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Differential control of H-reflex amplitude in different weight-bearing conditions in young and elderly subjects

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HIGHLIGHTS

- The soleus (SOL) maximum evoked H-reflex (H-max) was associated with the corresponding background EMG (bEMG) activity for the elderly subjects who increased the bEMG activity as they increased their body-weight-bearing conditions.
- The young subjects had an ability to modulate their descending tonic ongoing presynaptic inhibition imposed on the Ia afferents of the femoral nerve (FN) from non-weight-bearing condition to weight-bearing condition, whereas the elderly subjects did not.
- In the elderly group, it is considered that input from the vestibulospinal tract is insufficient to induce presynaptic inhibition upon Ia fibre connection to the motoneuron.

ABSTRACT

Objective: This study measured the modulation of conditioned (femoral nerve, paired-stimuli) and unconditioned soleus H-reflexes in young and elderly subjects when changing weight-bearing (WB) requirements and body position.
Methods: Conditioned and unconditioned H-reflexes were examined in 14 elderly subjects and 11 young subjects during six different WB conditions: (1) lying supine with no WB, (2) supine position inclined by 30° with 50% WB, (3) standing with 50%, (4) 75%, (5) 100% and (6) 125% WB.
Results: The elderly subjects had consistently higher background soleus EMG activity across the WB conditions compared to the young. Femoral nerve conditioning caused facilitation of the H-reflex that changed across WB conditions in the young subjects, but not in the elderly subjects. Finally, elderly subjects had less depression with paired-stimulation (PRD) across WB conditions, which was not observed in the young subjects.
Conclusions: The elderly may have more direct activation of motoneurons from descending pathways, coupled with less segmental spinal control of inhibitory interneurons, as evidenced by the increased background soleus activity, H/M-max ratios and the lack of modulatory control observed when conditioning the H-reflex.
Significance: There was an age-specific response from descending and segmental pathways during conditions that involved either different WB requirements or changes in body position.

1. Introduction

As humans age anatomical degeneration and changes in spinal excitability have deleterious effects on motor function (Sabbahi and Sedgwick, 1982). Reorganisation of motor unit pools and a decline in the number of muscle fibres are a well-documented consequence of the ageing process. Additionally, the greater decrease in the maximum evoked H-reflex (H-max), relative to the decrease in M-max, suggests that ageing negatively influences the Ia afferent pathway (Kido et al., 2004). This is evident in the differential modulation of H-reflex gain between young and old subjects (Angulo-Kinzler et al., 1998). Even within a group of elderly subjects there are differences in H-reflex gain, which was found to be associated with a larger deterioration in postural balance (Koceja et al., 1995).

Although the spinal mechanisms responsible for the differential changes in H-reflex magnitude between young and elderly have

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not been directly examined, the most plausible explanation is that there is presynaptic modulation of neurotransmitter release from the Ia afferent terminals. The presynaptic modulation of Ia afferents could be influenced by primary afferent depolarisation (PAD) interneurons or GABAergic interneurons via axo-axonic contacts with the terminal arborisations of the afferent fibres (Rudomin and Schmidt, 1999). Group Ib afferents, cutaneous afferents, vestibulospinal tract fibres and even the collaterals of Ia afferents themselves can excite both types of interneurons. These connections have been observed to inhibit the transmitter release from Ia presynaptic terminals during the standing position in young adults (Pierrot-Deseilligny and Burke, 2005; Stein, 1995). Alternatively, the absence of a decrease in the H-reflex in elderly subjects when transitioning to standing has been attributed to the decline in function of presynaptic inhibitory mechanisms.

One area that could be responsible for the decreased presynaptic inhibition in elderly is at the site of the PAD interneurons. Specifically, the first-order PAD interneurons receive excitatory inputs from the vestibulospinal tract, Ia and Ib afferents. On the other hand, inhibitory inputs to PAD interneurons come from other spinal interneurons that are excited by feedback from cutaneous afferents and from the descending corticospinal tract (Pierrot-Deseilligny and Burke, 2005; Rudomin, 2002). Consequently, in the elderly, changing postural orientation from prone to standing could be activating both the corticospinal and vestibulospinal tracts. The activation of these two tracts would cause counteracting inhibition and facilitation of the first-order PAD interneurons, leading to a decrease in the level of presynaptic inhibition. On the contrary, the increase in presynaptic inhibition observed when changing postural orientation in young adults could be due to vestibular inputs being more active and the corticospinal tract more inactive, resulting in more relative excitatory input to the inhibitory interneurons. The purpose of this study was to examine these mechanisms by demonstrating differential control of H-reflex modulation in young and elderly subjects by changing body position and weight-bearing (WB) loads. By adjusting body position and the WB load on the individual, we can independently manipulate activity in the vestibular and corticospinal tracts, respectively. In an effort to further explore the mechanisms responsible for the changes, soleus H-reflex modulation was examined with a conditioning stimulus of the femoral nerve (heteronymous facilitation), and through double stimuli to the same tibial nerve (paired-reflex depression (PRD)) during different body-WB positions.

