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# Corticospinal responses during passive shortening and lengthening of tibialis anterior and soleus in older compared to younger adults

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### What is the central question of this study?

Muscle spindle afferent feedback is dependent on changes in muscle length, which can, in turn, modulate corticospinal excitability. Aging is accompanied by several alterations in the nervous system influencing the transmission and integration of sensory information. Thus, this study aimed to assess whether there are age-related differences in corticospinal responses whilst passively changing muscle length.

### What is the main finding and its importance?

In contrast to young, older adults exhibited no modulation of corticospinal excitability in tibialis anterior during passive ankle movement. These data show impaired sensorimotor response in older adults during length changes of tibialis anterior, thus contributing to our understanding of age-related changes in sensorimotor control.

## ABSTRACT

Corticospinal responses have been shown to increase and decrease with passive muscle shortening and lengthening, respectively, as a result of changes in muscle spindle afferent feedback. The aging sensory system is accompanied by a number of alterations that might influence the processing and integration of sensory information. Consequently, corticospinal excitability might be differently modulated whilst changing muscle length. In 10 older adults (66±4 years), corticospinal responses (MEP/$M_{max}$) were evoked during a static position, passive shortening, and lengthening of soleus (SOL) and tibialis anterior (TA), and these data were compared to the re-analysed data pool of 18 younger adults (25±4 years; Škarabot et al. 2019, Exp Brain Res 237:2239-2254). Resting motor threshold was greater in SOL compared to TA ($p<0.001$), but did not differ between young and older ($p=0.405$). No differences were observed in MEP/$M_{max}$ between the static position, passive shortening or lengthening in SOL (young: all 0.02±0.01; older: 0.05±0.04, 0.03±0.02 and 0.04±0.01, respectively; $p=0.298$), and responses were not dependent on age ($p=0.090$). Conversely, corticospinal responses in TA were differently modulated between the age groups ($p=0.002$), with greater MEP/$M_{max}$ during passive shortening (0.22±0.12) compared to passive lengthening (0.13±0.10) and static position (0.10±0.05) in young ($p<0.001$), but unchanged in older adults (0.19±0.11, 0.22±0.11 and 0.18±0.07, respectively; $p\geq 0.867$). The present experiment shows that length-dependent changes in corticospinal excitability in TA of the young are not evident in older adults. This suggests impaired sensorimotor response during muscle length changes in older age that might only be present in ankle flexors, but not extensors.

## INTRODUCTION

The firing of muscle spindle afferents increases proportionally to the magnitude of the muscle stretch, but remains low during muscle shortening (Matthews, 2011). This behaviour influences corticospinal responses; in both upper and lower limb musculature, it has been shown that passive shortening and lengthening are accompanied by increased and decreased corticospinal excitability, respectively (Lewis, Byblow, & Carson, 2001; Lewis & Byblow, 2002; Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a). However, the magnitude of change in corticospinal excitability with passive movement might still depend on the muscle investigated (Chye, Nosaka, Murray, Edwards, & Thickbroom, 2010; Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a), with no modulation having been shown for soleus (SOL) in contrast to tibialis anterior (TA; Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a). Our recent work showed that passive ankle movement does not influence intracortical inhibitory or facilitatory neurons, or subcortical excitability, thus suggesting that modulation of corticospinal excitability with passive muscle length changes is mediated by the cortical neurons (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a). Based on primate data, information regarding changes in muscle length is integrated directly into the primary motor cortex via group II afferents, or indirectly into the sensorimotor cortex via Ia afferents mediated by inhibitory interneurons (Hore, Preston, & Cheney, 1976).

Healthy aging is characterised by alterations in both the motor pathway of the central nervous system (CNS) and proprioception, which can have significant implications for postural control (Henry & Baudry, 2019). Some evidence suggests that aging affects sensory compared to motor axons to a greater extent, as evidenced by prolonged latency of the H-reflex (Scaglioni, Narici, Maffiuletti, Pensini, & Martin, 2003). This change is possibly mediated by the age-related changes in conduction velocity (Boxer, Morales, & Chase, 1988;

