal arch of the foot.
Force was amplified 1,000 times, recorded with an open bandwidth (Delsys Bagnoli, Boston, MA), and digitized at the same rate as the EMG<sub>SM</sub> using the same collection equipment and software as for the EMG<sub>SM</sub>.

Isometric ramp-up, hold, ramp-down protocol. Each subject performed three isometric MVC F-AB contractions of the hallux. A minimum of 120 s was allowed for full recovery between each effort. The maximal force recorded during this task was used to normalize force levels during the subsequent isometric ramp-up, hold, ramp-down contractions.

Subjects were asked to conduct between three and five controlled isometric ramp-up (5 s), hold (3 s), ramp-down (5 s) F-AB contractions to 60% of MVC. This task was conducted while subjects followed visual feedback of the real-time force signal superimposed on a ramp template on a computer monitor. To record activity from a wider range of the AH motor unit pool, the position of the fine-wire electrodes was adjusted slightly after the completion of each trial by gently withdrawing the electrodes ~1 mm. Ramp contractions were then repeated, thereby analyzing the activity of a separate motor unit. This was conducted three to five times for each participant until at least five motor units had been collected. Immediately after completion of the subsequent fatigue task (described below), subjects were asked to complete the same ramp-up, hold, ramp-down contractions that were performed at 60% of the prefatigue MVC, following identical procedures.

Fatigue protocol. Subjects were asked to sustain a constant sub-maximal force, isometric F-AB contraction of the hallux. An SMU that could be clearly distinguished during the preceding ramp and hold contractions was selected as a target unit for the following fatigue trial. The target force was set at 1.5 times the recruitment threshold for the target unit. Participants were strongly encouraged to maintain the target force until failure, which was defined as when the force recording dropped by >5% of the target force trace for a period of >5 s and could not subsequently return to the target force level (Christie and Kamen 2009; Vila-Cha et al. 2010). In a number of the fatigue trials, additional motor units could be identified and discriminated from the beginning of the fatigue task. For these motor units, the target force did not correspond to 150% of their recruitment thresholds; however, given that they could be discriminated for the entire duration of the fatigue task, they were also included in the analysis.

Data analysis and statistics. Rate of force production was defined as the slope of the force time data from the onset of force production to the hold phase. Rate of force relaxation was defined as the slope from the end of the hold phase to when the force returned to baseline. The accuracy of the force-tracking task was calculated by subtracting the force signal from the target force trace. The tracking accuracy was defined as the mean root mean square (RMS) value of the residual force signal. This value was calculated for both the force production and relaxation phases of the ramp contractions.

EMG<sub>SM</sub> signals were decomposed semiautomatically, off-line, into trains of individual SMUs by using an interactive software program (EMGLAB; McGill et al. 2005) based in a MATLAB environment (The MathWorks, Natick, MA), which has been described in detail elsewhere (McGill et al. 2005; Oya et al. 2009). The signal was processed in 0.5-s segments, which were digitally high-pass filtered at 1 kHz. When decomposition of a segment was complete, the time window was advanced to the following 0.5-s segment. If SMU superimpositions could not be clearly resolved, the adjacent EMG<sub>SM</sub> channel from the quadrifilar electrodes was decomposed and used to aid in verifying the units involved.

Recruitment of SMUs was determined by moving a 0.5-s window of EMG<sub>SM</sub> signal forward in steps of 1 ms until the mean CV of ISIs within the 0.5-s window was <50%. Derecruitment was determined in the same manner, but by moving the window backward from the last segment of the SMU (Moritz et al. 2005). Forces corresponding to the calculated first and last discharge within each 0.5-s window were considered as recruitment and derecruitment thresholds, respectively. Recruitment and derecruitment thresholds, discharge rate at recruitment and derecruitment, and peak discharge rate were calculated during the ramp-up, hold, ramp-down contractions. The slope of the discharge rate as a function of the F-AB force was also calculated by dividing the amount of increase in the discharge rate by the amount of increase in the force from the recruitment threshold to peak discharge rate (Oya et al. 2009). This process was completed for both pre- and postfatigue ramp and hold isometric contractions.