2. Materials and methods

2.1. Subjects

Fourteen reportedly healthy, independent, community-dwelling elderly (mean age 67.2 and SD: 3.8 years, 4 men) and 11 young (mean age 22.8 and SD: 2.5 years, 8 men) subjects volunteered to participate in the study. Subjects were screened by completing a questionnaire and were excluded if they reported any neurological disease, disorder or injury. All subjects gave informed consent to the procedures as approved by the University's Committee for the Protection of Human Subjects.

2.2. Procedures

Bipolar surface electromyogram (EMG) electrodes (Ag) with a bar length of 10 mm, width of 1 mm and a distance of 1 cm between active recording sites (Delsys Bagnoli-4) were placed on the soleus (SOL), medial gastrocnemius (MG), tibialis anterior (TA) and rectus femoris (RF) muscles of the right leg. EMG electrodes were preamplified and routed through the EMG mainframe that additionally amplified (×1000) and band-pass filtered (20–450 Hz) the signals.

SOL H-reflexes were evoked according to the procedures outlined by Hugon (1973), with a 0.90-cm diameter-stimulating cathode electrode placed over the posterior tibial nerve (PTN) in the popliteal fossa. A 5-cm square anode dispersal pad was placed on the anterior midline of the knee, just above the patella. An electrical stimulator (Grass Instruments, S88) was used to generate a 1.0-ms duration square wave pulse to PTN. Once the optimal site of stimulation was established the recording and stimulating electrodes were not removed until the completion of the experiment. Initial measurements of H-max and maximal motor wave (M-max) amplitude were obtained for each body position. The intensity of stimulation was set to 15% of M-max for all of the control H-reflex trials to ensure that the same percentage of the motoneuron pool was activated for both elderly and young subjects.

The degree of presynaptic inhibition was examined by comparing the stand-alone SOL H-reflex with the SOL H-reflex facilitated by stimulation of the femoral nerve (FN-H-reflex). Because FN Ia afferents have monosynaptic excitatory projections to the heteronymous SOL motoneuron pool, the amount of ongoing presynaptic inhibition can be estimated by the change in H-reflex size when paired with FN stimulation (Hultborn et al., 1987; Koceja and Mynark, 2000). FN conditioning was performed with cathode stimulation just below the inguinal crease on the anterior superior aspect of the thigh, as described by Hultborn et al. (1987). A 5-cm square anode dispersal pad was placed on the back upper middle of the thigh. Specifically, FN location was determined by moving the electrode until the stimulus evoked a twitch in the RF muscle and not the sartorius muscle. Stimulus intensity was set at 1.1 × RF motor threshold, and the FN stimulus was elicited −5.5 ms prior to the PTN stimulus in order to account for the shorter conduction time required for FN due to the proximity of the stimulation site to the spinal cord.

A paired-reflex depression (PRD) protocol was used to examine the effect of altering body-weight supports and positions on the history-dependent activation of the Ia afferents (Trimble et al., 2000). This involved applying two consecutive stimuli to the PTN, separated by 80 ms, with a stimulus intensity of approximately 15% of M-max. The consecutive stimulation of the Ia afferents at this test interval results in a distinct suppression of the second H-reflex in unimpaired young adults.

The H-reflex protocols were evoked and measured during six different conditions: (1) lying supine with no load bearing, (2) lying supine and inclined by 30° of back support (BS), (3) standing with 50% body WB, (4) standing with 75% WB, (5) standing with 100% WB and (6) standing with 125% WB. In the first condition, the subject laid comfortably on a padded bench (KIN-COM 500H) in the supine position and the right foot was fixed to an immovable footplate at 0° of plantar flexion and the knee joint was set at 0° of flexion. For the second condition the subject laid supine, flat against glide-board back support. The glide-board could freely slide up and down with minimal friction in one plane (1° of freedom). The glide-board was inclined to 30° from the ground and the subject's feet were on a platform perpendicular to the board so that the ankle angle was in 0° of plantar flexion and the knee in 0° of flexion. With the gravitational force of the subject known, raising the board to an incline of 30° resulted in the gravitational force parallel to the slope of the glide-board being equal to 50%WB (body weight × *sin* 30°). The subject was required to stand quietly in conditions 3–6 and was instructed to maintain balance equally on both feet while maintaining a relaxed posture. For the third and fourth conditions the subject wore a harness that enabled them to be de-weighted by an air compressor (New Assist, Inter Reha, Tokyo, Japan), such that they supported 50% and 75% of WB, respectively (shown in Fig. 1 above). The subject was required to stand unsupported for the fifth condition, thereby supporting 100%WB. Finally,