Kim, Suzuki, & Kanda, 2007) and smaller axon diameters (Kim et al., 2007). In addition to that, cadaver studies have shown morphological changes in muscle spindles, with older adults exhibiting increased capsular thickness (Swash & Fox, 1972), a decrease in the number of intrafusal fibres (Swash & Fox, 1972) and diameter of muscle spindles (Kararizou, Manta, Kalfakis, & Vassilopoulos, 2005). Sensitivity of muscle spindles is also decreased with age in animals, with evidence pointing to a selective decrease in dynamic, rather than static sensitivity (Kim et al., 2007), however human data is lacking. Lastly, integration of the sensory signal in the CNS is also altered with age, both at the spinal level, as evidenced by reductions in complexity of interneuronal network (Terao et al., 1996), as well as at the level of the cerebral cortex (Brown, Neva, Feldman, Staines, & Boyd, 2018; Degardin et al., 2011). Given the number of aforementioned changes in the CNS with age, it is plausible that the modulation of corticospinal responses by variations in muscle spindle sensory input is attenuated, but this remains to be investigated.

Accordingly, the aim of the present experiment was to investigate corticospinal excitability in TA and SOL during passive ankle movement in older individuals. These muscles were chosen due to their integral role in locomotion (TA; Byrne, O'Keeffe, Donnelly, & Lyons, 2007) and postural stability (SOL; Capaday, Lavoie, Barbeau, Schneider, & Bonnard, 1999). The experimental setup was replicated from recent work in our laboratory investigating a similar research question in younger adults (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a). To allow for a direct comparison between young and older adults and importantly characterise any age-related alterations in function, previously published data from young individuals were pooled, and re-analysed (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a).

## METHODS

### Ethical approval

The procedures of this study were approved by Northumbria University Faculty of Health & Life Sciences Ethics Committee (BMS57UNNJSRD2016) in accordance with Declaration of Helsinki with the exception of registration in a database.

### Participants

Ten older adults (66 ± 4 years, range 61-73 years, 177 ± 14 cm, 75.5 ± 12.7 kg; 2 females) participated in the study and their data was compared to that of 18 younger adults from Škarabot *et al.* (2019*a*; 25 ± 4 years, range 20-32 years, 176 ± 8 cm, 81.2 ± 16.8 kg; 8 females). The groups did not differ in stature ($p = 0.820$) and body mass ($p = 0.357$). Participants were considered older if they were over 60 years of age (Hunter, Pereira, & Keenan, 2016). All participants were free from neurological conditions or musculoskeletal injury, were not taking any medications known to affect the nervous system and had no reported contraindications to transcranial magnetic stimulations (TMS). Premenopausal females were tested in the early follicular phase of the menstrual cycle where both oestrogen and progesterone concentrations are likely to be low, or whilst taking oral contraceptives, in order to minimise the potential influence of female sex hormones on TMS-evoked responses (Ansdell et al., 2019). Written informed consent was obtained from participants prior to the start of the study.

### Experimental design

Prior to the experiment, older participants attended a familiarisation session for habituation with stimulation procedures. In the experimental visit, single-pulse TMS was delivered over the primary motor cortex to evoke motor evoked potentials (MEPs) during a static position, passive shortening and passive lengthening of SOL and TA. The order of conditions was randomised. The data obtained in older adults was then compared to responses in younger individuals. To that end, data from a previous study (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a) were pooled from each participant's initial visit involving responses to single-pulse TMS during the same protocol of passive ankle movement.

## Procedures

### *Experimental setup*

Participants sat on an isokinetic dynamometer (Biodex System 4 Pro, New York, USA) with hip and knee at 60 and 90° flexion, respectively. The foot of the dominant leg, as determined by the lateral preference inventory (Coren, 1993), was placed onto a metal foot plate attached to the lever arm of the motor of the device, and strapped with Velcro. The dynamometer was programmed to move the foot plate throughout a 20° range-of-motion, between 10° plantar- and 10° dorsiflexion (anatomical zero being defined as the ankle joint at 90°), at $5°\cdot s^{-1}$. The movement velocity employed in the present experiment was chosen to ensure greater ability of relaxation and to avoid reflexive muscle activity related to passive movement (Pinniger, Nordlund, Steele, & Cresswell, 2001) and has been shown to result in linear changes in fascicle length of SOL and TA (~0.65 mm per degree of joint angle change; Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a), a surrogate of muscle spindle afferent feedback (Day, Bent, Birznieks, Macefield, & Cresswell, 2017). Electrical stimulation or TMS was delivered at anatomical zero (considered intermediate muscle length) during static position and passive ankle movement (shortening and lengthening of TA and SOL) with the order of conditions randomised. Stimulations were only delivered at anatomical zero since previous research has shown no muscle length-dependency of the responses during passive ankle movement throughout the 20° range-of-motion (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a). To minimise the differences in thixotropy between conditions and groups, participants rested in the starting position for at least 10 s before passive motion began (Proske, Morgan, & Gregory, 1993), with at least 15 s of rest given before each motion.