During the constant-force submaximal isometric fatigue task, mean discharge rate and the CV of ISIs were calculated from 5-s epochs at times corresponding to 0, 25, 50, 75, and 100% of contraction duration. The initial time epoch was considered to commence when the force attained the target level and remained stable for 5 s. The ability of the participant to match the rate of force increase and decrease during the ramp-up and ramp-down phases of the contraction was assessed using a one-way, repeated-measures analysis of variance (ANOVA). The same test was also applied to compare any differences in accuracy of the force production and relaxation phases. A two-way repeated-measures ANOVA was performed (discharge behavior vs. fatigue) to determine within-factors effects for discharge behavior (recruitment/peak/derecruitment discharge rates and recruitment/derecruitment force thresholds) and between-factors effects (pre- vs. postfatigue). Between-factors analysis was applied for pre- and post-fatigue comparisons, because we could not be certain that the same motor units were being decomposed following the fatigue task. Linear correlations were performed on both pre- and postfatigue data for the following variables: recruitment threshold, discharge rate at recruitment, peak discharge rate, and slope of increase in discharge rate as a function of force. Correlations were classified as weak, r = 0.1–0.3; moderate, r = 0.3–0.5; and strong, r > 0.5 (Cohen 1988). Alterations in mean discharge rate and the CV of ISIs occurring during the fatigue task were evaluated separately using a one-way repeated-measures ANOVA.

Sphericity (homogeneity of covariance) was verified by using the Mauchly’s test. If the assumption of sphericity was not met, the significance of F ratios was adjusted according to the Greenhouse-Geisser procedure. Pairwise comparisons, including Bonferroni corrections, were applied as post hoc analyses. For all analysis, the level of significance was set at P ≤ 0.05. Effect size (ES) was calculated using partial eta squared, to determine the magnitude and the practical relevance of the significant findings. Effect sizes were as follows: small, ±0.1–0.3; moderate, ±0.3–0.5; and strong, ±0.5–1.0 (Cohen 1988). All data are means ± SD unless otherwise stated.

RESULTS

A total of 42 motor units were recorded from the isometric ramp contractions before and immediately after the fatigue task. Additionally, 13 motor units (recorded from 5 subjects) could be followed for the duration of the fatigue task. Typically between six and eight motor units were collected from each participant during the ramp and hold contractions before and after the fatigue task, whereas one or two motor units were tracked during each fatigue task. Two individuals returned for a second data collection session 7 days after the initial session (see Table 1).

Isometric ramp-up, hold, ramp-down contractions. All subjects were able to satisfactorily follow the ramp templates, with force increasing (contraction) at a rate of 7.6 ± 1.2% MVC·s<sup>−1</sup> and decreasing (relaxation) at a rate of 8.2 ± 1.0% MVC·s<sup>−1</sup> (P = 0.12, Fig. 2). However, the ability to accurately track the contraction and relaxation ramps was significantly different, with force relaxation being more difficult. This was shown by mean RMS force residuals over the force relaxation ramp being significantly greater than those during the force development.
whereas the motor unit recorded from intramuscular EMG 27.2% maximum voluntary contraction (MVC) at a discharge rate of 8.8 Hz, 

The motor unit recorded from intramuscular EMG their instantaneous discharge rate is shown above each respective EMG trace. 

from quadrifilar fine-wire electrode inserted into abductor hallucis (2nd and 4th trace bottom trace) and 2 channels of intramuscular EMG showing force (ramp (3.3 894 ABDUCTOR HALLUCIS MOTOR UNIT DISCHARGE PROPERTIES 

