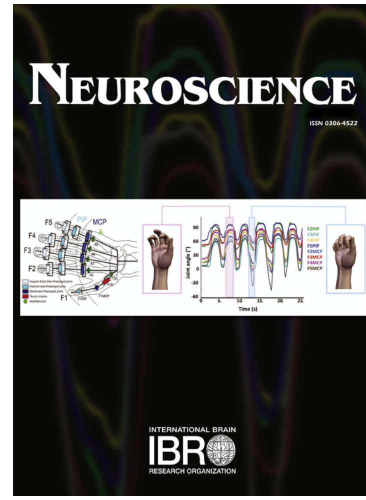


Proprioceptive acuity predicts muscle co-contraction of the tibalis anterior and gastrocnemius medialis in older adults' dynamic postural control

Chesney E. Craig, Daniel J. Goble, Michail Doumas

PII: S0306-4522(16)00176-7
DOI: http://dx.doi.org/10.1016/j.neuroscience.2016.02.036
Reference: NSC 16926

To appear in: *Neuroscience*

Accepted Date: 16 February 2016

Proprioceptive acuity predicts muscle co-contraction of the tibalis anterior and gastrocnemius medialis in older adults' dynamic postural control

Chesney E. Craig[a], Daniel J. Goble[b] & Michail Doumas[c]

[a] Department of Psychology, Queen's University Belfast, Belfast BT, UK, ccraig25@qub.ac.uk

[b] School of Exercise & Nutritional Sciences, San Diego State University, San Diego 92101, USA, dgoble@mail.sdsu.edu

[c] Department of Psychology, Queen's University Belfast, Belfast BT, UK, m.doumas@qub.ac.uk

Corresponding author: Chesney Craig

Rm LG.511, School of Psychology, Queen's University Belfast, David Keir Building, 18-30 Malone Road, Belfast, BT9 5BP

E: ccraig25@qub.ac.uk T: +44 (0)28 9097 4558 F: +44 (0)28 9097 5486

List of Abbreviations

ANOVA: analysis of variance

AP: anterior-posterior

CCI: co-contraction index(es)

COP: centre of pressure

EMG: electromyography

GM: gastrocnemius medialis

MVCs: maximum voluntary contractions

RVCs: reference voluntary contractions

TA: tibalis anterior

5XSTS: Five Times Sit to Stand

Abstract

Older adults use a different muscle strategy to cope with postural instability, in which they 'co-contract' the muscles around the ankle joint. It has been suggested that this is a compensatory response to age-related proprioceptive decline however this view has never been assessed directly. The current study investigated the association between proprioceptive acuity and muscle co-contraction in older adults. We compared muscle activity, by recording surface EMG from the bilateral tibalis anterior and gastrocnemius medialis muscles, in young (aged 18-34) and older adults (aged 65-82) during postural assessment on a fixed and sway-referenced surface at age-equivalent levels of sway. We performed correlations between muscle activity and proprioceptive acuity, which was assessed using an active contralateral matching task. Despite successfully inducing similar levels of sway in the two age groups, older adults still showed higher muscle co-contraction. A stepwise regression analysis showed that proprioceptive acuity measured using variable error was the best predictor of muscle co-contraction in older adults. However, despite suggestions from previous research, proprioceptive error and muscle co-contraction were negatively correlated in older adults, suggesting that better proprioceptive acuity predicts more co-contraction. Overall, these results suggest that although muscle co-contraction may be an age-specific strategy used by older adults, it is not to compensate for age-related proprioceptive deficits.

Keywords: posture, aging, muscular coactivation, proprioception, EMG

Postural control is a complex neural process that requires sensory information from visual, proprioceptive and vestibular systems, all of which are subject to age-related decline (Horak et al., 1989). Decline in proprioceptive acuity is particularly relevant in this task, as this is the sensory modality with the greatest contribution in postural control (Peterka, 2002). Accordingly, a breadth of research has shown an association between low proprioceptive acuity and reduced postural control in older adults (Lord et al., 1991; McChesney and Woollacott, 2000; Madhavan and Shields, 2005; Goble et al., 2009). Such findings extend to mobility in general, with studies suggesting that proprioception is associated with functional performance, as assessed in tasks such as 'Timed up and go' and stairs ascent/descent in older adults (Hurley et al., 1998). Older adults also demonstrate changes in the proprioceptive strategy used. For example, similar to patients with lower back pain, older adults show reduced reliance on lower back proprioceptive information and increased reliance on ankle joint information (Brumagne et al., 2004). Brumagne et al. (2004) state that it is unclear whether the proprioceptive strategy changes or back pain are witnessed first in patients however, so this potentially maladaptive proprioceptive alteration could explain older adults' susceptibility to spinal pain. Additionally, it has been suggested that proprioceptive decline could lead to abnormal joint biomechanics during gait which could eventually lead to joint degeneration (Skinner, 1993). More importantly, lower limb proprioceptive acuity has been shown to be predictive of fall accidents (Lord et al., 1999).

In order to avoid postural instability and falls, the aging body is likely to develop compensatory strategies, for instance when exposed to changes in their base of support, older adults 'co-contract' or co-activate the muscles around the ankle joint (Laughton et al., 2003; Benjuya et al., 2004; Nagai et al., 2011, 2013; Nelson-Wong et al., 2012). Muscle co-contraction refers to the simultaneous contraction of the agonist and antagonist muscle about a joint, which is often associated with stiffening of the joint (Melzer et al., 2001; Tucker et al., 2008; Cenciarini et al., 2010). However, the efficacy of this strategy in terms of postural control appears to be context-dependent (Chambers and Cham, 2007a; Nagai et al., 2013). In terms of the lower limbs, muscle co-contraction has been interpreted as a compensatory strategy for age-related decline in sensory acuity, especially proprioceptive acuity (Laughton et al., 2003; Benjuya et al., 2004; Madhavan and Shields, 2005), however the relationship between lower limb muscle co-contraction and proprioception has not been directly assessed by previous studies.

Age-related differences in lower limb muscle activation patterns in postural control tasks have been assessed by Benjuya et al. (2004). They showed that, in an upright standing task that was originally performed with eyes open, when visual information was withdrawn, young adults increased their postural sway more than older adults. This age difference in postural sway increase was accompanied by an age difference in muscle activation patterns, with older adults employing a different strategy from young adults whereby they co-contracted their lower leg muscles. The authors suggested that young adults increased postural sway in an attempt to gain more proprioceptive input from the lower limb muscles when one of the sources of sensory information (vision) was removed, whereas older adults did not increase their postural sway to the same degree, either due to an inability to utilise the additional lower limb proprioceptive input or a fear of reaching their limits of stability. Instead, they employed a muscle co-contraction strategy to prevent a further increase in postural sway by increasing the stiffness of the ankle joint. Benjuya et al (2004) suggest that this stiffening is a compensatory response for degraded proprioceptive input. Alternatively, other authors have suggested that co-contraction may compensate for proprioceptive deficits by *increasing* proprioceptive information from muscle spindles (Laughton et al., 2003;

Madhavan and Shields, 2005). Regardless of whether muscle co-contraction is employed in contrast to proprioceptive sense or in order to increase proprioceptive information, both of these arguments suggest that older adults who show reduced proprioceptive acuity would also show higher muscle co-contraction.

It is unclear how effective muscle co-contraction is as a compensatory postural strategy. On the one hand, it is also used by young adults when they are directly asked to minimize postural sway as much as possible, especially during difficult postural tasks (Reynolds, 2010). Similarly, both young and older adults increase muscle co-contraction in anticipation of a postural challenge, such as walking on a known slippery surface, and higher baseline co-contraction during walking on an unknown slippery surface is associated with less severe slips (Chambers and Cham, 2007b). This supports the proposition that it may be an adaptive strategy during postural instability. Additionally, evidence of its use in young adults suggests that it is not an age-specific strategy shift but may be a general strategy for larger postural challenges (Chambers and Cham, 2007b). Consequently, older adults may show higher muscle co-contraction as a result of their greater postural instability compared with young adults, as opposed to an effect of age.