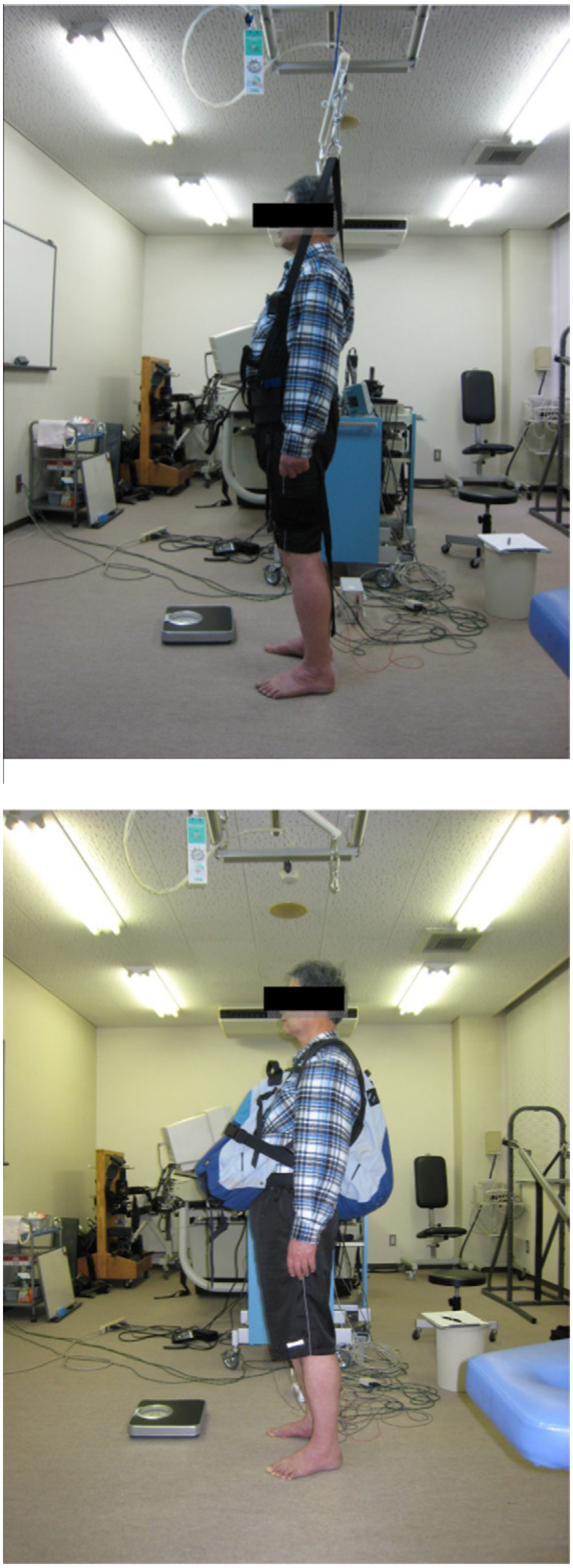

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Fig. 1. The system used for the weight bearing conditions. The subject wore the harness and was de-weighted by an air compressor until they only supported 50% or 75% of their body weight (above). The system used in the 125% weight bearing condition. Two backpacks were placed on the subject, one on the front of the body and one on the back. Each pack contained weights that were equal to 12.5% of the subject's body weight (25% total) (below).

in the last condition, a backpack was attached to each, the front and back of the body, with each backpack containing weight equal to 12.5% of the subject's body weight (25% of body weight total, Fig. 1). The subject was instructed to focus their gaze on a stationary target ~2 m in front of the subject.

Both H-max and M-max amplitude were obtained before testing each WB condition. The intensity of stimulation was set to approximately 15% of M-max and was adjusted until the amplitude of the control H-reflex was stable. Then, six to eight trials of control H-reflex were recorded, immediately followed by six to eight trials for each the FN-H-reflex and PRD conditioning protocols. There was a 10-s interval between each of the H-reflex trials. EMG signals were monitored online via the surface recording electrodes during each of the conditions to ensure that consistent signals were obtained.