Table 1. Data for individual motor units decomposed during the fatigue task 

<table>
<thead>
<tr>
<th>Subject</th>
<th>Session</th>
<th>Motor Unit</th>
<th>Fatigue Target Force, %MVC</th>
<th>Fatigue Task Duration, s</th>
<th>Prefatigue Recruitment Threshold, %MVC</th>
<th>Prefatigue Recruitment Discharge Rate, Hz</th>
<th>Prefatigue Recruit Discharge Rate, Hz</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
<td>36.5</td>
<td>432.0</td>
<td>24.7</td>
<td>6.9</td>
<td>13.3</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>2</td>
<td>36.5</td>
<td>432.0</td>
<td>37.7</td>
<td>8.7</td>
<td>15.6</td>
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<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>70.9</td>
<td>97.0</td>
<td>44.3</td>
<td>5.1</td>
<td>11.4</td>
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<tr>
<td>2</td>
<td>1</td>
<td>4</td>
<td>53.1</td>
<td>152.0</td>
<td>35.6</td>
<td>5.5</td>
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<tr>
<td>2</td>
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<td>5</td>
<td>53.1</td>
<td>152.0</td>
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<tr>
<td>3</td>
<td>1</td>
<td>6</td>
<td>37.7</td>
<td>212.0</td>
<td>25.5</td>
<td>8.6</td>
<td>12.3</td>
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<tr>
<td>3</td>
<td>1</td>
<td>7</td>
<td>37.7</td>
<td>212.0</td>
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<tr>
<td>3</td>
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<td>8</td>
<td>27.7</td>
<td>178.0</td>
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<td>5.8</td>
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<tr>
<td>3</td>
<td>2</td>
<td>9</td>
<td>27.7</td>
<td>178.0</td>
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<tr>
<td>4</td>
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<td>10</td>
<td>31.5</td>
<td>215.0</td>
<td>18.6</td>
<td>3.4</td>
<td>16.0</td>
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<tr>
<td>4</td>
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<td>11</td>
<td>31.5</td>
<td>215.0</td>
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<tr>
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<td>12</td>
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<td>345.0</td>
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<td>13</td>
<td>32.1</td>
<td>345.0</td>
<td>19.4</td>
<td>5.8</td>
<td>16.1</td>
</tr>
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</table>

Values are data for individual motor units decomposed during the fatigue task, including the subject and session from which each motor unit was recorded, as well as the duration and intensity of the task. Motor units correspond to those presented in Fig. 4. MVC, maximum voluntary contraction.

Mean motor unit discharge rates at recruitment (6.6 ± 1.8 Hz) and derecruitment (6.4 ± 1.1 Hz) were not significantly different from each other and ranged from 3.4 to 10.5 Hz at recruitment and from 4.0 to 8.6 Hz at derecruitment (P = 0.4). Motor unit discharge rate increased with increasing force and mean peak discharge rate (14.0 ± 2.3 Hz) was significantly higher than both recruitment and derecruitment discharge rates (P ≤ 0.05, ES = 0.86). Peak discharge rates ranged from 10.7 to 21.3 Hz for the ramp and hold contractions. A moderate positive correlation was evident between recruitment threshold and recruitment discharge rate, with higher threshold motor units discharging at a higher initial rates (r = 0.47, P ≤ 0.05, Fig. 3A). There was no correlation between recruitment threshold and peak discharge rate (r = 0.03, P = 0.89, Fig. 3B). However, a moderate positive correlation was evident between recruitment discharge rate and the slope of increase in discharge rate as a function of the force (r = 0.35, P ≤ 0.05), indicating that higher threshold motor units attained peak discharge frequency at a faster rate.

Fatigue task. The submaximal fatigue task was performed at a mean force level of 41.3 ± 15.3% MVC (range 27.7–70.9% MVC, Table 1), which resulted in a mean task duration of 233 ± 116.2 s (range 97–432 s). An increase in neural drive was indicated by the recruitment of new motor units in all of the fatigue trials, with eight additional motor units being detected by our electrodes. Recruitment of new motor units was not limited to the end of the fatigue task, with additional recruitment observed from 20% of task duration. However, most additional motor units discharged in periodic bursts; thus only motor units that could be identified and followed for the entire duration of the task were analyzed. Mean discharge rates and CVs of the ISIs are shown in Fig. 4. Mean motor unit discharge rate significantly decreased over the final 25% of task duration (P ≤ 0.05, ES = 0.72). Variability of the firing rate, as measured by CV of the ISI, was stable over the first 50% of the fatigue task and increased significantly during the final 25% of the fatigue task (P ≤ 0.05, ES = 0.71).