Despite some evidence showing that muscle co-contraction can be an effective strategy, alternative evidence suggests that it is often a maladaptive strategy. For example, co-contraction is not associated with decreased postural sway in young adults (Reynolds, 2010). In contrast, evidence suggests that co-contraction is typically associated with increased postural sway in both young (Warnica et al., 2014) and older adults (Laughton et al., 2003; Nagai et al., 2011). For example, both Laughton et al. (2003) and Nagai et al. (2011) found that older adults demonstrated significantly higher levels of co-contraction in the lower limb muscles compared with young adults, and this was correlated with their postural sway during quiet stance. Additionally, Nagai et al. (2011) extended this association to functional reach distance. Although neither of these studies can infer whether muscle co-contraction precluded postural sway due to the correlative nature of the findings,Warnica et al.'s (2014) study provided further insight into this issue by asking young adults to actively co-contract the muscles around the ankle joint. Results showed that higher muscle co-contraction was associated with increased sway amplitude and frequency. The authors suggest that this may occur as the increased ankle stiffness may degrade proprioceptive feedback and thus participants turn to other postural strategies, such as a hip strategy. In line with this, other authors (Tucker et al., 2008) have suggested that the increase in ankle rigidity associated with co-contraction may impede adaptive responses to postural perturbations, which could explain the associations between higher co-contraction and a tendency to fall (Ho and Bendrups, 2002) and increased fall risk (Nelson-Wong et al., 2012). This suggests that in everyday life muscle co-contraction is an ineffective and risky postural strategy.

Together, evidence suggests that muscle co-contraction in postural control is more likely to be maladaptive. This observation raises the question: why have older adults developed a bias towards this strategy? One possibility is that co-contraction may result from age-related decline in proprioceptive acuity (Laughton et al., 2003; Benjuya et al., 2004; Madhavan and Shields, 2005), however little is known about the relationship between the two. A link between proprioceptive acuity and postural performance in older adults has been demonstrated by previous studies (Lord et al., 1991; Gauchard et al., 1999; McChesney and Woollacott, 2000; Madhavan and Shields, 2005). However, little is known about the relationship between proprioceptive acuity and lower limb muscle co-contraction during upright stance. Madhavan and Shields (2005) assessed the relationship between proprioceptive acuity and balance measures, such as standing/single-limb standing with eyes open/closed in young and older adults. Proprioceptive acuity was assessed using a passive ('dynamic') position sense task, during which the authors reported significant use of muscle co-contraction in the lower leg. However, the relationships between muscle co-contraction, proprioceptive acuity and balance measures were not examined.

The main aim of the present study was to assess the relationship between proprioceptive acuity and lower limb muscle co-contraction in young and older adults' postural control. The studies reviewed above suggest that muscle co-contraction may be a compensatory strategy for proprioceptive acuity decline, thus, co-contraction and proprioceptive error should be positively correlated. However, as this prediction is solely based on interpretations and indirect evidence, and we cannot predict the causal direction of the relationship between these two variables, we performed exploratory correlations, which included the possibility of a negative correlation. Additionally, as previous studies have been unable to elucidate whether co-contraction is an age-specific strategy or merely a response to high instability, the present study employed a postural manipulation with the aim of making the task more difficult for young adults and thus inducing equivalent amounts of postural sway in young and older adults. This manipulation ensured that any age-differences in muscle activation would be solely due to age-specific muscle activation patterns, rather than differences in sway. Co-contraction was assessed by measuring electromyographic (EMG) activity of the tibalis anterior (TA) and gastrocnemius medialis (GM) muscles.

2. Experimental Procedures

2.1. Participants

Sixteen young and sixteen older adults volunteered to participate in the present study. Participants were excluded if they had a history of any medical conditions or medication use that could impair postural performance. Our key exclusion criteria were: fall accidents within the last 6 months, hip replacement, Parkinson's disease, the use of tricyclic antidepressants or tranquilisers, polyneuropathy, stroke, paralysis, dizziness, osteoarthritis and the use of orthopaedic shoes. Participants were also screened for ADHD, diabetes, epilepsy, depression, cardiac arrhythmias, heart attack in the last year, hyper-/hypotension, osteoporosis and operations in the past year, with further questioning used to determine whether these criteria necessitated participant exclusion. Leg dominance was identified by asking participants which was their preferred foot to kick a ball (Peters, 1988). All older adults scored 25+ on the *Mini-Mental State Examination (MMSE*) and were independent, as assessed by the *Katz Basic Activities of Daily Living* test (Katz et al., 1963) and the *Instrumental Activities of Daily Living Scale* (Lawton and Brody, 1969). Additionally, all older adults completed the *Rapid Assessment of Physical Activity* (RAPA, available from http://depts.washington.edu/hprc/rapa) and *Five Times Sit-to-Stand Test* (5XSST). Written informed consent was obtained from all participants in line with the 1964 Declaration of Helsinki and the study was approved by the School of Psychology's Ethics Committee. Participant characteristics are summarised in Table 1.

Table 1. *Sample means and standard deviations (in parentheses)*

	Young Adults	Older Adults
Age	22.69 (4.14)	70.5 (3.91)
Sex (male, female)	8, 8	5, 11
Height (cm)	173.94 (10.78)	166.13 (11.67) *
Weight (kg)	69.88 (11.13)	69.25 (14.81)
BMI	22.98 (2.00)	25.04 (3.89)
Footedness (right, left)	13, 3	14, 2
MMSE	N/A	29.05 (1.06)

ADL	N/A	5 (1.46)
IADL	N/A	8 (0)
RAPA	N/A	8 (0)

Note: * $p < .05$. BMI = body mass index; MMSE = Mini Mental State Examination; ADL = Katz Basic Activities of Daily Living; IADL = Instrumental Activities of Daily Living; RAPA = Rapid Assessment of Physical Activity

2.2. Apparatus and Tasks

2.2.1. Proprioceptive Acuity Assessment

Proprioceptive acuity was assessed using an active contralateral concurrent joint position sense task, during which participants were asked to match the joint angle prescribed by their dominant foot by moving their non-dominant foot at a self-selected speed. This was achieved using a custom-made foot support (Figure 1), similar to that used by Boisgontier and Nougier (2013). The device consisted of two rotating light-weight polymer paddles, which were attached to precision linear potentiometers which served as ankle position transducers after converting the voltage output signal to angular displacement using software custom-written in MATLAB. This resulted in an angle resolution of 0.0001^{o}.

-Insert Figure 1 about here-

Participants were seated in a height-adjustable chair, with their hips at a 90^{o} angle and their feet strapped comfortably to the pedals. The reference (dominant) foot was placed on a fixed support at one of two angles: 10^{o} or 15^{o} above horizontal. During testing, participants wore a blindfold and headphones and held a push-button in their dominant hand, which they were instructed to press whenever they believed the matching foot had reached the same angle as the fixed reference foot. Signals from the potentiometers and push-button were recorded at 1000Hz. The matching foot was placed at a starting angle of 10^{o} below horizontal for all trials.

2.2.2. Postural Assessment

Postural control was assessed using a Smart Balance Master (NeuroCom International, Inc., Clackamas, OR, USA), which employs an 18"x18" dual force plate. The system records vertical forces exerted on the force plate at a sampling frequency of 100Hz, from which the centre of pressure (COP) trajectories in both medio-lateral (COP-X) and antero-posterior (COP-Y) directions can be derived. Data were collected over two 3-minute blocks, the first of which employed a stable support, followed by a sway-referenced-support block. Sway-referencing was induced using a servo-controlled motor, which introduced platform tilt in the sagittal plane about the ankle joint axis, in proportion to the participant's expected centre of mass sway angle (Nashner et al., 1982). Centre of mass was approximated from the immediate COP-Y trajectory using a proprietary second-order Butterworth low-pass filter with a cut-off frequency of 0.85 Hz (Nashner et al., 1982; Doumas and Krampe, 2010). Delays in surface response time due to the electro-mechanical delay of the system or the filter (Clark and Riley, 2007) amount to a maximum of ~31ms.