### *Electromyography*

Bipolar surface electrodes (8 mm diameter, 20 mm inter-electrode distance; Kendall 1041PTS, Tyco Healthcare Group, USA) were used to record electromyographic (EMG) activity of SOL and TA. The electrodes were placed over the belly of SOL and TA according to SENIAM recommendations (Hermens, Freriks, Disselhorst-Klug, & Rau, 2000), with the ground electrode placed over the medial malleolus. Prior to placement of electrodes, the recording site was shaved, abraded with preparation gel and wiped clean with an alcohol swab to ensure appropriate impedance (< 2 kΩ). To ensure participants were relaxed during passive ankle movement, EMG activity was visually inspected during the experiment. If EMG activity was observed, the trial was discarded and repeated. The EMG signal was amplified (×1000), band pass filtered (20-2000 Hz; Neurolog System, Digitimer Ltd, UK), digitised (5 kHz; CED 1401, CED, UK), acquired and analysed off line (Spike2, v8, CED, UK).

### *Percutaneous nerve stimulation*

To account for changes at the skin-electrode interface, maximal compound action potentials ($M_{max}$) were elicited in SOL and TA via percutaneous nerve stimulation (1 ms pulse duration; Digitimer DS7AH, Hertfordshire, UK). Responses in SOL were evoked with the cathode (2.5 cm$^2$; Nidd Valley Medical Ltd., Bordon, UK) placed over the tibial nerve in the popliteal fossa and the anode (5×9 cm) positioned over the patella. To elicit responses in TA, a 40 mm cathode/anode arrangement (Digitimer, Hertfordshire, UK) was placed over the common peroneal nerve below the head of the fibula. $M_{max}$ was elicited separately for SOL and TA by gradually increasing the intensity of percutaneous stimulation until the EMG response plateaued, upon which the intensity was further increased by 30%. Since $M_{max}$ is sensitive to changes in static positions (Gerilovsky, Tsvetinov, & Trenkova, 1989), but not shortening and lengthening when stimuli are delivered at the same joint angle (Pinniger et al., 2001), $M_{max}$ was elicited only at anatomical zero where MEPs were subsequently evoked. Three responses were elicited in each muscle and their average used as a representative $M_{max}$ value.

### *Transcranial magnetic stimulation*

Single-pulse TMS was delivered using a Magstim 200$^2$ magnetic stimulation (Magstim Co., Ltd., Whitland, UK). A concave double-coin coil was positioned over the leg area of the primary motor cortex contralateral to the target dominant leg and was oriented to induce posterior-to-anterior cortical current. The centre of the coil was placed 1 cm lateral and posterior to the vertex as per the reported optimal spot for activation of lower leg muscles (Devanne, Lavoie, & Capaday, 1997). After that, the coil was moved medio-laterally and posterior-anteriorly in small steps around the initial position until the spot consistently evoking the greatest MEP in the target muscle, i.e. SOL or TA, was identified (hotspot). Upon identification of the hotspot, the back of the coil was marked directly on the scalp to ensure consistent placement throughout the trial. Resting motor threshold (rMT) was established with the ankle positioned at anatomical zero and determined as the intensity that elicited a MEP amplitude $\geq$50 μV in 3 out of 5 trials (Rossini et al., 1994). The hotspot and rMT were determined separately for SOL and TA. During the experimental trials, intensity of TMS was standardised to 1.2 × rMT in the static position, as this intensity corresponds with the ascending limb of the stimulus-response curve (Han, Kim, & Lim, 2001), making the responses susceptible to changes with passive ankle movement. A total of ten MEPs were elicited in each condition. This number of trials has previously been shown to result in excellent intra-session reliability in healthy populations (Lewis, Signal, & Taylor, 2014). The variability of responses (CV%) was comparable to published data in lower leg musculature at rest (e.g. Lewis et al., 2014; Škarabot, Ansdell, Brownstein, Thomas, et al., 2019), for both older (SOL: 26 ± 10, 27 ± 10 and 32 ± 16%; TA: 36 ± 18, 42 ± 21 and 31 ± 19% during static position, passive shortening and lengthening, respectively) and younger individuals (SOL: 32 ± 12, 37 ± 14 and 30 ± 10%; TA: 39 ± 15, 35 ± 17 and 41 ± 15% during static position, passive shortening and lengthening, respectively).