Isometric ramp-up, hold, ramp-down contractions following the fatigue task. Maximal voluntary force producing capacity declined to 73.6 ± 4.2% of prefatigue MVC value (P ≤ 0.05, ES = 0.91). Mean recruitment (25.2 ± 14.6% MVC) and derecruitment (25.7 ± 13.3% MVC) thresholds during the
ramp and hold contractions performed immediately after the fatigue trial were not significantly different from each other (range 8.3–51.3 and 6.8–52.0% MVC, respectively, \( P = 0.25 \)). These threshold values were not significantly different from the same measures made over the same type of contraction protocol before the fatigue task was performed (\( P = 0.25 \)).

Mean discharge rates at recruitment and derecruitment (5.8 ± 1.5 and 6.3 ± 1.7 Hz, respectively) for ramp and hold contractions after the fatigue task were not significantly different from each other (range 3.2–10.1 and 4.1–10.7 Hz, respectively, \( P = 0.4 \)). There was also no difference between these values and the prefatigue task recruitment and derecruitment discharge rates (\( P = 0.4 \)). Mean peak discharge rate (13.3 ± 2.3 Hz) remained unchanged after the fatigue trial (post fatigue range 7.8–18.5 Hz, \( P = 0.12 \)) and was significantly higher than recruitment and derecruitment discharge rates (both \( P \leq 0.05 \)). A moderate positive linear correlation was still evident between recruitment threshold and peak discharge rate over the last 25% of the fatigue task (\( r = 0.63, P \leq 0.05 \)).

During this task (i.e., recruitment threshold and recruitment discharge rate (both \( r = 0.47, P \leq 0.05 \)) and after the fatigue task (open symbols, \( r = -0.43, P \leq 0.05 \)). After the fatigue task, a negative correlation was evident between recruitment threshold and peak discharge rate (open symbols, \( r = -0.43, P \leq 0.05 \)).

**DISCUSSION**

We describe the recruitment and discharge characteristics of motor units in AH, a muscle with a postural function (Kelly et al. 2012) that also possesses a low number of motor units (Johns and Fuglevand 2011). Similarly to other postural muscles (Dalton et al. 2009; Maciefeld et al. 2000; Oya et al. 2009), motor units in AH displayed low peak discharge rates and were resistant to fatigue. The anatomic configuration of a low number of motor units, relative to PCSA (Johns and Fuglevand 2011), that are also fatigue resistant, may allow this muscle to generate and sustain moderate to large amounts of force for prolonged periods of time, to provide postural support for the foot.

Recruitment threshold and discharge characteristics. In the current study we did not observe any difference between recruitment and derecruitment thresholds or between discharge rates at recruitment and derecruitment for AH motor units. Although similar findings have been reported previously (Jesunathadas et al. 2010; Oya et al. 2009) during isometric ramp up-down contractions, derecruitment generally occurs at higher force levels and at lower discharge rates (Adam 2005; Moritz et al. 2005; Oya et al. 2009; Riley et al. 2008b). It is suggested that this is due to the amplifying effects of persistent inward currents (PIC) (Gorassini et al. 2002; Heckman et al. 2008) as well as late adaptation of the motoneuron (Kernell and Monster 1984, 2004). Our finding may indicate that, similar to another lower limb postural muscle, the soleus (Oya et al. 2009), the

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**Fig. 3.** A: moderate positive linear correlation between recruitment threshold and discharge rate at recruitment for ramp and hold contractions before (filled symbols, \( n = 42 \) units, \( r = 0.45, P \leq 0.05 \)) and after the fatigue task (open symbols, \( n = 42, r = 0.47, P \leq 0.05 \)). B: no significant correlation was observed between recruitment threshold and peak discharge rate before the fatigue task (filled symbols, \( r = 0.03, P = 0.89 \)). After the fatigue task, a negative correlation was evident between recruitment threshold and peak discharge rate (open symbols, \( r = -0.43, P \leq 0.05 \)).