The mechanical compliance of the system to postural sway was determined by the pre-selected *gain factor* of the test. A typical gain factor of 1.0 results in exact coupling between COP-Y movement and the degree of platform tilt. This prevents any change in ankle joint angle, thus near-eliminating a key proprioceptive signal used in postural control (Peterka and Loughlin, 2004). Gain factors larger than 1.0 result in a more compliant support surface, resulting in greater surface rotations and thus greater postural sway (Clark and Riley, 2007). The current study utilized distinct gain factors for each age group; a gain setting of 1.0

for older adults and 1.6 for young adults. This was determined from previous pilot testing and using evidence from previous studies (Clark and Riley, 2007; Doumas et al., 2008; Doumas and Krampe, 2015). The aim of using distinct gain levels for each group was to achieve equivalent levels of postural sway in the two age groups in order to examine whether muscle co-contraction results from increased postural sway or is an age-specific response. A blindfold and safety harness were worn during all experimental blocks. The safety harness did not restrict movements.

2.2.3. EMG Recordings

Co-contraction was measured by recording surface electromyography (EMG) signals from the bilateral tibalis anterior (TA) and gastrocnemius medialis (GM) muscles during the postural control task. Surface EMG was recorded using disposable Ag-AgCl electrodes (Cleartrace, CONMED, Utica, NY, USA), with an inter-electrode distance of 3cm and the ground electrode placed on the right knee joint. The EMG signal was pre-amplified at a gain of 2000 using a differential amplifier (EMG100C, Biopac Systems, Inc., Santa Barbara, CA). The signal was initially band-pass filtered at 1.0-500Hz and sampled at 4 kHz. EMG data was then normalised in relation to the maximum values recorded during three reference voluntary contractions from each muscle.

2.3. Procedure

Testing commenced by recording three maximum voluntary contractions (MVCs) from each TA muscle during seated maximal isometric dorsiflexion of the ankle, with the knee flexed at 90^{o}. As discussed by Nelson-Wong et al. (2012), only reference voluntary contractions (RVCs) could be reliably obtained from each GM muscle. This was achieved using three replications of a standing single leg heel raise on each leg. Then, the active proprioceptive matching task commenced, during which participants were asked to actively move their non-dominant foot to match the position of their stable dominant (reference) foot as accurately as possible. Participants were instructed to press the push-button to indicate whenever they believed the matching foot had reached the same angle as their reference foot, which could be fixed at one of two positions. Participants were asked to initiate movement after the onset of an audio beep, which was played through the headphones. Initial practice trials were given for each target angle, during which participants were given feedback about the magnitude and direction of their error in degrees. In line with Verschueren et al. (2002), practice trials were given until participants pressed within 2^{o} of the target during 2 consecutive trials. Following practice at both target angles, the experimental trials commenced. Participants completed 5 trials in each target angle (10^{o}/15^{o}) without feedback. The target angle order was counterbalanced. EMG activity was recorded from the bilateral tibalis anterior and gastrocnemius medialis muscles during both the proprioceptive matching and postural control tasks. EMG was assessed during the proprioceptive matching task to ensure the reference foot was relaxed.

The postural control task was assessed at the end of each session, during which participants were instructed to stand as still as possible. Participants were given three 1-minute practice trials of increasing difficulty before testing commenced; the first at a low gain (0.4 for older and 1.0 for young adults) with eyes open, followed by low gain eyes closed and finally high gain eyes closed (1.0 for older and 1.6 for young adults), which was the same setting used in the experimental trials. An extra practice of high gain eyes closed was given if a loss of stability occurred. Following this, the experimental trials commenced, starting with 3 minutes on a stable platform, followed by a 3-minute sway-referenced trial.

During testing, in the event of a loss of stability, the platform was immediately stopped and the trial was repeated. Two such cases were recorded, one in the young and one in the older adult group. Additionally, older adults completed the Mini-Mental State Examination (MMSE) and Five Times Sit to Stand test (5XSTS) at the start of the session. The 5XSTS was performed in a chair that was 39cm high. In line with standardised protocol, the test commenced with the participant's back against the chair and their arms folded across their chest (Guralnik et al., 1994). Participants were instructed "I want you to stand up and sit down 5 times as quickly as you can when I say 'Go'". Participants were told to stand up fully between each repetition and not to touch the back of the chair whilst returning to the sitting position. The timer started on the statement of the 'Go' signal and was stopped as soon as the buttocks touched the chair after the 5th repetition.

2.4. Data Analysis

Proprioceptive acuity was expressed in terms of absolute error, calculated as the angular disparity between the matching and reference foot positions and variable error, calculated as the standard deviation of error across trials. COP-Y data, reflecting COP displacement in the Anterior-Posterior (AP) direction was low-pass filtered at 4Hz using a 4th order Butterworth filter. Postural performance was initially assessed using the average AP path length of the COP for each condition. This was followed up with a 30-s time window analysis, in order to examine how path length evolved over time in each block.

All raw EMG data (including RVCs) was full-wave rectified and linear envelopes were created using a 2nd order Butterworth filter with a cut-off frequency of 4Hz. Experimental trials were then normalised as a percentage of each participant's peak RVCs. Co-contraction indexes (CCI) were calculated using Equation 1, which was derived from an equation commonly used in the literature (Lewek et al., 2004; Nelson-Wong et al., 2012). This equation enables the quantification of CCI without the identification of agonist and antagonist muscle pairs.

Equation 1

$$\mathrm{CCI}(N) = \mathrm{avg}\left(\frac{\mathrm{EMG}_{\mathrm{low}_i}}{\mathrm{EMG}_{\mathrm{high}_i}}\right)\left(\mathrm{EMG}_{\mathrm{low}_i} + \mathrm{EMG}_{\mathrm{high}_i}\right)$$

In Equation 1, N is the selected time window, $\mathrm{EMG}_{\mathrm{low}}$is the lower EMG value from the two muscles (TA and GM) at the ith data point and $\mathrm{EMG}_{\mathrm{high}}$ is the higher EMG value at the ith data point. CCI was initially calculated for 1-s time windows (N), which included 4000 data points (i) in each, for the duration of each postural assessment block (3-minutes). For each ith point, the ratio of the low over the high value from each muscle pair was calculated and then multiplied by the sum of both values. Due to the longer duration of our CCI assessment compared with previous studies (Lewek et al., 2004; Nelson-Wong et al., 2012), the mean CCI value of these products was calculated, rather than the overall sum. This demonstrated the same pattern as the summated data but resulted in output values more similar to other muscle co-contraction studies, such as Benjuya et al. (2004). As there was no significant difference in CCI values from both legs, activity was averaged across both. The 1-s mean CCI values were then used to assess the overall mean CCI value for each 30s of the overall data acquisition block.

2.5. Statistical Analysis

Age differences in absolute and variable error in proprioceptive performance were assessed using a 2-way mixed ANOVA, with target angle (10^{o}/15^{o}) as the within-subjects factor and age group as the between-subjects factor. Similarly, AP path length and CCI were assessed using 3-way mixed ANOVAs, with support condition (stable/sway-referenced) and time window (per 30s) as within- and age group as between-subjects factors. All significant effects and interactions were explored further using two-way ANOVAs split by age group and Bonferroni post hoc tests. Two-tailed Pearson product-moment correlations were used to explore the relationship between each of the three dependent variables (proprioception: absolute and variable error; muscle co-contraction: CCI; and posture: AP path length). Two- rather than one-tailed correlations were performed because our main hypothesis was based on suggestions and interpretations from previous studies regarding the relationship between muscle co-contraction and proprioceptive acuity, rather than direct evidence. Thus, we could not exclude the possibility of a correlation in the opposite direction to the one hypothesised. A linear regression analysis was run to examine the key predictors of muscle co-contraction.