2.3. Data acquisition and analysis

Data were recorded online with 16-bit resolution using Powerlab data collection software program (Chart v5.5.5, AD Instruments) at a sampling rate of 2 kHz that went through the AD board and was stored on a computer for off-line analyses. The root-mean-square (RMS) values of background EMG (bEMG) signals for all muscles 100 ms prior to initiation of the test stimulus were normalised to the corresponding muscle's activity in the supine position. The peak-to-peak amplitudes (mV) of H-max, control H-reflex, FN-H-reflex and PRD H-reflex were normalised to the peak-to-peak amplitude (mV) of M-max for each subject.

A 2 × 5 (age × condition) mixed-measures analysis of variance (ANOVA) design was used to examine comparisons between young and elderly individuals and each of the WB conditions (BS, 50%, 75%, 100% and 125% WB) independently for each muscle. Five positions were compared because the bEMG signals were normalised to the corresponding muscles' activity in the supine position. A 2 × 6 (age × condition) mixed-measures ANOVA design within subjects crossed with the WB conditions (supine, BS, 50%, 75%, 100% and 125% WB) was used to examine differences in the ratio of H/M-max. Furthermore, a 2 × 3 × 6 (age × protocol × condition) mixed-measure ANOVA design within subjects crossed with the conditions was used to measure differences in the control, PRD- and FN-H-reflex. Where appropriate, the Dunnett's post-hoc test was used to measure any significant differences for each position (Keppel and Wickens, 2004). All statistical tests were performed at the 0.05 level of probability.

3. Results

3.1. Background EMG activity

Representative bEMG traces from SOL for one elderly subject are displayed in Fig. 2. All six WB conditions are shown and the data were taken from trials while obtaining H-max. Across all conditions, the mean bEMG in SOL for the elderly subjects was greater than that of the young subjects. The elderly group displayed a larger increase in SOL bEMG when changing from the supine condition (100% as normalised) to the 125% WB condition (141%), compared to the young group (115%). The results demonstrated a significant difference between age groups across all conditions in SOL bEMG ($F(4,92) = 3.80$, $p < 0.01$). Specifically, elderly subjects significantly increased SOL bEMG during the standing with 100% and 125% WB conditions compared with the young subjects ($F(1,119) = 6.42$, $p < 0.05$ and $F(1,119) = 16.3$, $p < 0.01$, respectively). The Dunnett's post-hoc test revealed that the elderly group significantly increased SOL bEMG during standing conditions with 100% and 125% WB compared with the BS condition. In contrast, no significant differences were found across WB conditions compared with the BS condition for the young group. Young and old group

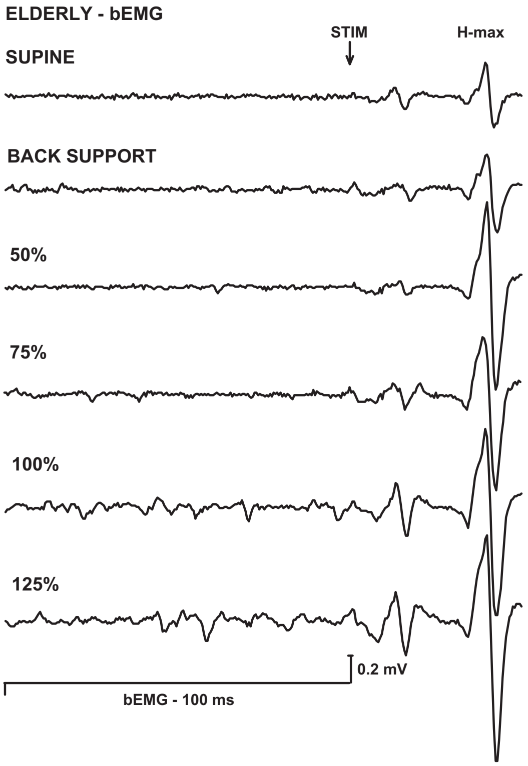

Fig. 2. Representative soleus EMG traces for one elderly subject during each of the conditions. Soleus background EMG activity was measured 100 ms prior to the test stimulus when H-max was recorded. Note the increase in the amplitude of the soleus background EMG during the 100% and 125% WB conditions.