## Data analysis

Pre-stimulus EMG activity was quantified as root-mean-square in the 100 ms epoch prior to stimulus artefact. If $RMS_{EMG}$ was >2 standard deviations (SD) compared to mean baseline values, the evoked response following it was discarded. This was the case for 10 out of 1680 trials across individuals (0.6% of total number of trials). Peak-to-peak amplitudes of MEPs and $M_{max}$ were calculated. The average peak-to-peak amplitude of ten MEPs in each condition was expressed relative to representative $M_{max}$ value (MEP/$M_{max}$).

## Statistical analysis

Normality of data was assessed using Shapiro-Wilks test. In the case of non-normal distribution, transformations were performed using common logarithm. A paired-sample T-test was used to assess differences in stimulus intensity at rMT between SOL and TA. Sphericity was assessed using Mauchly's test of sphericity. In the case of violation, a Greenhouse-Geisser correction was employed. A 2-way repeated measures ANOVA was used to assess differences in stimulus intensity at rMT between SOL and TA in young and older adults. Differences in normalised evoked responses between resting position and passive shortening and lengthening, between young and older adults were assess with a 2 × 3 repeated measures ANOVA. To ensure robustness of the results, simple random sampling (without replacement) was additionally performed to generate 10 different samples of 10 young individuals for comparison with 10 older adults, thus making the sample size equitable. The first ten random samples that were generated were used for further analyses, which involved running 10 separate 2 × 3 repeated measures ANOVAs. Significance was set at an alpha level of 0.05. All analyses were performed using SPSS (v20, SPSS Inc., Chicago, IL, USA). All data are presented as means ± SD. Partial eta squared ($\eta_p^2$) was calculated to estimate effect sizes associated with ANOVA.

## RESULTS

The stimulus intensity at rMT was higher in SOL (54 ± 10% of stimulus output) compared to TA (49 ± 9% of stimulus output; $F_{1,28} = 16.9$, $p < 0.001$), with no differences between young and older adults ($F_{1,28} = 0.7$, $p = 0.405$). $RMS_{EMG}$ did not differ among static position, passive shortening and lengthening in SOL ($F_{1.0, 28.1} = 0.7$, $p = 0.396$, $\eta_p^2 = 0.09$) and TA ($F_{2, 56} = 2.6$, $p = 0.088$, $\eta_p^2 = 0.10$), with no differences between young and older ($p = 0.558$; Table 1). Example responses are shown in Figure 1. The MEPs were modulated during passive ankle movement in TA in young individuals (Figure 1B), whereas the remaining traces do not show differences between conditions. Passive movement of the ankle did not influence corticospinal responses in SOL ($F_{1.2, 33.1} = 1.7$, $p = 0.298$, $\eta_p^2 = 0.05$), and this was not different between the age groups (*movement* × *age group interaction*: $F_{1.2, 33.1} = 2.9$, $p = 0.090$, $\eta_p^2 = 0.09$). Older individuals displayed larger responses in resting SOL compared to the young ($F_{1, 28} = 21.8$, $p < 0.001$, $\eta_p^2 = 0.45$). Corticospinal responses with passive movement in TA differed between the groups (*movement* × *age group interaction*: $F_{2, 56} = 6.9$, $p = 0.002$, $\eta_p^2 = 0.18$), such that MEP/$M_{max}$ was greater during passive shortening compared to passive lengthening ($p < 0.001$) and static position ($p < 0.001$) in the young (Figure 1F), whereas responses were unchanged in older adults ($p \geq 0.867$). The results were similar when 10 random samples of 10 young individuals were compared to 10 older adults (SOL interaction: $F_{2,36} = 1.0 – 1.7$, $p = 0.203 – 0.328$; TA interaction: $F_{2,36} = 3.5 – 7.5$, $p = 0.002 – 0.040$).