3. Results

3.1. 5XSTS

Older adults showed a mean time of 11.08s with a standard deviation of 1.73 on the 5XSTS. These times were comparable with those typically found in community-dwelling older adults of this age range – 11.4s for 60-69, 12.6s for 70-79 and 14.8s for 80-89 (Bohannon, 2006a).

3.2. Proprioceptive acuity

Figure 2A depicts the mean absolute error scores in young and older adults for both target angles. There was no main effect of target angle (p= .54) or age group (p= .63) and no interactions (p= .70). Similar results were found for variable error (Fig. 2B), with no main effect of age (p= .70). However, as indicated in Figure 2B there was a reliable main effect of target angle F(1,30) = 6.81, p=.014, $\eta_p^2 = .19$ followed by a target angle by age interaction

F(1,30) = 9.20, p=.005, $\eta_p^2 = .24$, whereby the effect of target angle was only significant for the older group (t(15) = 3.6, p=.003), for whom error was significantly higher during the 10° target (M= 1.93) compared with the 15° target (M= 1.24).

-Insert Figure 2 about here-

3.3. Postural sway

Figure 3A depicts mean anterior-posterior (AP) path length in all conditions for both young and older adults. The sway reference manipulation induced an increase in AP path length compared with the stable condition as shown by a main effect of condition F(1,30) = 190.07, p<.001, $\eta_p^2 = .86$ but no effect of age group (p= .59) or age by condition interaction (p= .56). This suggests that our goal of inducing similar levels of postural sway in the two groups was successful.

-Inset Figure 3 about here-

The same analysis was performed for AP path length when the 3-min trial was divided in 30-s time windows (Figure 3B & C) to examine how AP path length changes over time. This time period was chosen as it is the typical length of a posturography trial. Data depicted in Figure 3B (young) and C (older adults) show that the two groups performed similarly across both conditions, however, the change in sway over time was different in young and older adults as shown by a main effect of window F(5,150) = 16.09, p<.001, $\eta_p^2 = .35$ followed by a significant 3-way interaction between condition, window and age F(5,150) = 4.01, p=.002, $\eta_p^2 = .12$. Examination of the simple effects per posture condition was then performed. In the stable condition the analysis revealed a main effect of window

F(5,150) = 2.82, p=.018, $\eta_p^2 = .09$, but no main effect of age or age by window interaction. However, in the sway-referenced condition results showed a main effect of window F(5,150) = 14.54, p<.001, $\eta_p^2 = .33$, and a window by age interaction F(5,150) = 4.58, p=.001, $\eta_p^2 = .13$. Bonferroni post-hoc analyses showed that there was only a significant difference between windows 1 and 2 for young adults (p=.009), suggesting their level of postural sway was quite consistent overall, whereas older adults showed a significant difference between window 1 and all following windows, with postural sway gradually decreasing up to window 4 (p=.007-.001) and then increasing slightly (p=.008) but always remaining below the initial postural sway levels of the first 30 seconds.

3.4. Age differences in Muscle Co-contraction (CCI)

The CCI (Figure 3D) data also showed greater CCI in the sway referenced compared with the stable condition as shown by a main effect of condition F(1,30) =57.48, p<.001, $\eta_p^2 = .66$. However, in this measure, there was also a main effect of age F(1,30) = 4.71, p=.038, $\eta_p^2 = .14$, whereby older adults employed greater levels of muscle co-contraction in both conditions (stable M= 3.64, sway-referenced M= 6.53) compared with young adults (stable M= 2.87, sway-referenced M= 4.90). Additionally, examination of CCI across 30-s time windows (Figure 3E & F), showed a main effect of window F(3.51,105.36) = 6.32, p<.001, $\eta_p^2 = .17$ and a condition by window interaction F(3.31,99.22) = 5.32, p=.001, $\eta_p^2 = .15$. Simple effects analysis revealed a significant effect of window during sway-referencing only F(3.36,100.69) =6.62, p<.001, $\eta_p^2 = .18$, within which CCI significantly decreased from window 1 to 2 (p= .001) and then plateaued.

3.5. Association between muscle co-contraction and proprioceptive acuity

Pearson product-moment correlations demonstrated large significant *negative* associations between proprioceptive variable error values and CCI values during sway-referencing (r= -.69, p= .003) conditions for older adults (Figure 4), which remained significant after controlling for age and 5XSTS score (r= -.67, p= .009). Neither age group showed significant correlations between either proprioceptive acuity measure and CCI during stable conditions (p= .13 - .79). Additionally, only older adults showed a positive relationship between their CCI levels during stable conditions and their CCI levels during sway-referencing (r= .56, p= .025). Older adults also showed a positive correlation between CCI levels and AP path length during the stable condition (r= .60, p= .015). There was no correlation between neither CCI nor proprioceptive measures and path length during sway-referencing for either age group (p= .10 - .38). This lack of correlation remained even when examining path length in the most unstable first 30 second window. The correlation between CCI and path length during stable conditions was lost when examining the first 30 second window only (r= .43, p=.10).

-Insert Figure 4 about here-

A forward stepwise regression model found a significant model, F(2,13) = 12.25, p= .001, in which variable proprioceptive error was the strongest predictor of CCI during sway-referencing, t(13)= -4.12, p=.001, beta = - .673, and absolute proprioceptive error was also a significant predictor, t(13)= -2.61, p=.022, beta = -.427. Together these variables predict 65% of the variance in CCI during the sway-referenced condition. Age, path length and 5XSTS measures were not significant predictors of CCI.

4. Discussion

The main aim of the present study was to investigate whether reduced proprioceptive acuity is predictive of greater muscle co-contraction during postural control in older adults, as hypothesised previously (Laughton et al., 2003; Benjuya et al., 2004; Madhavan and Shields, 2005). We found that proprioceptive acuity was the best predictor of co-contraction in older adults' unstable postural control. However, we found a strong *negative* correlation between proprioceptive variable error and CCI during sway-referencing in older adults. This correlation suggests that older adults who demonstrated better proprioceptive acuity showed higher co-contraction during unstable posture. Additionally, we investigated whether muscle co-contraction is an age-specific strategy shift, as opposed to a sway-induced postural response, by using a paradigm that introduced equivalent levels of postural sway in young and older adults. This paradigm revealed that despite successfully inducing similar levels of postural sway in both age groups, older adults still showed consistently higher levels of co-contraction. Both age groups showed higher co-contraction during the first 30 seconds of sway-referencing, suggesting that muscle co-contraction is a reactive early response to high postural sway levels, however, given that older adults consistently employed higher levels of co-contraction overall, this supports an age-specific bias towards this strategy. Our results emphasise an age-specific co-contraction bias when controlling for the amount of postural sway.

Our findings contradict the recurrent prediction that muscle co-contraction is a compensatory strategy for age-related proprioceptive decline by emphasising that co-contraction is employed more by older adults with good proprioception. We postulate that older adults with greater proprioceptive acuity may show higher co-contraction due to their proficiency at using this sensory channel. Thus, they weight this channel highly and even in stable conditions they use muscle co-contraction to increase proprioceptive information in the absence of visual information. Concurrently, older adults with poor proprioceptive acuity may be less reliant on this channel and instead become more dependent on other sensory channels, such as the vestibular pathway, to maintain postural control (Horak and Hlavacka, 2001). Future work is required to expand on this and explore why these differences in co-contraction may exist in a larger older adult sample. This relationship may be mediated by muscle strength (Butler et al., 2008; Nagai et al., 2011), however, the differences in the current study could not be explained by age or 5XSTS score, which is often used as an indirect measure of lower limb muscle strength (Csuka and McCarty, 1985; Bohannon, 2006b). Alternatively, 5XSTS can also be used to assess postural control and functional mobility (Goldberg et al., 2012), which supports our finding that postural measures could not predict muscle co-contraction.