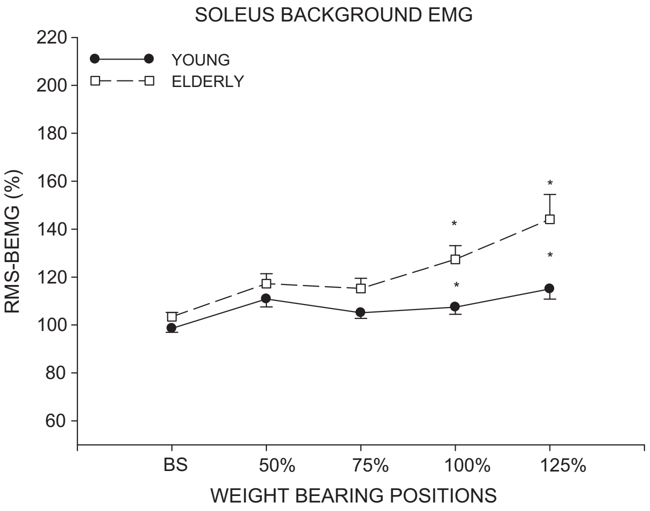

Fig. 3. Soleus background EMG activity for both age groups and across WB conditions. There were significant age group differences in the 100% and 125% WB conditions. In addition, within the elderly group the BS condition was different from the 100% and 125% WB conditions. Error bars denote the standard error of the mean.

SOL bEMG activity for the five conditions, normalised to the SOL bEMG in the supine position, is shown in Fig. 3.

There were no significant differences observed in MG muscle bEMG between the two age groups. However, collapsed across age groups, MG bEMG significantly increased during the standing conditions with 100% and 125% WB (130% and 158%, respectively). There was no interaction and no main effects observed in the TA bEMG for both age groups and WB conditions. This was the same for RF bEMG, as no specific differences were noted between age groups or across conditions.

3.2. Reflex and motor responses

As expected, the raw SOL H-reflex responses of the elderly subjects were lower in amplitude overall than those observed in the young subjects. The mean values of M-max and H-max for each of the WB conditions are shown in Table 1 for the two age groups. No statistical interaction in M-max was observed for age or WB conditions, whereas there was a significant interaction across WB conditions and age groups for H-max ($F(5,140) = 10.4$, $p < 0.001$).

3.3. Ratio of H-max to M-max

The ratio of H-max to M-max significantly decreased during all of the standing WB conditions as compared with the supine condition for the young subject group. In contrast, H/M-max significantly increased in the elderly subject group for all of the standing WB conditions compared with the supine condition. Additionally, a difference in H/M-max was noted between the young and old groups (60.5% vs. 35.7%, respectively) for the BS condition, in which the subject had back support accounting for approximately half of their bodyweight. On the other hand, no differences were noted during the standing condition with 50% WB between groups (50.2% young vs. 43.5% elderly). No differences in H/M-max between the two age groups were found for the 75%, 100% and 125% WB conditions; as such, only the H/M-max for the supine, BS and 50% WB conditions for both age groups are displayed in Fig. 4.

3.4. Conditioned H-reflexes

A significant three-way interaction was found between the age groups and conditioned H-reflexes across WB conditions ($F(10,280) = 2.89$, $p < 0.01$). Specifically, during the standing condition with 125% WB, PRD-H-reflexes were greater, indicating less Ia afferent depression, for the elderly compared to the young subjects ($F(1,504) = 4.89$, $p = 0.027$). Furthermore, the PRD-H-reflex was greater during 125% WB condition compared to the supine condition. No differences were observed for the young subjects across any of the WB conditions. The PRD-H-reflex results are shown in Fig. 5 for each age group. There were significant differences in the FN-H-reflex between two age groups during the supine, BS and 125% WB conditions ($F(1,504) = 8.44$, $p = 0.004$; $F(1,504) = 22.6$, $p < 0.001$; $F(1,504) = 4.45$, $p = 0.035$, respectively). Specifically, the young subjects demonstrated greater facilitation with FN conditioning. Additionally, the FN-H-reflex was significantly depressed during the standing conditions with 50% and 75% WB compared with the supine position in the young group, whereas no difference across WB conditions was observed in the elderly (Fig. 6).

4. Discussion

4.1. Soleus background EMG

The primary result emerging from this study was that the young and elderly subjects demonstrated differential control of bEMG for the different WB conditions. MG bEMG activity consistently increased for both age groups as the subjects had to support a greater percentage of their body weight. However, the elderly subjects also significantly increased SOL bEMG with greater WB. The divergent SOL bEMG results could be explained by the physiological consequences of ageing on the motor system. Specifically, as there is an overall loss of strength with ageing, the SOL muscle may be

Table 1
Mean values of H-max and M-max for young and elderly groups (with standard deviations in parentheses).

