

Modulation of Soleus H-Reflex during Shortening and Lengthening Muscle Actions in Young and Older Adults

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Abstract

The Hoffmann reflex (H-reflex) is dependently modulated during isometric and anisometric muscle actions. However, the manner of the H-reflex modulation during dynamic muscle movements in relation to ageing is less stated in the literature. This study was designed to investigate the effects of ageing on soleus (SOL) H-reflex modulation during dynamic muscle actions. Twenty young (24 ± 4 years of age) and 20 older adults (73 ± 5 years of age) voluntarily participated in the study. The SOL H-reflex was measured during passive and active shortening and lengthening muscle actions in a sitting position. The older group showed a lower ratio of the maximal amplitude of H-reflex to M-wave ($\text{SOL } H_{\max}/M_{\max}$) during the passive lengthening than that during the passive shortening (shortening: 0.40 ± 0.22 vs. lengthening: 0.15 ± 0.10 , $P < 0.05$), whereas the $\text{SOL } H_{\max}/M_{\max}$ ratio of the young group was significantly higher during the shortening than that during the lengthening contractions at maximal effort (shortening: 0.51 ± 0.26 vs. lengthening: 0.37 ± 0.18 , $P < 0.05$). These results suggested different modulations of group Ia afferent inputs to the SOL motoneurons during passive and active dynamic muscle actions between young and older adults.

Key Words: ageing, dynamic muscle contraction, H-reflex, passive movement, plantarflexion

Introduction

The Hoffmann reflex (H-reflex) test is used to assess neural control strategy *via* the Ia afferent spinal loop (3, 6). Changes in muscle fiber length have been demonstrated to affect the H-reflex modulation during passive (37) and active muscle actions (11, 39). It has been observed that the soleus (SOL) H-reflex is depressed during passive lengthening movement, compared with that during passive shortening movement (36, 37). Similar modulation of the SOL H-reflex was also found during shortening and lengthening contractions with voluntary effort at submaximal (36) and maximal (11) levels. It has been suggested that the movement-related changes in the H-reflex response during shortening and lengthening muscle actions are

mainly influenced by presynaptic inhibition of Ia afferents (10) and homosynaptic post-activation depression (HPAD) (24).

Ageing is an inevitable physiological process in human life. This process results in deterioration of the neuromuscular functions and decreased physical capacity at older ages (23, 31, 35). In comparison with young adults, older persons show slower cognitive processing (40), motor response generation (30, 44), nerve conduction velocity (38) and electromechanical delay (32, 45), and decreased muscle strength (17) and power (33). As a result, older adults have less ability in performing motor tasks and executing daily physical activities. Although existing evidences indicate deterioration of neuromuscular functions with ageing, older adults may adopt different strategies in

performing motor tasks as a result of compensatory adaptations (13, 41). For example, in comparison with young adults, Scaglioni *et al.* (41) demonstrated lower maximal amplitude of the H-reflex (H_{\max}) and M-wave (M_{\max}) responses associated with a decrease of the plantarflexors twitch torque in older individuals. However, the ratio of twitch torque to the H-reflex amplitude in older adults was higher. The observation in the Scaglioni's study indicated a preservation of mechanical efficiency in the motor system as a result of physiological compensation during the ageing process.

Age-related changes in the SOL H-reflex modulation have been reported during submaximal voluntary isometric contractions (1, 13), postural tasks (5, 14, 28) and walking (4). Older adults demonstrated specific manners of reflex modulation during different functional tasks, compared with their young counterparts. For example, the size of SOL H-reflex response in young adults is depressed from lying to upright standing but not in older adults (28). Presynaptic inhibition affected by supraspinal or segmental mechanisms may be an explanation for the age-related differences of H-reflex modulation (5). The influences of ageing and type of muscle contraction on H-reflex excitability are also confirmed (25). Kallio *et al.* (25) reported that in older adults the SOL H-reflex response was lower than that of young adults during submaximal dynamic plantarflexion. Coincidentally, depression of spinal excitability was also revealed during lengthening muscle contractions in both age groups. Whether older adults use a different neural strategy to modulate the Ia afferent inputs during dynamic plantarflexion at maximal contraction intensity, however, is still unclear, since variations of motor output regulation have been revealed during anisometric muscle contractions at submaximal and maximal intensities (8).