An alternative explanation could be that older adults with higher proprioceptive acuity may show higher muscle co-contraction as they were more affected by the inaccurate proprioceptive information about body sway induced by sway-referencing, and thus employed this strategy in an attempt to minimise postural sway. However, no associations between proprioceptive acuity and path length during sway-referencing were found. Additionally, the strong association between CCI during sway-referencing and CCI during stable conditions suggests that older adults who show higher co-contraction during sway-referencing also do so during stable conditions, reinstating that a response to sway-referencing cannot be the only cause of this divergent correlation. This nondiscriminant use of muscle co-contraction is in accordance with Benjuya et al.’s (2004) finding that older adults used co-contraction regardless of task difficulty (size of base of support).

It is important to note that despite these suggestions as to why some older adults may employ muscle co-contraction more than others, the current study cannot elucidate cause and effect between the two variables – proprioceptive acuity or muscle co-contraction. Thus, it is possible that rather than explaining co-contraction, this association is caused by high co-contraction leading to improved proprioceptive information from the muscle spindles. However, EMG activity was monitored during the proprioceptive task and no muscle co-contraction was witnessed. Additionally, one would expect that if this was the case then those who showed high co-contraction would also show a larger postural sway response to the proprioceptive manipulations induced by sway-referencing, however the current sample size did not permit such an analysis. This could be investigated in future research by examining differences among a larger older adult sample during a sway-referencing task.

Regardless of why co-contraction is employed, we do not imply that co-contraction is a proficient postural strategy. Conversely, the finding that CCI levels and path length during stable conditions are positively correlated could suggest that muscle co-contraction is a maladaptive strategy that leads to higher postural sway overall. This supports previous literature in young (Warnica et al., 2014) and older adults (Laughton et al., 2003; Nagai et al., 2011). Alternatively, one could argue that co-contraction is a response to postural sway, however, if this was the case, one would expect this correlation to be witnessed early in the block (first 30 seconds) where postural sway is the highest. This was not found. Furthermore, as this was during the stable condition, this cause is unlikely as generally path length was small.

Somewhat surprisingly, the present study found no age differences in proprioceptive acuity. Most other studies that have examined absolute error in lower leg active proprioceptive matching have reported significant age differences (Petrella et al.; Kaplan et al., 1985; Meeuwsen et al., 1993; You, 2005; Goble et al., 2009). However, it is worth noting that only two of these studies examined the ankle joint (Meeuwsen et al., 1993; You, 2005). Other studies examining ankle joint proprioceptive error during active matching have reported no age differences (Deshpande et al., 2003; Boisgontier et al., 2012). Boisgontier et al. (2012) suggest that this may be due to the maintenance of the reference position between trials, which was also the case in the current study. This would concur with previous findings that repetition of trials at the same target (Meeuwsen et al., 1993) and maintaining a stable position for a prolonged period of time without visual feedback (Goble et al., 2010) increases proprioceptive accuracy in older adults, perhaps due to the development of neural representations of the reference limb location. Thus, it is important to acknowledge that our findings might have been different if we had returned the reference foot to an initial start position following each trial. Future studies could benefit from fewer practice trials and the use of an alternative target angle for practice trials compared with experimental trials.

Our study had a number of limitations, including biomechanical differences between our proprioceptive acuity assessment and the postural control task. It is unclear how well the proprioceptive signal generated from our proprioceptive acuity task compares to the signal generated during our postural control task. However, this type of non-weight-bearing joint position sense task is canonical in assessing the relationship between proprioceptive acuity and postural control (Lord et al., 1991; McChesney and Woollacott, 2000; Madhavan and Shields, 2005). Also, the present study only examined one source of somatosensory input. It is known that cutaneous information, such as mechanoreceptor input from the soles of the feet, also plays an important role in postural control (Magnusson et al., 1990) and poor tactile acuity has been associated with falls in older adults (Melzer et al., 2004). Hence, in future studies it would be instructive to assess how tactile acuity interacts with muscle co-contraction use in older adults. Additionally, the contribution of lower limb muscle spindles to proprioceptive acuity could be assessed by utilising tendon vibration during joint position matching, as previously examined by Verschueren et al. (2002). The relationship between reliance on muscle spindle input and employment of co-contraction during postural testing could then be investigated.

Another key limitation of the current study is the lack of assessment of the postural strategy employed. For example, it is widely documented that older adults are more likely to use a hip strategy compared with young adults (Horak and Nashner, 1986), thus proprioceptive acuity in the ankle joint may be less relevant to postural control in older adults compared with young adults. Despite this, it seems unlikely from the current data that older adults were employing a hip strategy compared with young adults, as a hip strategy is typically associated with larger AP COP excursions, yet there were no age differences in AP path length. Additional evidence suggests that older adults show rigid postural strategies in response to perturbations, whereas young adults demonstrate a flexible movement strategy (Wu, 1998). However, this could not be elucidated in the current study as we did not examine the movement of individual body segments. Furthermore, it is possible that different strategies could be employed within the older adult group, for example differences may exist between older adults who show high or low muscle co-contraction, though the current study could not clarify this due to the sample size. The strategy employed could be assessed in future studies by utilising kinematic measures, such as motion capture, and using a larger older adult sample to assess whether differences exist between those who show high muscle co-contraction and those who do not. Another limitation of the present study was the gender bias in the older adult group. Although this is common in ageing research, it would be beneficial in future studies to ensure gender-matching or examine only female participants to avoid any effects of gender differences.

These suggestions are currently implemented in a follow-up study, which will examine the relationship between proprioceptive acuity during active matching and co-contraction during postural adaptation to sway-referencing and postural after-effects. In light of the current results that older adults with better proprioceptive acuity show greater co-contraction during unstable conditions, which we hypothesize may be due to a heavier reliance/weighting on this sensory channel, we predict that these older adults may also show distinct after-effects in response to adaptation to sway-referencing. Such after-effects could have implications on the efficacy of balance training programmes. For example, a recent study showed that an 8-week balance training intervention in nursing home residents resulted in decreased muscle co-contraction during the functional reach task but not during quiet standing or the functional stability boundary task (Nagai et al., 2012). However, our results suggest that intragroup differences in CCI levels may exist which could affect these outcomes. The study did not report whether baseline differences in CCI were examined. Similar decreases in CCI have been reported in a 3-week Tai Chi intervention (Gatts and Woollacott, 2006). The authors argue that this decrease in CCI demonstrates improved neuromuscular responses, which mediates the relationship between Tai Chi training and reduced fall risk in older adults (Wolf et al., 1996; Wolfson et al., 1996). This could also be relevant to studies demonstrating that other types of ‘proprioceptive training’, such as, yoga and ‘soft’ gymnastics can improve performance on dynamic posture tasks (Gauchard et al., 1999).

The present study highlights the need for future studies to examine intragroup differences in proprioceptive acuity at baseline, as these may affect the efficacy of training programmes. Furthermore, if older adults with greater proprioceptive acuity do show higher co-contraction due to a reliance on this channel, future balance training should focus on sensory reweighting techniques that promote the use of accurate sensory channels, rather than overreliance on one specific channel. Future research should also examine the relationship between the postural strategy employed (e.g. rigid/flexible) and muscle co-contraction (Wu, 1998). Perhaps similarly to their flexible movement strategies, young adults are more likely to use flexible co-contraction strategies in different muscle groups. This could be investigated by assessing EMG activity in various muscle groups, including proximal muscles, such as the trunk muscles, during postural assessment with motion capture to examine differential body segment movement in young and older adults.