## DISCUSSION

The aim of the present study was to assess age-related differences in corticospinal excitability during passive ankle movement between young and older adults. The results showed no changes in corticospinal excitability during passive shortening and lengthening of both SOL and TA in older adults, whereas young individuals exhibited modulation in TA. As such, the present data suggest that aging is accompanied by alterations in processing and/or transmission of sensory information related to muscle length changes, or cortical and spinal integration of such information.

In younger individuals, passive ankle movement modulated corticospinal excitability in TA (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a), in agreement with previous reports in passive movement of upper limb joints (Lewis et al., 2001; Lewis & Byblow, 2002). We previously showed that corticospinal modulation during passive movement in TA in young individuals is not accompanied by changes in intracortical inhibition or facilitation, subcortical and spinal excitability, concluding it was mediated at the cortical level of the corticospinal tract (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a). Based on primate data, it was suggested that corticospinal modulation in response to changes in muscle length is mediated through inhibitory connections to area 4 of the cerebral cortex either directly by group II afferents or indirectly, via area 3a, by the group Ia afferents (Hore et al., 1976). Differences in corticospinal modulation between young and older adults during passive movement thus implies that the information transmission from group Ia and/or group II afferents, or cortical integration of that information, is impaired in older age.

Previous work indicated that cortical integration of cutaneous stimuli is impaired in older adults (Brown et al., 2018). However, when muscle spindles are activated through vibration, the corticospinal responses have been shown to be similar between young and older individuals (Brown et al., 2018). The vibration stimulus is thought to preferentially activate Ia afferents (Bove, Nardone, & Schieppati, 2003), and as such vibration-based feedback is more likely to be integrated into area 3a of the cerebral cortex (Hore et al., 1976). Somewhat dichotomously, previous work in humans suggested greater loss of Ia afferents in older adults, based on observation of prolonged H-reflex latencies (Scaglioni et al., 2003). However, more recent work showed no alterations in peripheral sensory conduction times with older age (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019b). Since peripheral sensory conduction time is based on a combination of H-reflex latency and F-wave-derived peripheral motor conduction time, it will be primarily dependent on transmission efficacy of Ia afferents, thus suggesting no age-related alterations in this afferent type. Conversely, aging mice exhibit a decrease in group II afferents, increased number of Ia afferents that fail to maintain their annulospiral structures, but a lower degeneration rate of group Ia compared to group II afferents (Vaughan, Stanley, & Valdez, 2017). The greater age-related degeneration rate of group II compared to Ia observed in mice, combined with human data not supporting alterations in Ia afferent transmission (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019b) or cortical integration (Brown et al., 2018), suggest that the results of the present experiment might represent an age-related alteration of group II afferent feedback. This could occur through the loss of transmission efficacy of these fibres due to an age-related decrease in number (Vaughan et al., 2017), or the integration of information conveyed by this group of afferents into the area 4 of the cerebral cortex (Hore et al., 1976). However, direct measures are required to confirm this hypothesis. To gain insight into the responsiveness of muscle spindle afferents in older age, future studies could consider using microneurography to directly record the activity of different afferent fibres. Given muscle spindle receptors are considered the primary source of proprioceptive information (Henry & Baudry, 2019), and their involvement in triggering rapid postural responses to unexpected perturbations (Stapley, Ting, Hulliger, & Macpherson, 2002), the impairment in processing and integration of information from muscle spindles could be considered a contributing factor in altered postural control in older age.

The age-related differences were limited to the TA muscle, whilst no differences were noted in SOL. It is difficult to discern the reason for such a difference, but these two muscles have been shown to differ in various aspects, e.g. quantity of muscle spindles (Banks, 2006), reciprocal spindle afferent input (Yavuz, Negro, Diedrichs, & Farina, 2018), motor unit properties (Burke, 1967; Dum & Kennedy, 1980), and distribution of direct corticomotoneuronal projections (Brouwer & Ashby, 1992), among others, which could have changed differently between muscle with age and thus influenced the responses observed in the present experiment. It should be noted however, that previous data in young individuals showed no modulation in SOL corticospinal responses during passive movement (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a). This observation, combined with greater between-subject variability of responses in the older group, a known characteristic of an aging population (Hunter et al., 2016), makes it less likely that the difference between young and older adults, if there is one, could be detected in this muscle.