Duclay and Martin (11) utilized an angular velocity of 60°/s and a wide range of ankle joint movement (between plantarflexion 30° and dorsiflexion 30°) to investigate movement-related changes in the SOL H-reflex in young adults. However, this wide range of motion (ROM) may not be appropriate in testing older adults due to their limited ROM at the ankle joint (18). The present study adopted similar methods with a modification of the joint angle range (between plantarflexion 20° and dorsiflexion 20°) to examine the age-related changes in the SOL H-reflex modulation during dynamic ankle movements. This range of movement was close to the maximal recovery angle of the ankle joint ($16.3^\circ \pm 1.5^\circ$) during upright standing (32). Since the ability to maintain balance and control posture is critical to older adults in daily activities, it is necessary to advance our knowledge in the effects of ageing on motor performance during dynamic ankle muscle actions.

Therefore, the aim of the present study was to investigate the effects of ageing on the SOL H-reflex modulation during passive and active shortening and lengthening muscle actions. We hypothesized that [1] older adults would demonstrate a lower level of the SOL H-reflex ratio during passive ankle movement and maximal dynamic muscle contractions in comparison with young adults; and [2] in comparison of muscle action type, the SOL H-reflex ratio would be higher during the shortening muscle action than lengthening muscle action in young and older adults.

Materials and Methods

Participants

Healthy adults aged 20 ~ 40 years and 65 ~ 85 years with regular physical activity were included in this study. A young group of twenty (10 males, 10 females, age: 24.4 ± 4 years, height: 168 ± 6.6 cm, weight: 63.2 ± 12.9 kg) and an older group of twenty (10 males, 10 females, age: 73.3 ± 5 years, height: 166.1 ± 7 cm, weight: 74.8 ± 12.6 kg) healthy volunteers participated in the study. An established health status screening questionnaire was used to identify any contraindication to participation. Exclusion criteria included the presence of neuromuscular disorders, true vertigo, acute illness, current lower extremity injury, current use of medications known to impair neuromuscular function (*e.g.* antidepressants) and the use of a walking aid. All volunteers were recruited from a local community in the Northern River region of New South Wales, Australia. The volunteers who met the inclusion criteria and had no contraindication to participation signed an informed consent form and undertook a familiarization session prior to the testing session. All participants were instructed to refrain from taking caffeine-containing substances and smoking within 2 h of the testing session, and were asked not to perform strenuous exercise activity for 24 h before the testing session. The study was approved by the Human Research Ethics Committee of the University's Institutional Review Board and was performed in accordance with the Declaration of Helsinki.

In the passive lengthening test, the SOL H-reflex response could not be elicited from two female participants in the older group. Data from these two participants were excluded from data analysis. Therefore, data used for the statistical analysis was from 20 young and 18 older participants instead.

Experiment Settings

A Biodex dynamometer (System 3; Biodex Medical System, Shirley, NY, USA) was used to set ankle joint positions for isometric voluntary muscle

contraction. Participants sat on the Biodex chair in a semi-reclined position with the right leg fitted into the ankle attachment. The back tilt of the seat was set at 55° (0° for flat). The left foot was resting on the foot-rest attachment. The right foot was placed in the foot-plate and stabilized by Velcro straps and the heel cups. The thigh was supported by the support arm which was fitted proximally to the knee with the knee joint angle at 140° (180° as full extension). A Velcro strap was applied to the thigh against the support arm. A strap over the trunk and a strap over the hip of the testing leg were used to minimize body movement. The transverse axis of the ankle joint (a line through the lateral and the medial tibial condyles) was carefully aligned with the rotational axis of the dynamometer. Constant angular velocity was set at $60^\circ/\text{s}$. This velocity was chosen due to the high level of reproducibility of H-reflex test during maximal dynamic muscle actions under this condition (11), and the validity of isokinetic ankle strength measurement in older adults (22). To monitor the torque a computer screen was placed at a distance of approximately 2.0 m in front of the participants at the eye level.

The SOL H-reflex response was elicited by an electrical impulse applied to the tibial nerve *via* a constant-current electrical stimulator (DS7AH, Digitimer, Herfordshire, UK) with a single rectangular pulse of 200 μs in width and an output voltage of 400 V. The current output was adjustable in the range of 0 ~ 999 mA. A reusable rubber-based self-adhesive electrode with the size of 20×20 mm (Uni-Patch EP 84177, MN, USA) was placed on the popliteal fossa as the cathode, while another reusable rubber-based self-adhesive electrode with the size of 50×50 mm (Axelgaard Model 895220, CA, USA) was positioned over the patella as the anode. Because no difference of the H-reflex amplitude between the right and left legs has been reported, all participants were measured on the right leg for the SOL H-reflex to ensure consistency (34).