**Fig. 4.** Mean (solid line) and the corresponding 13 individual motor unit responses (broken lines) for discharge rate (A) and coefficient of variation (CV) of the interspike interval (ISI) (B), calculated during a submaximal contraction to task failure. *\( P \leq 0.05 \), significant decrease in mean discharge rate over the last 25% of the fatigue task. **\( P \leq 0.05 \), significant increase in CV ISI over the last 25% of the fatigue task.
effects of PICs and late adaptation are minimal within AH. However, an alternative explanation for the lack of difference between recruitment and derecruitment thresholds, or between discharge rates at recruitment and derecruitment, relates to the accuracy of force development and relaxation in the ramp-up and ramp-down phases of the isometric contractions. In our study, despite extensive task familiarization, the accuracy of force tracking during force production was significantly greater than that during force relaxation. Thus it is possible that a less accurate relaxation of force may have influenced both the threshold and discharge rate at derecruitment.

Discharge rate at recruitment was positively associated with recruitment threshold over the range of force tested. This result is in contrast to the “onion skin” hypothesis, which describes lower-threshold motor units discharging at higher initial and peak discharge rates in muscles such as vastus lateralis and tibialis anterior (Adam and Deluca 2005; De Luca and Hostage 2010; Erim et al. 1996). However, the positive correlation between recruitment threshold and recruitment discharge rate has previously been demonstrated in other muscles such as soleus (Oya et al. 2009), muscles of the hand (Monster and Chan 1977; Moritz et al. 2005), biceps brachii (Kukulka and Clamann 1981; Riley et al. 2008b), and adductor pollicis (Kukulka and Clamann 1981). The finding that lower-threshold motor units discharge at lower initial rates fits with the theoretical organizational properties of a motoneuron pool, because these motor units possess longer contraction and half-relaxation times (Bakels and Kernell 1993; Kernell et al. 1999) and would therefore summate and fuse at lower firing rates compared with higher-threshold units with shorter contraction and half-relaxation times (Grimby et al. 1979). It has been hypothesized previously that this level of organization helps to achieve efficient gradation of force across a wide variety of contraction strengths (Moritz et al. 2005; Oya et al. 2009).

Peak discharge rate. The peak discharge rates reported in our study are at the lower end of the range of peak discharge rates (between 10 and 25 Hz) described in other lower limb muscles (Connelly et al. 1999; Dalton et al. 2009; Roos et al. 1999) during isometric contractions at similar contraction intensities. Our observed low peak discharge rates may be related to the postural function of this muscle (Kelly et al. 2012), because some postural muscles are known to discharge at relatively low rates (Dalton et al. 2009; Oya et al. 2009) for sustained periods to resist gravitational forces and maintain upright posture (Sherrington 1915).

Previous studies have reported both positive (Gydikov and Kosarov 1974; Moritz et al. 2005; Oya et al. 2009) and negative (De Luca and Hostage 2010; Stock et al. 2012) linear relationships between recruitment threshold and peak discharge rate. However, in AH we found no relationship between peak discharge rate and recruitment threshold, with all motor units converging to similar peak discharge rates regardless of recruitment threshold. When considering this finding, it must be recognized that we have only recorded data from contractions up to 60% of MVC. Thus it is possible that our latter recruited motor units may have eventually attained higher discharge rates if the contraction force was increased to levels beyond 60% MVC. Our finding that higher threshold motor units obtained peak discharge rate more rapidly supports this suggestion. Regardless, the relatively small increase in discharge rate after recruitment for all motor units suggests that rate coding as a method of force gradation may be somewhat limited in AH. Thus recruitment may be the dominant factor in force generation (Bellemare et al. 1983; De Luca et al. 1982), despite the fact that AH has relatively few motor units (Johns and Fuglevand 2011). This suggestion is further supported by the continued recruitment of motor units during the fatigue task, despite a minimal change in discharge rate. Because of its postural function, AH is required to generate and sustain relatively large forces to support body weight. The organization of a low number of large motor units relative to its PCSA may allow for generation of substantial forces while maintaining fatigue resistance (Gordon et al. 1990; Sirca et al. 1990).