### *Limitations*

In the present experiment, only responses to single-pulse TMS were assessed to gain insight into age-related alterations in sensorimotor processing with muscle length changes. As modulation of motor responses during passive movement in young individuals is likely mediated by the cortical areas (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a), it was assumed that sensorimotor integration is altered in aging cortical areas. However, other levels of the neural axis were not assessed. It is unclear whether lack of modulation in intracortical activity and spinal excitability observed during passive ankle movement in young (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019a) would translate to older populations. However, sensorimotor integration has been previously shown not to be altered in older age when intracortical inhibition and facilitation were assessed in response to vibration (Brown et al., 2018). Given that the complexity of interneuronal networks has been shown to be reduced in an aging CNS (Terao et al., 1996), it is possible that sensorimotor integration is also altered at the spinal level. Indeed, it has been suggested that presynaptic inhibition is differently affected in older compared to young adults in response to vibration (Butchart, Farquhar, Part, & Roberts, 1993), and differences in presynaptic activity of older adults have previously been suggested during active muscle length changes (Škarabot, Ansdell, Brownstein, Hicks, et al., 2019b). However, the aforementioned findings are mainly based on the changes in H-reflex amplitude, whereas the data using the conditioning H-reflex technique to more directly assess presynaptic inhibition showed no difference between young and older adults (Baudry, Maerz, & Enoka, 2010).

The movement velocity of 5°.s$^{-1}$ was chosen to promote relaxation and prevent reflexive muscle activity. However, muscle spindles are not only sensitive to the extent of muscle stretch, but also on the rate of stretch (Matthews, 2011). As such, the data should be interpreted within the constraints of the velocity employed. Further work could elucidate whether the present findings can be extended to faster movement velocities.

### *Conclusion*

The present data in older adults when compared to the young suggest that aging is accompanied by altered sensorimotor response during passive changes in the tibialis anterior, but not soleus muscle length. Given differential age-related alterations in group Ia and II afferents reported previously, it is conceivable that aging adults exhibit impairment in transmission or integration of information originating from group II afferents into the primary motor cortex. The age-related alteration shown in the present study contributes to our understanding of age-related changes in sensorimotor control.