4.1. Conclusions

The present study has demonstrated an age-specific bias in muscle co-contraction levels in older adults during a postural task that induced similar levels of postural sway in young and older adults. Importantly, our results contradicted the previous assumption that muscle co-contraction is a strategic bias employed by older adults to overcome their proprioceptive deficits. Rather, co-contraction was used more during unstable conditions by older adults with better proprioceptive acuity. This may be due to different sensory weightings in older adults who do and who do not show age-related proprioceptive decline. Future work is required to explore these differences within the older adult group.

Acknowledgements

This work was supported by a Department of Employment and Learning PhD studentship to C. Craig, British Academy/Leverhulme Small Research Grant R1067PSY to M. Doumas and the School of Psychology, Queen's University Belfast Staff Incentivisation Scheme.

Conflict of interest

The authors declare no conflict of interest.

5. References

Benjuya N, Melzer I, Kaplanski J (2004) Aging-induced shifts from a reliance on sensory input to muscle cocontraction during balanced standing. journals Gerontol A, Biol Sci Med Sci 59:166–171.

Bohannon RW (2006a) Reference values for the five-repetition sit-to-stand test: A descriptive meta-analysis of data from elders. Percept Mot Skills 103:215–222.

Bohannon RW (2006b) Reference values for the five-repetition sit-to-stand test: a descriptive meta-analysis of data from elders. Percept Mot Skills 103:215–222 Available at: http://www.ncbi.nlm.nih.gov/pubmed/17037663 [Accessed November 30, 2015].

Boisgontier M, Nougier V (2013) Ageing of internal models: from a continuous to an intermittent proprioceptive control of movement. Age (Omaha) 35:1339–1355 Available at: http://dx.doi.org/10.1007/s11357-012-9436-4.

Boisgontier MP, Olivier I, Chenu O, Nougier V (2012) Presbypropria: the effects of physiological ageing on proprioceptive control. Age (Dordr) 34:1179–1194.

Brumagne S, Cordo P, Verschueren S (2004) Proprioceptive weighting changes in persons with low back pain and elderly persons during upright standing. Neurosci Lett 366:63–66 Available at: http://www.sciencedirect.com/science/article/pii/S0304394004005828 [Accessed January 15, 2016].

Butler AA, Lord SR, Rogers MW, Fitzpatrick RC (2008) Muscle weakness impairs the proprioceptive control of human standing. Brain Res 1242:244–251 Available at: http://www.ncbi.nlm.nih.gov/pubmed/18499088 [Accessed October 24, 2014].

Cenciarini M, Loughlin PJ, Sparto PJ, Redfern MS (2010) Stiffness and damping in postural control increase with age. IEEE Trans Biomed Eng 57:267–275 Available at: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3070169&tool=pmcentrez&rendertype=abstract [Accessed November 18, 2015].

Chambers AJ, Cham R (2007a) Slip-related muscle activation patterns in the stance leg during walking. Gait Posture 25:565–572 Available at: http://www.gaitposture.com/article/S0966-6362(06)00131-7/abstract [Accessed October 28, 2014].

Chambers AJ, Cham R (2007b) Slip-related muscle activation patterns in the stance leg during walking. Gait Posture 25:565–572.

Clark S, Riley MA (2007) Multisensory information for postural control: sway-referencing gain shapes center of pressure variability and temporal dynamics. Exp brain Res 176:299–310 Available at: http://www.ncbi.nlm.nih.gov/pubmed/16874512 [Accessed January 6, 2015].

Csuka M, McCarty DJ (1985) Simple method for measurement of lower extremity muscle strength. Am J Med 78:77–81 Available at:

http://www.sciencedirect.com/science/article/pii/0002934385904656 [Accessed October 27, 2015].

Deshpande N, Connelly DM, Culham EG, Costigan PA (2003) Reliability and validity of ankle proprioceptive measures. Arch Phys Med Rehabil 84:883–889.

Doumas M, Krampe RT (2010) Adaptation and reintegration of proprioceptive information in young and older adults' postural control. J Neurophysiol 104:1969–1977.

Doumas M, Krampe RT (2015) Ecological Relevance Determines Task Priority in Older Adults' Multitasking. J Gerontol B Psychol Sci Soc Sci 70:377–385 Available at: http://www.ncbi.nlm.nih.gov/pubmed/24149518.

Doumas M, Smolders C, Krampe RT (2008) Task prioritization in aging: Effects of sensory information on concurrent posture and memory performance. Exp Brain Res 187:275–281.

Gatts SK, Woollacott MH (2006) Neural mechanisms underlying balance improvement with short term Tai Chi training. Aging Clin Exp Res 18:7–19 Available at: http://www.ncbi.nlm.nih.gov/pubmed/16608131 [Accessed April 17, 2015].

Gauchard GC, Jeandel C, Tessier A, Perrin PP (1999) Beneficial effect of proprioceptive physical activities on balance control in elderly human subjects. Neurosci Lett 273:81–84 Available at: http://www.deepdyve.com/lp/elsevier/beneficial-effect-of-proprioceptive-physical-activities-on-balance-FC4t52ttIM [Accessed November 4, 2014].

Goble DJ, Coxon JP, Wenderoth N, Van Impe A, Swinnen SP (2009) Proprioceptive sensibility in the elderly: Degeneration, functional consequences and plastic-adaptive processes. Neurosci Biobehav Rev 33:271–278 Available at: http://www.sciencedirect.com/science/article/pii/S0149763408001450.

Goble DJ, Noble BC, Brown SH (2010) Where was my arm again? Memory-based matching of proprioceptive targets is enhanced by increased target presentation time. Neurosci Lett 481:54–58 Available at: http://www.ncbi.nlm.nih.gov/pubmed/20600603 [Accessed August 21, 2015].

Goldberg A, Chavis M, Watkins J, Wilson T (2012) The five-times-sit-to-stand test: validity, reliability and detectable change in older females. Aging Clin Exp Res 24:339–344 Available at: http://www.ncbi.nlm.nih.gov/pubmed/23238309 [Accessed October 25, 2015].

Guralnik JM, Simonsick EM, Ferrucci L, Glynn RJ, Berkman LF, Blazer DG, Scherr PA, Wallace RB (1994) A short physical performance battery assessing lower extremity function: association with self-reported disability and prediction of mortality and nursing home admission. J Gerontol 49:M85–M94 Available at: http://www.ncbi.nlm.nih.gov/pubmed/8126356 [Accessed January 27, 2015].

Ho CY, Bendrups AP (2002) Ankle reflex stiffness during unperceived perturbation of standing in elderly subjects. J Gerontol A Biol Sci Med Sci 57:B344–B350.

Horak FB, Hlavacka F (2001) Somatosensory loss increases vestibulospinal sensitivity. J Neurophysiol 86:575–585.

Horak FB, Nashner LM (1986) Central programming of postural movements: adaptation to altered support-surface configurations. J Neurophysiol 55:1369–1381 Available at: http://www.ncbi.nlm.nih.gov/pubmed/3734861 [Accessed January 9, 2015].

Horak FB, Shupert CL, Mirka A (1989) Components of postural dyscontrol in the elderly: a review. Neurobiol Aging 10:727–738 Available at: http://www.ncbi.nlm.nih.gov/pubmed/2697808 [Accessed January 9, 2015].

Hurley M V, Rees J, Newham DJ (1998) Quadriceps function, proprioceptive acuity and functional performance in healthy young, middle-aged and elderly subjects. Age Ageing 27:55–62.

Kaplan FS, Nixon JE, Reitz M, Rindfleish L, Tucker J (1985) Age-related changes in proprioception and sensation of joint position. Acta Orthop Scand 56:72–74 Available at: http://www.ncbi.nlm.nih.gov/pubmed/3984706 [Accessed September 8, 2015].