		Supine	BS	50%	75%	100%	125%
M-max (mV)	Young	4.72 (1.84)	4.75 (1.76)	5.16 (2.00)	4.99 (2.08)	5.07 (1.79)	5.13 (1.82)
	Elderly	2.82 (1.20)	2.88 (1.24)	3.10 (1.10)	2.94 (1.18)	2.85 (1.07)	2.93 (1.02)
H-max (mV)	Young	2.96 (1.56)	2.82 (1.31)	2.47 (1.05)	2.42 (1.06)	2.43 (1.06)	2.57 (1.11)
	Elderly	0.97 (.66)	1.05 (.73)	1.31 (.59)	1.19 (.66)	1.28 (.65)	1.30 (.63)

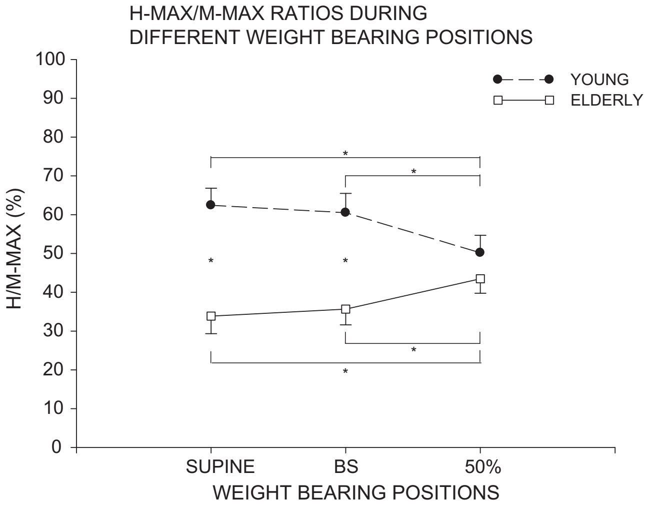

Fig. 4. H/M-max values for the supine, BS, and 50% weight bearing conditions for both age groups. Significant differences within each group were present when comparing the supine condition to the weight bearing conditions. Significant differences were also observed between the two age groups. Error bars denote the standard error of the mean.

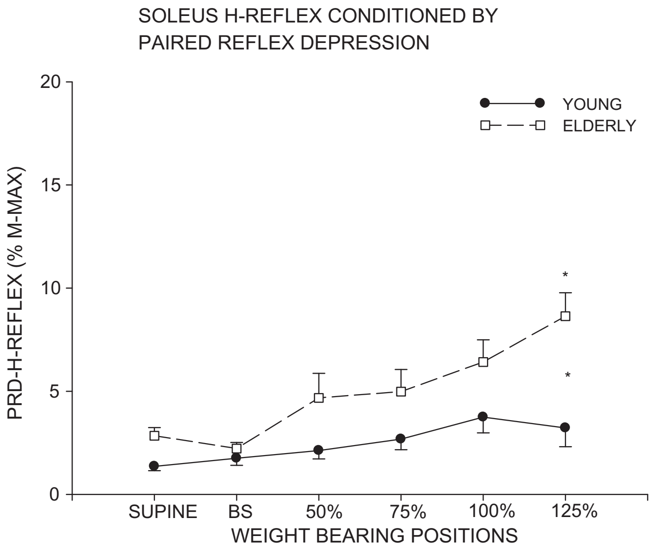

Fig. 5. Soleus H-reflex conditioned by paired reflex depression (PRD). Elderly subjects showed significantly less depression of the test H-reflex during the standing 125% weight bearing condition. In this condition the elderly subjects also had significantly less depression than the young subjects. Error bars denote the standard error of the mean.

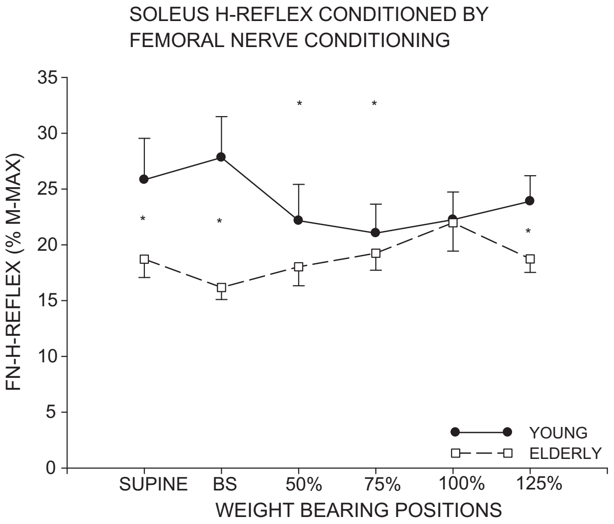

Fig. 6. Soleus H-reflex conditioned by femoral nerve conditioning (FN-H-reflex). Young subjects displayed less facilitation in the 50% and 75% weight bearing conditions compared with the supine condition, whereas no change in facilitation was found for the elderly group. Error bars denote the standard error of the mean.

required to assist other lower limb muscles in maintaining balance and postural stability. The SOL is a relatively homogeneous muscle with respect to slow twitch motor units (Fladby and Jansen, 1990; Proske and Waite, 1974), and the motor axons of this muscle could be preserved without substantial collateral reinnervation in the elderly subjects, regardless of a loss of strength and deterioration of contractile properties (Dalton et al., 2008). In contrast, it was not necessary for the young subjects to increase SOL activity as they have enough strength provided by other muscles (such as MG), and this may enable them to use a better motor skill to stabilise the centre of mass in the body.