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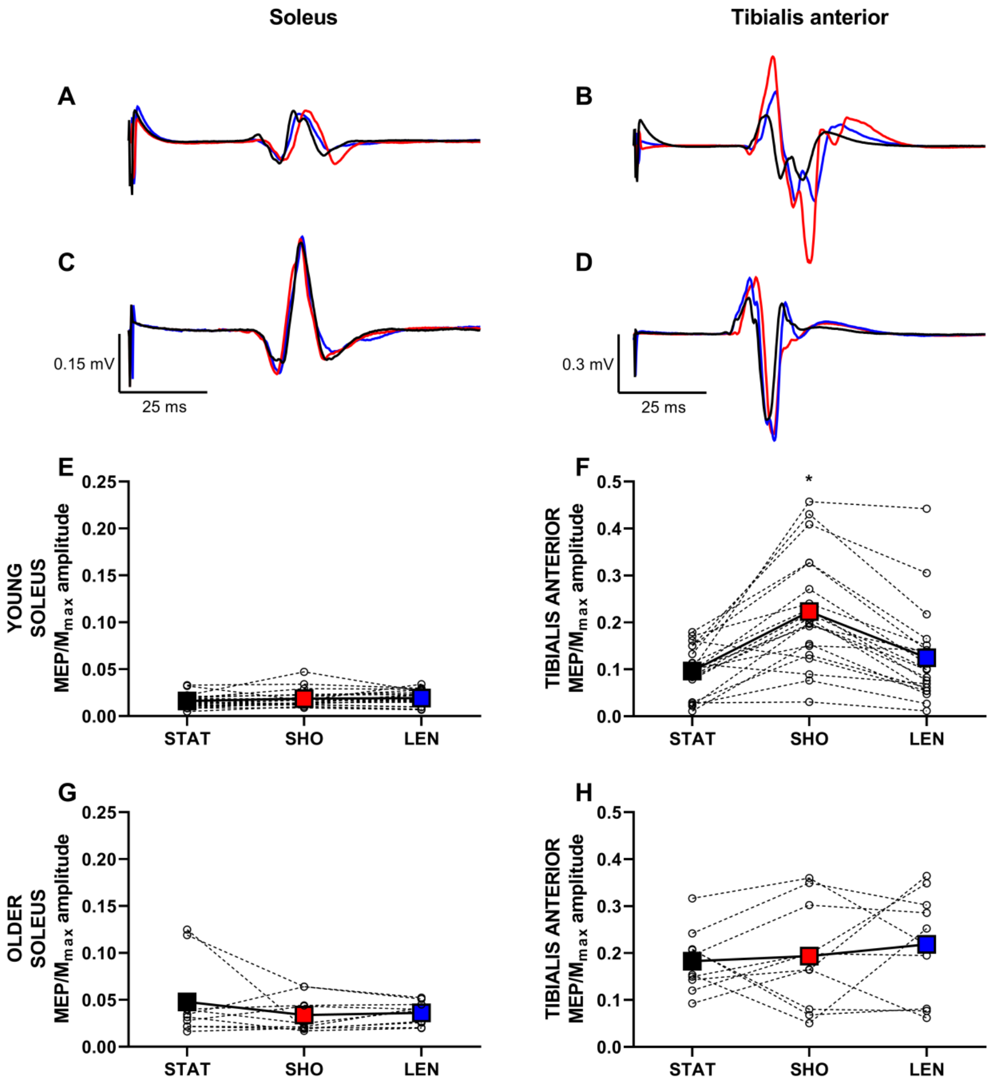
**Table 1**. Root-mean-square electromyographic activity (mV; mean ± SD) in the 100 ms preceding the stimulus.

| | YOUNG | OLDER |
|---|---|---|

| | | |
|---|---|---|
| | SOL | |
| Static position | 0.0130 ± 0.0020 | 0.0112 ± 0.0017 |
| Passive shortening | 0.0132 ± 0.0020 | 0.0116 ± 0.0020 |
| Passive lengthening | 0.0132 ± 0.0020 | 0.0115 ± 0.0019 |
| | TA | |
| Static position | 0.0045 ± 0.0003 | 0.0045 ± 0.0006 |
| Passive shortening | 0.0045 ± 0.0006 | 0.0045 ± 0.0008 |
| Passive lengthening | 0.0048 ± 0.0007 | 0.0045 ± 0.0011 |



Figure

**Figure 1. Motor evoked potentials during a static position, passive shortening and passive lengthening in soleus and tibialis anterior.** A - D: Averaged traces in response to single pulse transcranial magnetic stimulation during static position (black line), passive shortening (red line) and passive lengthening (blue line) in soleus (A, C) and tibialis anterior (B, D) in a young (A, B) and an older (C, D) adult that best represent the sample mean. Each representative trace is an average of 10 waveforms. E – H: Amplitude of motor evoked potential expressed relative to the amplitude of maximal compound action potential (MEP/$M_{max}$) during a static position (STAT), passive shortening (SHO) and passive lengthening (LEN) in soleus (left panel) and tibialis anterior (right panel) in young (E, F) and older (G, H) adults. Squares and solid lines represent the sample mean, whilst open circles and dashed lines denote individual responses (n = 10 and n = 18 for young and older,

respectively). To allow for easier comparison, data for soleus and tibialis anteior are presented in a 1:2 ratio. *p < 0.001 compared to STAT and LEN.

## Competing interests

The authors declare no conflict of interest, financial or otherwise.

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## Author Contributions

Experiments were performed in the Neurophysiology Laboratory at Northumbria University. JŠ, GH, SG and RD conceived and designed the work; JŠ and PA acquired the data; JŠ prepared figures and tables; JŠ and RD analysed and interpreted the data; JŠ drafted the manuscript; JŠ, PA, GH, SG and RD revised the final manuscript. All authors approved the final version of manuscript and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy and integrity of any part of the work are appropriately investigated and resolved. All persons designated as author qualify for authorship, and all those who qualify for authorship are listed.