Motor unit discharge properties during the fatigue task. During the fatigue task an increase in central drive to the motoneuron pool was evidenced by recruitment of eight additional motor units. Despite this increase in central drive, only two of these motor units displayed an increase in discharge rate during the fatigue task. During the final 25% of the task we observed a decrease in motor unit discharge rate in 11 of the 13 motor units. This anomalous decrease in SMU discharge rate observed concurrently with an increase in central drive has been observed previously in upper (Carpentier et al. 2001; Mottram 2004; Riley et al. 2008a) and lower limb muscles (Christie and Kamen 2009; Dalton et al. 2010; Kuchinad et al. 2004) and is possibly due to reduced spinal motoneuron responsiveness, which impairs the ability to integrate increased cortical input (McNeil et al. 2011a, 2011b). Reduced spinal motoneuron responsiveness may occur as a result of intrinsic motoneuron adaptation (due to repetitive discharge) (Kernell and Monster 1982; McNeil et al. 2011b) and reflex inhibition by group III and IV afferents (Rotto and Kaufman 1988). We must also recognize that motor units recruited during the later stages of the fatigue may have actually increased their discharge rates, to compensate for the decrease in discharge rate of the existing motor units. Regardless, it is worth noting that AH motor units were able to maintain moderate to high levels of force (40% MVC for 233 s) for periods and intensities similar to those of the fatigue-resistant soleus (40–60% MVC for 292 s) (Kuchinad et al. 2004) and considerably longer than those of the biceps brachii (17% MVC for 117 s) (Riley et al. 2008a).

Despite increasing central drive, discharge rate variability also remained relatively unchanged until late in the fatigue contraction, when it was observed to increase significantly in the final 25% of the task. Discharge variability arises as a result of fluctuations in synaptic noise due to an increase in both excitatory and inhibitory input (Berg et al., 2008), causing variability in the motoneuron membrane potential (Calvin and Stevens, 1968). Our findings that both discharge rate and discharge rate variability of AH motor units remains relatively stable until just prior to task failure, indicates that AH is able to sustain a relatively constant and moderate output for prolonged periods. It appears that it is only in the late phase of a sustained contraction that significant alterations in synaptic input and intrinsic motoneuron properties occur, disturbing the balance of repetitive discharges.

Maximal voluntary force production was reduced by 27% following the fatigue tasks. However, recruitment thresholds of the recorded units during ramp and hold contractions following the fatigue task were not significantly different from those prefatigue. Our finding of no change in recruitment thresholds
following the fatigue task suggests that additional motor units, other than those detected by our fine-wire electrodes, may have been recruited to generate 60% of prefatigue MVC (equivalent to 83% postfatigue MVC). However, this suggestion cannot be quantified in the current study, because we have not collected surface EMG data. Regardless, the 27% decline in MVC following a sustained moderate- to high-intensity fatigue task is similar to that of the fatigue-resistant soleus (Kuchinad et al. 2004), highlighting the fatigue resistance properties of this muscle.

After the fatigue trial we observed a moderate negative correlation between recruitment threshold and peak discharge rate. This relationship was not evident before the fatigue task, when all motor units attained similar peak discharge rates, thus indicating a fatigue-related alteration in the discharge behavior of higher-threshold motor units. The divergence in discharge behavior between lower- and higher-threshold motor units may be explained by the fact that higher-threshold motor units generally innervate faster-twitch muscle fibers, which are less fatigue resistant (Bakels and Kernell 1993).

**Conclusion.** We have described the discharge characteristics of motor units from AH, a postural muscle in the foot that is known to have relatively few motor units. This muscle is comparatively fatigue resistant and appears to rely predominantly on recruitment to generate force, optimizing the use of slow-twitch, fatigue-resistant fibers to generate moderate to large amounts of force for sustained periods of time.

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**DISCLOSURES**

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

**AUTHOR CONTRIBUTIONS**


**REFERENCES**


Motor-unit activity differs with load type during a fatiguing contraction. 