Katz S, Ford AB, Moskowitz RW, Jackson BA, Jaffe MW (1963) Studies of illness in the aged. The index of ADL: A standardised measure of biological and psychological function. JAMA 185:914–919 Available at: http://www.ncbi.nlm.nih.gov/pubmed/14044222 [Accessed January 9, 2015].

Kurlowicz L, Wallace M (1999) The Mini Mental State Examination (MMSE). Director 7:62.

Laughton CA, Slavin M, Katdare K, Nolan L, Bean JF, Kerrigan DC, Phillips E, Lipsitz LA, Collins JJ (2003) Aging, muscle activity, and balance control: Physiologic changes associated with balance impairment. Gait Posture 18:101–108.

Lawton MP, Brody EM (1969) Assessment of Older People: Self-Maintaining and Instrumental Activities of Daily Living. Gerontol 9 :179–186 Available at: http://gerontologist.oxfordjournals.org/content/9/3_Part_1/179.short.

Lewek MD, Rudolph KS, Snyder-Mackler L (2004) Control of frontal plane knee laxity during gait in patients with medial compartment knee osteoarthritis. Osteoarthritis Cartilage 12:745–751 Available at: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3123521&tool=pmcentrez&rendertype=abstract [Accessed October 26, 2014].

Lord SR, Clark RD, Webster IW (1991) Postural stability and associated physiological factors in a population of aged persons. J Gerontol 46:M69–M76.

Lord SR, Rogers MW, Howland a, Fitzpatrick R (1999) Lateral stability, sensorimotor function and falls in older people. J Am Geriatr Soc 47:1077–1081.

Madhavan S, Shields RK (2005) Influence of age on dynamic position sense: evidence using a sequential movement task. Exp brain Res 164:18–28 Available at: http://www.researchgate.net/publication/7959173_Influence_of_age_on_dynamic_position_sense_evidence_using_a_sequential_movement_task [Accessed November 4, 2014].

Magnusson Mån, Enbom Håk, Johansson R, Pyykkö I (1990) Significance of Pressor Input from the Human Feet in Anterior-Posterior Postural Control: The Effect of Hypothermia on Vibration-Induced Body-sway. Acta Otolaryngol Available at: http://www.tandfonline.com/doi/abs/10.3109/00016489009122535 [Accessed December 7, 2015].

McChesney JW, Woollacott MH (2000) The effect of age-related declines in proprioception and total knee replacement on postural control. J Gerontol A Biol Sci Med Sci 55:M658–M666 Available at: http://www.ncbi.nlm.nih.gov/pubmed/11078095 [Accessed January 14, 2015].

Meeuwsen HJ, Sawicki TM, Stelmach GE (1993) Improved foot position sense as a result of repetitions in older adults. J Gerontol 48:P137–P141 Available at: http://www.ncbi.nlm.nih.gov/pubmed/8482823 [Accessed September 8, 2015].

Melzer I, Benjuya N, Kaplanski J (2001) Age-related changes of postural control: effect of cognitive tasks. Gerontology 47:189–194.

Melzer I, Benjuya N, Kaplanski J (2004) Postural stability in the elderly: a comparison between fallers and non-fallers. Age Ageing 33:602–607 Available at: http://ageing.oxfordjournals.org/content/33/6/602.abstract.

Nagai K, Yamada M, Mori S, Tanaka B, Uemura K, Aoyama T, Ichihashi N, Tsuboyama T (2013) Effect of the muscle coactivation during quiet standing on dynamic postural control in older adults. Arch Gerontol Geriatr 56:129–133.

Nagai K, Yamada M, Tanaka B, Uemura K, Mori S, Aoyama T, Ichihashi N, Tsuboyama T (2012) Effects of balance training on muscle coactivation during postural control in older adults: a randomized controlled trial. J Gerontol A Biol Sci Med Sci 67:882–889 Available at: http://www.ncbi.nlm.nih.gov/pubmed/22389467 [Accessed October 20, 2014].

Nagai K, Yamada M, Uemura K, Yamada Y, Ichihashi N, Tsuboyama T (2011) Differences in muscle coactivation during postural control between healthy older and young adults. Arch Gerontol Geriatr 53:338–343 Available at: http://www.sciencedirect.com/science/article/pii/S0167494311000045 [Accessed October 22, 2014].

Nashner LM, Black FO, Wall C (1982) Adaptation to altered support and visual conditions during stance: patients with vestibular deficits. J Neurosci 2:536–544 Available at: http://www.jneurosci.org/content/2/5/536?ijkey=92c2884ae94f14faf7ddeed3a786dde216ac5053&keytype2=tf_ipsecsha [Accessed August 27, 2015].

Nelson-Wong E, Appell R, McKay M, Nawaz H, Roth J, Sigler R, Third J, Walker M (2012) Increased fall risk is associated with elevated co-contraction about the ankle during static balance challenges in older adults. Eur J Appl Physiol 112:1379–1389 Available at: http://queens.ezp1.qub.ac.uk/login?url=http://ovidsp.ovid.com/ovidweb.cgi?T=JS&CSC=Y&NEWS=N&PAGE=fulltext&D=medl&AN=21811766.

Peterka RJ (2002) Sensorimotor integration in human postural control. J Neurophysiol 88:1097–1118 Available at: http://www.ncbi.nlm.nih.gov/pubmed/12205132 [Accessed January 9, 2015].

Peterka RJ, Loughlin PJ (2004) Dynamic regulation of sensorimotor integration in human postural control. J Neurophysiol 91:410–423.

Peters M (1988) Footedness: asymmetries in foot preference and skill and neuropsychological assessment of foot movement. Psychol Bull 103:179–192.

Petrella RJ, Lattanzio PJ, Nelson MG Effect of age and activity on knee joint proprioception. Am J Phys Med Rehabil 76:235–241 Available at: http://www.ncbi.nlm.nih.gov/pubmed/9207711 [Accessed September 8, 2015].

Reynolds RF (2010) The ability to voluntarily control sway reflects the difficulty of the standing task. Gait Posture 31:78–81.

Skinner HB (1993) Pathokinesiology and total joint arthroplasty. Clin Orthop Relat Res:78–86 Available at: http://www.ncbi.nlm.nih.gov/pubmed/8458157 [Accessed January 15, 2016].

Tucker MG, Kavanagh JJ, Barrett RS, Morrison S (2008) Age-related differences in postural reaction time and coordination during voluntary sway movements. Hum Mov Sci 27:728–737 Available at: http://www.sciencedirect.com/science/article/pii/S0167945708000304 [Accessed October 15, 2014].

Verschueren SMP, Brumagne S, Swinnen SP, Cordo PJ (2002) The effect of aging on dynamic position sense at the ankle. Behav Brain Res 136:593–603 Available at: http://www.sciencedirect.com/science/article/pii/S0166432802002243.

Warnica MJ, Weaver TB, Prentice SD, Laing AC (2014) The influence of ankle muscle activation on postural sway during quiet stance. Gait Posture 39:1115–1121.

Wolf SL, Barnhart HX, Kutner NG, McNeely E, Coogler C, Xu T (1996) Reducing frailty and falls in older persons: an investigation of Tai Chi and computerized balance training. Atlanta FICSIT Group. Frailty and Injuries: Cooperative Studies of Intervention Techniques. J Am Geriatr Soc 44:489–497 Available at: http://www.ncbi.nlm.nih.gov/pubmed/8617895 [Accessed July 31, 2015].

Wolfson L, Whipple R, Derby C, Judge J, King M, Amerman P, Schmidt J, Smyers D (1996) Balance and strength training in older adults: intervention gains and Tai Chi maintenance. J Am Geriatr Soc 44:498–506 Available at: http://www.ncbi.nlm.nih.gov/pubmed/8617896 [Accessed September 29, 2015].

Wu G (1998) Age-related differences in body segmental movement during perturbed stance in humans. Clin Biomech 13:300–307 Available at: http://www.sciencedirect.com/science/article/pii/S0268003398000680 [Accessed January 15, 2016].