Electromyogram (EMG) signals from the SOL and tibialis anterior (TA) muscles were recorded by using a Bagnoli-8 EMG system (Delsys, Boston, MA, USA) with single differential surface electrodes (DE 2.1, Delsys). The electrode housing contained two parallel silver bars (99.9% pure silver) of 10 mm in length and 1 mm in diameter as the EMG sensors, spaced 10 mm apart. The electrode housing was internally shielded and contained a pre-amplifier. A self-adhesive conductive disk electrode 50 mm in diameter (Dermatode, Delsys) was placed over the medial condyles of the femur bone of the same leg as the reference. The electrode placement on the TA muscle was at 1/3 distance from the head of the fibula to the medial malleolus and ~ 2 cm lateral to the tibial crest. The electrode on the SOL muscle was placed at 2/3

distance from the medial condyles of the femur to the medial malleolus and at the central position in the medial-lateral direction of the SOL muscle border (7). The sites for placement of the electrodes were cleaned with alcohol wipes. Conductive gel was rubbed on the silver bars of the EMG sensors to improve electrode-skin contacts. In addition to application of the double-sided adhesive electrode-skin interface, a surgical adhesive tape was used to secure the electrode positions on the skin.

There is a consideration regarding the antagonist muscle activity during shortening and lengthening muscle actions. Afferent inputs from the antagonistic muscle during movement can cause inhibitory modulation of the agonist motoneuron pool (6). Therefore, the TA muscle was recorded to identify the degree of antagonist involvement during the H-reflex test.

The EMG signal was filtered with a band-pass range of 20 to 450 Hz, amplified with a gain of 1,000 times, and sampled at an analogue to digital conversion rate of 5 kHz. To capture the EMG signals, a custom-written LabView program (8.2 ver, National Instruments, Austin, TX, USA) was used to synchronize the electrical stimulation trigger and EMG recording.

Passive and Active Dynamic Muscle Actions

In the passive ankle movement test, the ankle joint movement was set with a ROM of 40° . Passive shortening movement was defined as the ankle movement from dorsiflexion 20° to plantarflexion 20° , whereas the passive lengthening movement was defined as the ankle movement in the opposite direction. H-reflex and M-wave (H/M) recruitment curve was established during the passive shortening and lengthening movement (Fig. 1). Electrical stimulation was delivered when the ankle joint passed through the neutral position (0°) to ensure all evoked potentials were elicited at identical muscle length throughout the test. The stimulation intensity was progressively increased, with increments of 10 mA, from the threshold of H-reflex to where there was no more increase in the M-wave amplitude. The intensity for eliciting the H_{max} was subsequently checked by using 2-mA increments. The mean value of SOL H_{max} and M_{max} was determined by averaging four repetitions in the passive shortening or lengthening condition and was used for data analysis. To preclude any influence of HPAD, a minimum of 10 s inter-stimulus interval was used (24).

In the shortening contraction test, the participant's ankle joint was rested at the dorsiflexion 20° as the initial position. When a verbal instruction "go" was given, the participant immediately performed a shortening muscle contraction with a maximal effort

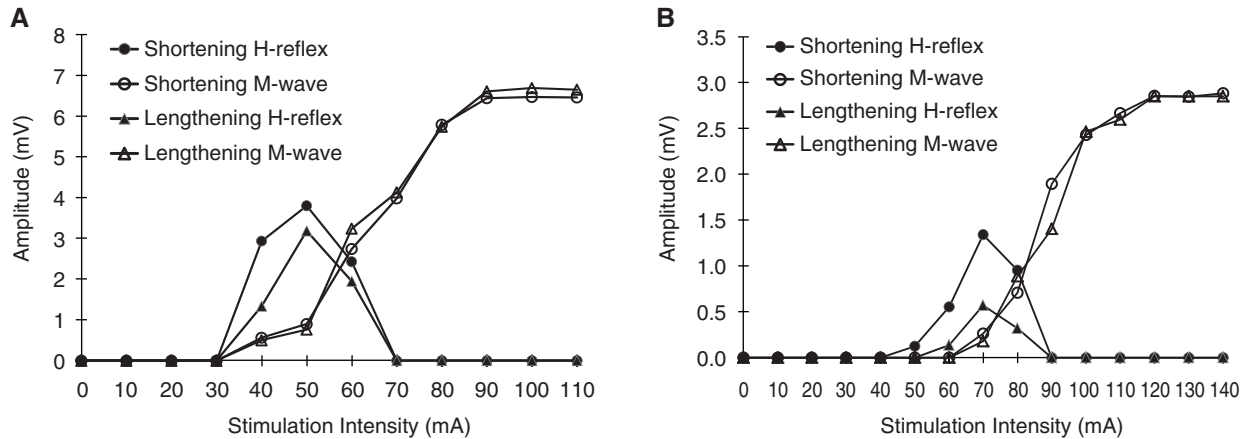


Fig. 1. H-reflex and M-wave recruitment curves during passive shortening (H-reflex: ●; M-wave: ○) and lengthening (H-reflex: ▲; M-wave: △) actions from representative one young (A) and one older (B) participants. Please note the differences in Y and X scales.