Based on the interpretation of the bEMG results it is important to consider the methods used to compare conditions and age groups. It would be preferable to normalise the EMG signals from the muscles to their maximum values obtained from a maximal force contraction. However, this would not have been reliable assessment of maximal EMG activity considering the difficulty in isolating plantar flexion and not compensating with other actions such as knee extension. As such, bEMG during the different WB conditions was normalised to bEMG in the supine condition as this condition provided the most stable signal for a baseline measurement.

4.2. H-reflex protocols during WB conditions

Prior to discussing the results of the conditioning H-reflex protocols used in the present study, it is important to mention the effect of WB on other spinal pathways and circuitry such as group II afferents from the muscle spindle and group Ib afferents from the Golgi-tendon organ. For instance, it has been suggested that input from group II afferents contributes to the control of upright postural balance more than input from group Ia afferents. Marchand-Pauvert et al. (2005) observed that standing with a slight backward or forward lean, causing co-contraction of heteronymous muscles such as TA and RF, preferentially excited the group II afferents. However, the design of the present protocol may not have caused sufficient group II excitation, even during the 125% WB condition, since the subjects remained upright and did not intentionally lean in any one direction. This is reinforced by the lack of modulation observed in RF and TA bEMG for both elderly and young subjects.

Group Ib inhibition is another mechanism that must be considered relative to these results, particularly since it offsets group Ia excitation, and ultimately the compound excitatory post-synaptic potential at the motoneuron. However, it has been shown that high-threshold motoneurons are most susceptible to Ib inhibition (McNulty et al., 2008); so it is less likely to affect a motor pool such as the SOL which was studied here. Furthermore, Faist et al. (2006) reported that Ib inhibition was minimal when load-bearing for both standing and supine positions. This is congruent with the present results where bEMG was greater when the percentage of WB was progressively increased.

Specific to reflex modulation, significant differences in H/M-max were observed between young and elderly subjects across the WB conditions. The H/M-max ratio actually decreased from supine to WB in young subjects while it increased with WB in elderly. However, these results must be taken in context since it has been reported that the ratio of H-max to M-max decreases with ageing due to the decrease in H-max outpacing that of M-max (Kido et al., 2004). The motor response evoked by an electrical percutaneous stimulation appears sooner than the H-reflex response in the recruitment curve in elderly (Maffiuletti et al., 2000; Scaglioni et al., 2003; Tsuruike et al., 2006), which indicates that the diameter of afferent fibres have deteriorated to the point where there is a compression of axon sizes and the concurrent activation of motor axonal fibres and Ia afferent fibres (Pierrot-Deseilligny and Mazevet, 2000). Consequently, it is hypothesised that the increase in H/M-max in elderly with WB is a result of the ratio being small in the supine condition. As the elderly group transitions to standing and increased WB more stability is required, and this is accomplished by increasing supraspinal motor drive, as evidenced by the change in SOL bEMG activity. Alternatively, in young group the H/M-max ratio is higher at baseline (supine), and to prevent instability when standing and WB due to too much afferent activity, the ratio of H/M-max is decreased. These results demonstrate a neural adaptation in elderly that increases stability and appears to counteract the negative consequences of ageing.

An important consideration based on the smaller H/M-max in the elderly subjects lying supine is that the stimulation intensity used in the study was similar relative to each age group. If H-max is much smaller relative to M-max in elderly as compared to young subjects, then a stimulation intensity of 15% of M-max would result in a larger afferent volley to the motor pool. However, the mean control H-reflex size, relative to M-max, was 18.2% for young subjects and 15.4% for elderly across all of the conditions. Alternatively, the mean control H-reflex size, relative to H-max, was 32.6% for the young group and 42.0% for the elderly. As confirmed by these data, setting test H-reflex size relative to H-max would have been inappropriate. Even with setting both groups' stimulation intensity relative to M-max, the test H-reflexes still ranged from 25% to 50% of H-max on the upsloping portion of the recruitment curve, which indicated there were no saturation effects and minimal cancellation from antidromic collision (Crone et al., 1990).