from the initial position to the plantarflexion 20° (terminal position). The ability to generate maximal muscle force has been reported to correlate to the ability of balance recovery in response to disturbance during upright standing (32). When the trial was completed at the terminal position, a 60 s rest interval was given before the ankle position was shifted to the initial position for the next trial. Electrical stimulation was delivered when the ankle joint passed through the neutral position. Four successful trials were recorded for the H-reflex and the M-wave, respectively. The stimulation intensity used for the H-wave was that induced H_{\max} during the passive movement, whereas that for the M-wave was the supra-maximal stimulation (1.5 times of M_{\max} stimulation intensity) used during the passive movement.

In the lengthening contraction test, the initial and terminal ankle positions were converted to the plantarflexion 20° and the dorsiflexion 20°, respectively. The testing procedure was identical to the shortening contraction test, except it was a lengthening contraction.

It is understood that alteration of the spatial relationship between stimulation electrode and the targeted nerve during muscle contraction can shift the H-wave and M-wave recruitment curve from that established at rest (3). Furthermore, the stimulation intensity that can induce the maximal amplitude of H-reflex during passive muscle action might not be identical to that during maximal muscle contraction. However, it would be difficult to establish the H/M recruitment curve and H_{\max} under various conditions in one day due to the time required and the possibility of fatigue that may affect the testing outcomes (19). Therefore, we limited our study to the H-reflex evoked by the same stimulation intensity for the purpose of comparison.

Data Analysis

A 100 ms background EMG (bEMG) prior to the onset of stimulus artifact was recorded for measuring baseline muscle activation in passive and active dynamic muscle actions (7). Root mean square calculation was used to determine the bEMG amplitude.

The mean values of H_{\max} , M_{\max} , H_{\max}/M_{\max} , $M_{\text{at}H_{\max}}/M_{\max}$ and bEMG were measured off-line for the respective experimental conditions. The peak-to-peak amplitude of M-wave and H-reflex was determined. The $M_{\text{at}H_{\max}}$ is an M-wave response associated with the H_{\max} . The calculation of $M_{\text{at}H_{\max}}/M_{\max}$ ratio is used to determine the proportion of spinal motoneuron pool being activated by electrical percutaneous stimulation during different types of muscle actions (11).

The digital EMG data was transferred to Excel datasheets and then all variables were measured on the Excel sheets (Microsoft Office, 2007 version). The original EMG traces of the SOL H-reflex in all testing conditions from a representative young and one older participant, respectively, are demonstrated in Fig. 2.

Statistical Analyses

The data was checked for normal distribution. If a suspicious outlier data was found, that might be caused by other influential factors, the Grubbs test was used to confirm and eliminate the significant outliers. The Grubbs test was used with a probability level of 0.05 to determine any outlying value (20). Statistical analysis was performed on the data following elimination of the significant outliers.

Descriptive data was presented as mean \pm

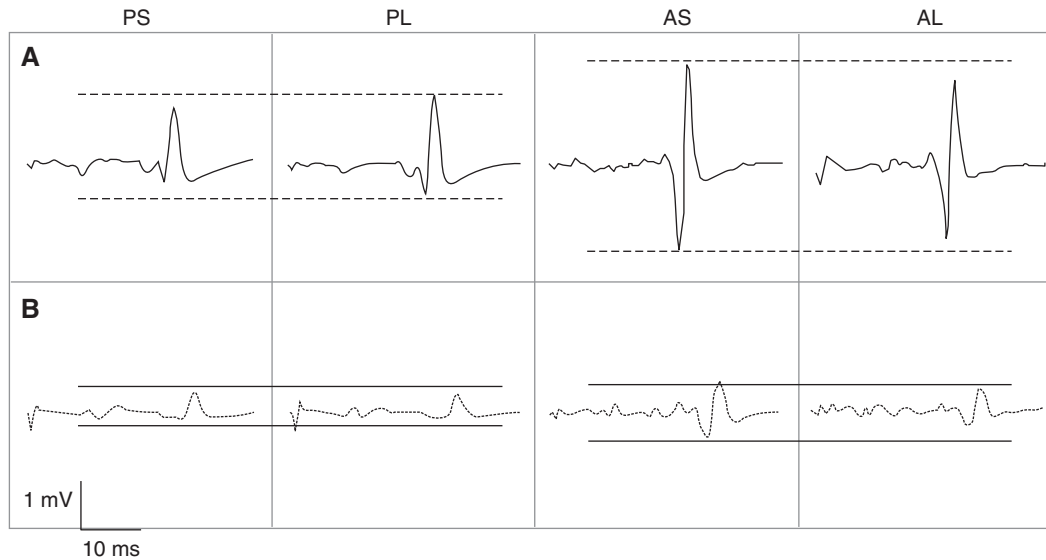


Fig. 2. Representative raw EMG traces of the maximal SOL H-reflex during passive and active dynamic muscle activities from one young (solid lines: A) and one older (dotted lines: B) participants. PS: passive shortening action; PL: passive lengthening action; AS: active shortening action; AL: active lengthening action.

standard deviation (SD). A two-factor [group (2) \times action type (2)] repeated measurements analysis of variance (RMANOVA) was performed to determine the main effect of age and action type, and the interaction between these factors on the SOL H_{\max} , M_{\max} , H_{\max}/M_{\max} ratio, $M_{\text{at}}H_{\max}/M_{\max}$ ratio, SOL bEMG and TA bEMG. When a significant interaction was found, a *post-hoc* analysis with Bonferroni adjustment was conducted to identify where the differences between the mean values occurred. An alpha value of $P \leq 0.05$ was set for significant differences between the means. All data were analysed by using SPSS software for Windows (SPSS Inc, ver. 16.0, Chicago, IL, USA).

Results

Passive Dynamic Muscle Action Test

The peak-to-peak amplitude of H_{\max} and M_{\max} responses were significantly lower in the older group than that in the young group ($P < 0.05$) in all types of passive movement.

For the comparison between passive shortening and lengthening movements, the size of SOL H_{\max} was similar in the young group ($P > 0.05$) but not in the older group ($P = 0.001$). The M_{\max} and $M_{\text{at}}H_{\max}/M_{\max}$ ratio in both age groups did not significantly differ between passive shortening and lengthening movements (Table 1).

The SOL H_{\max}/M_{\max} ratio during the passive movement demonstrated a significant “group by action type” interaction ($P = 0.001$) (Fig. 3A). The

post-hoc comparisons with Bonferroni adjustment showed that the young group had a higher SOL H_{\max}/M_{\max} ratio than that of the older group during the lengthening action ($P < 0.05$). No significant between-group difference was found in the SOL H_{\max}/M_{\max} ratio during the passive shortening action ($P > 0.05$). The SOL H_{\max}/M_{\max} ratio during the passive shortening movement was significantly higher than that during the passive lengthening movement in the older group ($P < 0.05$; shortening: 0.40 ± 0.22 > lengthening: 0.15 ± 0.10). In contrast, the young group demonstrated no significant difference of the SOL H_{\max}/M_{\max} ratio between the passive shortening and lengthening movements (0.45 ± 0.19 and 0.48 ± 0.20 , respectively; $P > 0.05$).

Active Dynamic Muscle Action Test

The size of H_{\max} and M_{\max} responses during shortening and lengthening contractions were lower in the older group than that in the young group ($P < 0.05$). However, a movement-related difference of the SOL H_{\max} response was found in the young group but not in the older group. There were no statistical differences of the M_{\max} and $M_{\text{at}}H_{\max}/M_{\max}$ ratio between maximal shortening and lengthening contractions in both aged groups (Table 1).

There was no significant “group by action type” interaction ($P > 0.05$) for the SOL H_{\max}/M_{\max} ratio during active dynamic muscle actions. However, a main effect of “action type” was found ($P < 0.05$, Fig. 3B). The SOL H_{\max}/M_{\max} ratio of the young group was significantly higher during shortening contraction than

Table 1. Mean values and standard deviation (values in the brackets for measurement variables) for the maximal amplitude of SOL H-reflex (H_{\max}), maximal amplitude of SOL M-wave (M_{\max}), and SOL $M_{\text{at}H_{\max}}/M_{\max}$ ratio ($M_{\text{at}H_{\max}}$ is an M-wave response accompanied with the H_{\max}) during passive dynamic movements and maximal voluntary dynamic contractions

	Passive dynamic muscle actions		Active dynamic muscle actions	
	Shortening	Lengthening	Shortening	Lengthening
<i>Young group (n = 20)</i>				
SOL H_{\max} (mV)	2.10 (± 1.02)	2.19 (± 1.25)	3.15 (± 1.59)	2.68 (± 1.48) [†]
SOL M_{\max} (mV)	4.61 (± 1.55)	4.53 (± 1.58)	6.90 (± 1.90)	7.09 (± 1.75)
SOL $M_{\text{at}H_{\max}}/M_{\max}$ ratio	0.14 (± 0.07)	0.13 (± 0.09)	0.17 (± 0.16)	0.17 (± 0.14)
<i>Older group (n = 18)</i>				
SOL H_{\max} (mV)	0.74 (± 0.59)*	0.26 (± 0.17)* [†]	1.10 (± 0.60)*	0.96 (± 0.52)*
SOL M_{\max} (mV)	1.78 (± 0.67)*	1.76 (± 0.64)*	2.78 (± 1.08)*	2.64 (± 0.98)*
SOL $M_{\text{at}H_{\max}}/M_{\max}$ ratio	0.19 (± 0.10)	0.20 (± 0.14)	0.24 (± 0.13)	0.23 (± 0.14)

*: $P < 0.05$, differ significantly from the young group. †: $P < 0.05$, differ significantly from the shortening muscle action.