It is interesting to note that the increase in SOL H-max was associated with a corresponding increase in bEMG activity as WB increased in the elderly subjects. This indicates that reflex gain, defined as the change in the H-reflex relative to the change in the bEMG activity (Angulo-Kinzler et al., 1998), remained relatively constant when WB (see Table 1). In contrast, reflex gain was significantly lower when the elderly were in the supine condition compared to all of the WB conditions. There was no association between H-max and the corresponding bEMG with increased WB in the young group. In this case, there may be other spinal mechanisms causing the dissociation between naturally occurring drive to the motoneurons and the H-reflex during standing (Earles et al., 2001). This may be due to an increase in vestibulospinal inputs to the first-order PAD interneurons, resulting in a smaller compound excitatory postsynaptic potential and subsequent H-reflex. Alternatively, the first-order interneurons are turned off other interneurons receiving inputs from the corticospinal tract.

4.3. Ongoing presynaptic inhibition

The FN-H-reflex did not change across WB conditions in the elderly group, whereas the young subjects significantly increased the FN-H-reflex with additional WB. Morita et al. (1995) pointed out that presynaptic inhibition progressively increases with ageing, which could be an adaptation prompted by other changes in the nervous system. However, the FN-H-reflex was evoked when the subjects sat on a chair with the foot at rest. It still cannot be concluded, based on one static position, whether the dynamic modulation of presynaptic inhibition on heteronymous Ia afferents is increased with ageing. Elderly subjects have been shown to have less modulation of the FN-H-reflex in both supine and standing positions (Koceja and Mynark, 2000). In contrast, young subjects show significant facilitation in the FN-H-reflex while supine, and no significant facilitation when standing (indicating more ongoing presynaptic inhibition in standing). These results illustrate the ability of young subjects to modulate their descending tonic presynaptic inhibition imposed on the Ia afferents of FN from non-WB to WB, an adaptive process not present in the elderly (Hultborn et al., 1987).

4.4. Paired-reflex depression

The two age groups displayed differential modulation of the activation history-dependent PRD-H-reflex across the WB conditions as well. The depression observed in the test H-reflex when it is preceded by a control H-reflex only 80 ms prior has been attributed to refractoriness from the afterhyperpolarisation phase, and/or the depletion of neurotransmitters at the Ia terminals (Stein et al., 2007; Trimble et al., 2000). However, PRD is substantially reduced during voluntary contractions (Hultborn et al., 1996; Trimble et al., 2000). PRD is further minimised when standing versus being seated with the same level of muscle contraction (Stein et al., 2007). In the present study, the level of SOL bEMG was so great in the 125% WB condition (144%), compared with the supine condition, that it was likely that the corticospinal input enhanced the net excitability of SOL motoneuron pool and thus eliminated the effect of PRD.

4.5. H/M-max with equivalent WB and different positions

The experiments were designed such that the BS condition and standing 50% WB condition required similar support of WB. Although theoretically the bEMG should be similar, slight differences were observed in both age groups (Fig. 4). Furthermore, there was a significant interaction between age group and condition for H/M-max (BS and 50%WB conditions, Fig. 5). The increase of H/M-max in the elderly group from the BS condition to the standing 50%WB condition was significant and accompanied by a slight increase in SOL bEMG activity. Based on our overall results it is hypothesised that H/M-max is more responsive to background muscle activation level in elderly, and by body position in young subjects. The dissociation between age groups is attributed to the difference in relative supraspinal inputs between age groups. In the elderly group, input from the vestibulospinal tract is insufficient to mediate ongoing presynaptic inhibition of the Ia afferent connection to the motoneuron. This inference is made based on the results of the present study where vestibular activity was presumed different in the BS and 50% standing conditions, while corticospinal tract activity was controlled by the WB demands.

In conclusion, young subjects and elderly subjects respond to changes in body position and WB differently. The strategy employed by both age groups included increasing activation of the medial gastrocnemius muscle in response to additional WB, though the elderly subjects displayed concurrent increases in SOL muscle activity. Presumably, the change in SOL activation evoked by Ia afferents was due to the decline in vestibulospinal input to first-order PAD interneurons in the elderly. Additionally, the elderly subjects exhibited an increase in H/M-max with greater WB, while less segmental control was observed based on the lack of facilitation with FN conditioning. Finally, the PRD-H-reflex in the SOL progressively increased as body loading increased in the elderly, matching the corresponding levels of background activity in the SOL. Although there is a progressive physiological consequence of the ageing process, the results of the present study suggest that there are also some compensatory adaptations to help maintain upright stance with WB in elderly. The adaptations may not present an optimal energetic strategy for postural control (e.g. co-activation of SOL and MG), but at the least they might be a first line of defence against losing balance and falling.

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