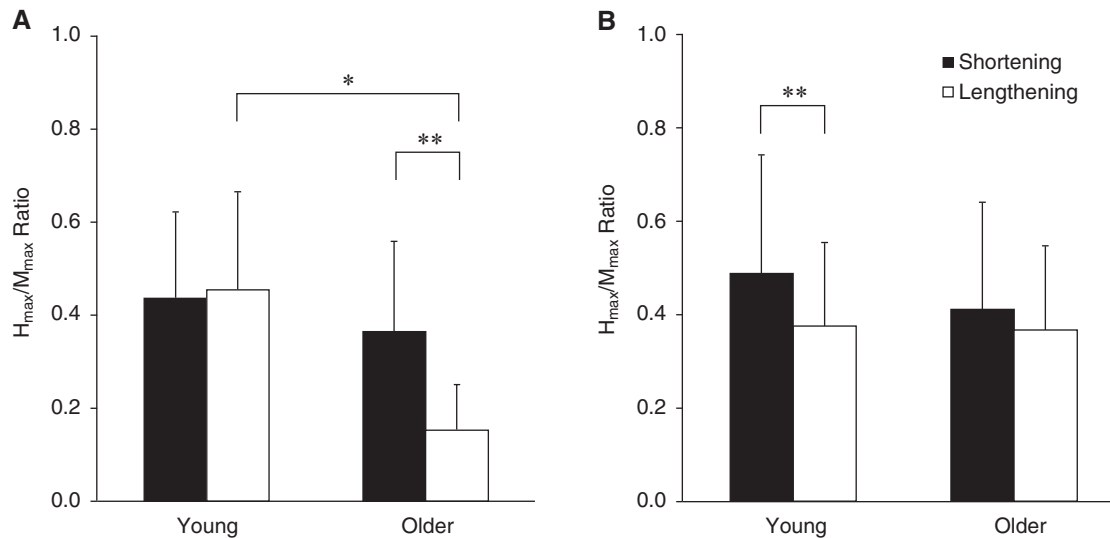


Fig. 3. The SOL H_{\max}/M_{\max} ratio during dynamic muscle actions. A) passive shortening and lengthening movements and B) voluntary shortening and lengthening muscle contractions. Data are presented as mean values and standard deviations (Young group: n = 20; Older group: n = 18). *: $P < 0.05$, between both groups. **: $P < 0.05$ between action types.

that during lengthening contraction ($P < 0.05$; shortening: $0.51 \pm 0.26 >$ lengthening: 0.37 ± 0.18). There was no significant difference in the SOL H_{\max}/M_{\max} ratio found between the shortening and lengthening muscle contractions in the older group ($P > 0.05$; shortening: $0.40 \pm 0.22 >$ lengthening: 0.36 ± 0.18).

Background EMG

Results showed a significant main effect of action type for the SOL bEMG during passive and active muscle actions ($P < 0.05$). However, the *post-hoc* comparisons with Bonferroni adjustment revealed no significant differences of the SOL bEMG during passive

muscle actions and the TA bEMG during passive and active conditions in both groups (Fig. 4). The mean values of bEMG in the SOL muscle between the shortening and lengthening muscle contractions differ significantly in the young ($P < 0.05$; shortening: $118.8 \pm 68.1 \mu\text{V} >$ lengthening: $89.1 \pm 45.9 \mu\text{V}$) and the older groups ($P < 0.05$; shortening: $84.9 \pm 27.2 \mu\text{V} >$ lengthening: $75.4 \pm 31.1 \mu\text{V}$).

Discussion

There were movement-related differences in the SOL H-reflex modulation during passive and active shortening and lengthening actions. The modulation

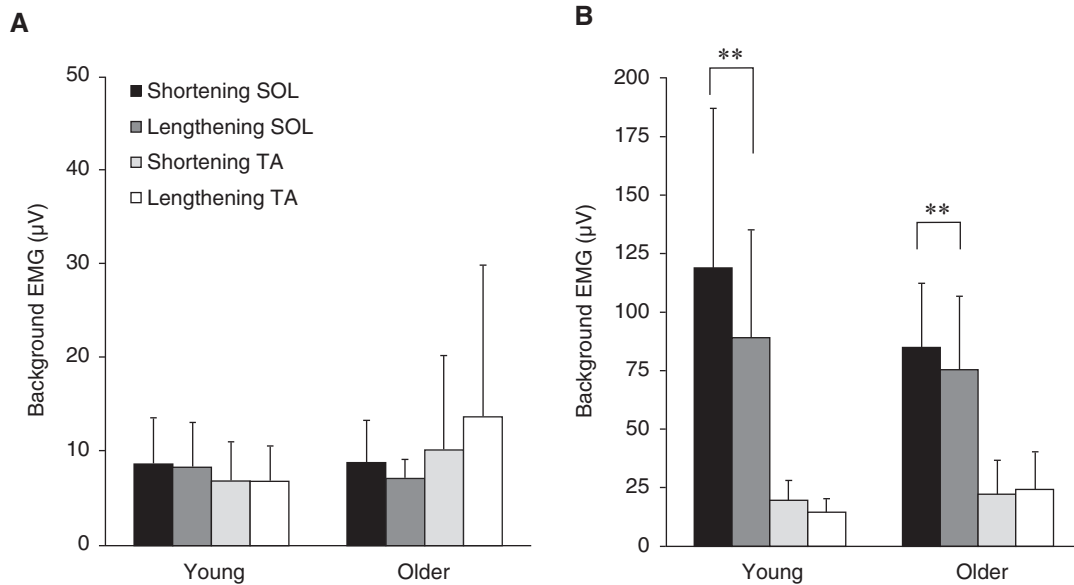


Fig. 4. The electromyogram activities of the soleus and tibialis anterior muscles. (A) passive plantarflexors movements and (B) maximal dynamic plantarflexors contractions. Data are presented as mean values and standard deviations (Young group: $n = 20$; Older group: $n = 18$). Please note the difference in Y-scale. **: $P < 0.05$ between action types.

of the group Ia monosynaptic projection in older adults was affected by the type of muscle action (shortening and lengthening) during passive movement but not during maximal voluntary contraction, while in young adults movement-related change of the SOL H-reflex was observed during active contraction but not during passive movement. Furthermore, older adults have a lower SOL H_{\max}/M_{\max} ratio than younger population during passive lengthening movement but not for passive shortening movement and maximal dynamic contractions.

Passive Dynamic Plantarflexors Actions

It has been previously suggested that the size of SOL H-reflex response was reduced during passive lengthening than passive shortening (11, 36, 37). Decrease in Ia afferent inputs to spinal motoneuronal activation is a functional adjustment for accurate motor performance during lengthening muscle activation. Presynaptic inhibition through primary afferent depolarization and HPAD contributed to the SOL H-reflex depression during passive lengthening movement as observed in young adults. Conversely, our finding of the young group showed a similarity of the SOL H-reflex size during passive dynamic muscle actions. The absence of H-reflex modulation indicates no change in inhibitory effect on the spinal excitability between passive shortening and lengthening trials. It was possibly due to discrepancy of thixotropic effect between passive shortening and lengthening trials in the present study. Previous studies implemented a submaximal

effort of voluntary muscle contraction before passive dynamic plantarflexors actions in an attempt to ensure similar muscle length before conditional trials (11, 36, 37). Changes in muscle length can affect muscle spindle discharge rates and the Ia afferent inputs because the preceding muscle spindle activity leads to different levels of presynaptic and postsynaptic inhibitions of the spinal motoneurons *via* peripheral and central regulations (21). The lack of reflex modulation observed in the present study may be explained by differences in sensitivity between the experimental settings utilized to measure the H-reflex response.

It is interesting to find that the older group demonstrated movement-related changes in the SOL H_{\max}/M_{\max} ratio during passive actions. Previous studies have suggested that presynaptic inhibition of Ia afferent is a primary factor to affect H-reflex modulation during passive muscle actions (36, 37). However, presynaptic mechanisms may not be an appropriate explanation for the movement-related difference of SOL H-reflex ratios in the older group due to ageing effect on presynaptic inhibitory function. Evidence with the H-reflex assessment suggests that older adults have shown less engagement of the presynaptic inhibitory mechanisms to modulate the Ia afferent inputs at the spinal level during rest and functional performance (1, 5, 13, 29). This phenomenon is possibly related to descending control on the inhibitory function of the primary afferent depolarization interneurons during movements.

Reciprocal inhibition may be a neurophysiological factor to reduce the size of SOL H-reflex response

(9). Older adults increase co-activation of antagonistic muscles associated with decrease in muscle strength of agonistic muscles (27). In the present study, the bEMG in the older group demonstrated that co-activation of TA muscle was stronger than that in the young group despite no statistical difference in comparison of group means. However, the reciprocal inhibition may not be a contributor to cause such movement-related change in older population. Because the influence of reciprocal inhibitory mechanisms on spinal excitability is reduced with advancing ageing, such age-related change is not supported by this observation (26).

If presynaptic inhibition or reciprocal inhibition is not a factor contributing to the reduction of H-reflex response during passive lengthening movement found in older adults, it raises a question of what had caused the reflex modulation in this case. Burke *et al.* (2) observed that muscle spindle afferent discharge was quiescent during passive shortening activity but it increased rapidly during passive lengthening activity. Because the length extensibility of ankle muscle-tendon unit decreased with age, the range of ankle joint movement engaged in our study may lead to a great facilitation of muscle spindle discharge in older participants (18). The difference of muscle spindle afferent discharge between muscle actions might be a possible mechanism for the reduction of the H-reflex amplitude during passive lengthening movement in older adults. However, the neural control of lengthening exercise in older adults is not well understood in the current literature. We speculated that the movement-related change in muscle spindle discharge may play a major role in the SOL H-reflex modulation in the older group.

Active Dynamic Plantarflexors Actions

When the SOL H_{\max}/M_{\max} ratio was assessed during maximal voluntary shortening and lengthening contractions, differences were found between young and older adults. The SOL H_{\max}/M_{\max} ratio of the young group during the shortening contraction was significantly higher than that during the lengthening contraction. However, this contraction-related change of the SOL H_{\max}/M_{\max} ratio was not significant in the older participants. Significant change in the SOL H_{\max}/M_{\max} ratio of the young group is in agreement with the previous studies that demonstrated a depression of the SOL H-reflex during lengthening muscle contraction at submaximal and maximal levels, in comparison to that during shortening contraction at the same intensities (11, 36, 39). Presynaptic inhibition of Ia terminals and HPAD were the two possible mechanisms underlying the depression of SOL H-reflex during voluntary lengthening contractions. The in-

fluence of HPAD on the spinal excitability, however, may be minimized during voluntarily control of movement (43). Potential mechanism that can explain the decrease of spinal motoneuron excitability during maximal lengthening muscle contraction is the presynaptic inhibition of Ia afferents and is possibly mediated by the supraspinal mechanisms. Evidences with motor evoked potentials (MEPs) (12, 42) and electroencephalogram (EEG) (15, 16) assessments suggested specific neural control of voluntary lengthening contraction mainly regulated by cortical mechanisms. For example, Sekiguchi *et al.* (42) reported that the size of MEPs induced by transcranial magnetic stimulation decreased during lengthening plantarflexion, compared to that during shortening plantarflexion, although the SOL and TA bEMG values were similar between the two contraction types. This decrease in MEPs may indicate a reduction of the cortical descending inputs when the calf muscle voluntarily contracts in a lengthening action. Thus, it appears that descending inputs may be involved in the neural modulation at the spinal level during maximal dynamic muscle contractions in young adults.

Results of the present study showed that, in contrast to the young group, the contraction-related motor regulation, controlled by the supraspinal mechanisms, was not different between maximal shortening and lengthening contractions in the older group. This observation may indicate that older adults used specific descending commands to adjust synaptic inputs in the spinal motoneuron pool during lengthening contractions. Differently to the passive movement, it has been shown that the supraspinal control of presynaptic inhibition in Ia-motoneuron system during voluntary muscle contraction is preserved in the older population (13). The shift of spinal inhibitory mechanisms could lead to strong neural modulation in the Ia afferent pathway. Therefore, it is likely that the absent modulation of the SOL H_{\max}/M_{\max} ratio between maximal shortening and lengthening contractions found in the older group is related to central regulation of motor output.

Methodological Considerations

Methodological concerns for recording condition should be addressed in the H-reflex measurement (6). Electrical stimulation applied at different joint position during ankle movement can cause a bias to test motoneuron excitability (7). Our study used the $M_{\text{at}}H_{\max}/M_{\max}$ ratio to confirm that same proportion of motoneuron pool was activated by artificial electrical stimulations. The determination to use the $M_{\text{at}}H_{\max}/M_{\max}$ ratio was to ensure the validity of H-reflex measurement during the dynamic muscle actions. In the present study, the result in both groups showed no difference of the

$M_{at}H_{max}/M_{max}$ ratio and M_{max} between the muscle action types during passive and active tasks. The findings supported that the test method in our study was appropriated.

In conclusion, this study demonstrated the influence of shortening and lengthening plantarflexions on the SOL H-reflex modulation in older adults. Dissimilar modulations of the SOL H-reflex during passive dynamic movements and voluntary maximal dynamic contractions were found between young and older adults. These findings suggest an age-related neural adaptation during dynamic plantarflexion muscle actions.

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