You SH (2005) Joint position sense in elderly fallers: a preliminary investigation of the validity and reliability of the SENSERite measure. Arch Phys Med Rehabil 86:346–352 Available at: http://www.ncbi.nlm.nih.gov/pubmed/15706567 [Accessed November 4, 2014].

Figure Captions

Fig 1.

Proprioceptive matching device used to assess proprioceptive acuity using an active contralateral concurrent matching paradigm. Participants moved their non-dominant foot (participant's right in image) at a self-selected speed to match their stable dominant foot, which was held at one of two angles (10/15^{o} above horizontal).

Fig 2.

Proprioceptive acuity measures as a function of target angle (10^{o}/15^{o}) and age group.

(A) Absolute error(deg), defined as the angular disparity between the matching and reference foot positions at the button press
(B) Variable error (standard deviation), defined as the standard deviation of error across trials

* p< .05

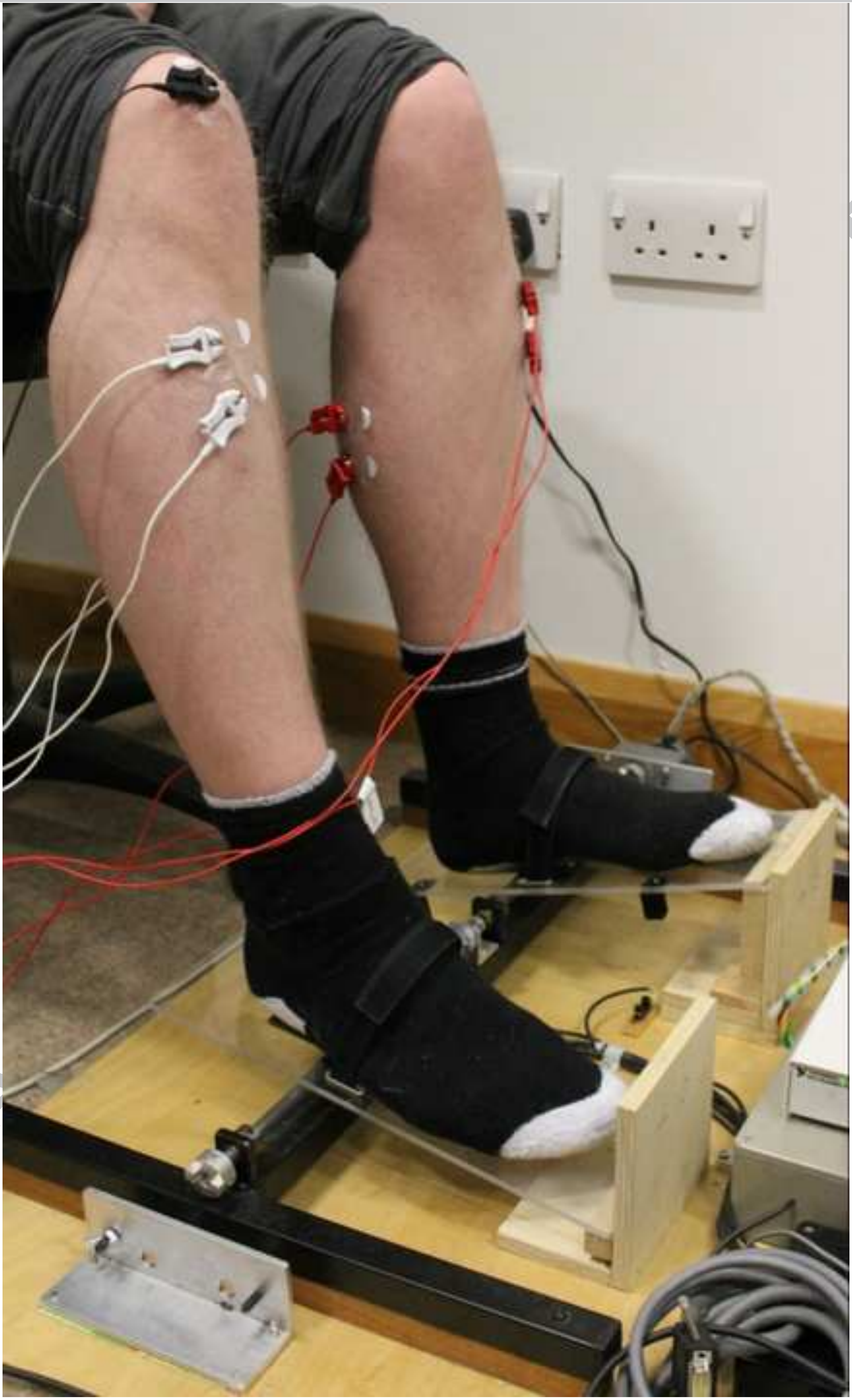
Fig 3.

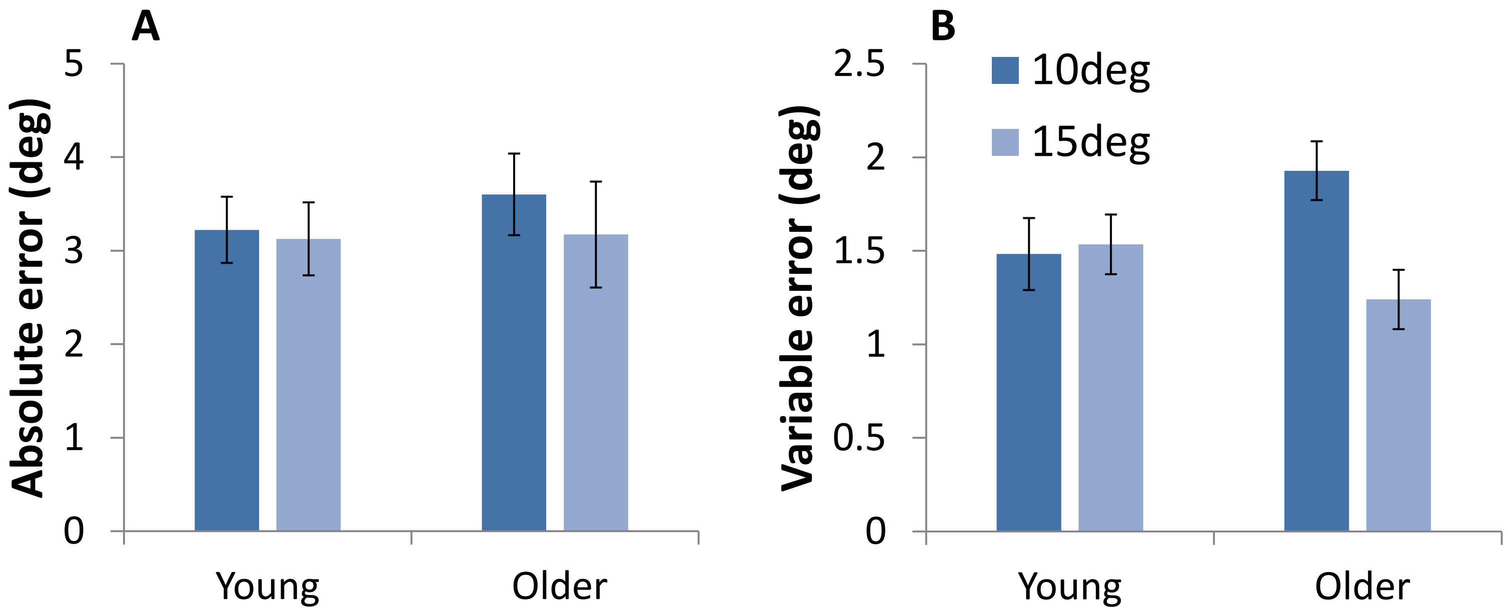
AP-path length (top panels) and CCI (bottom panels) for the whole 3-min trial (left panels) and divided into 30-s windows (middle and left panels).

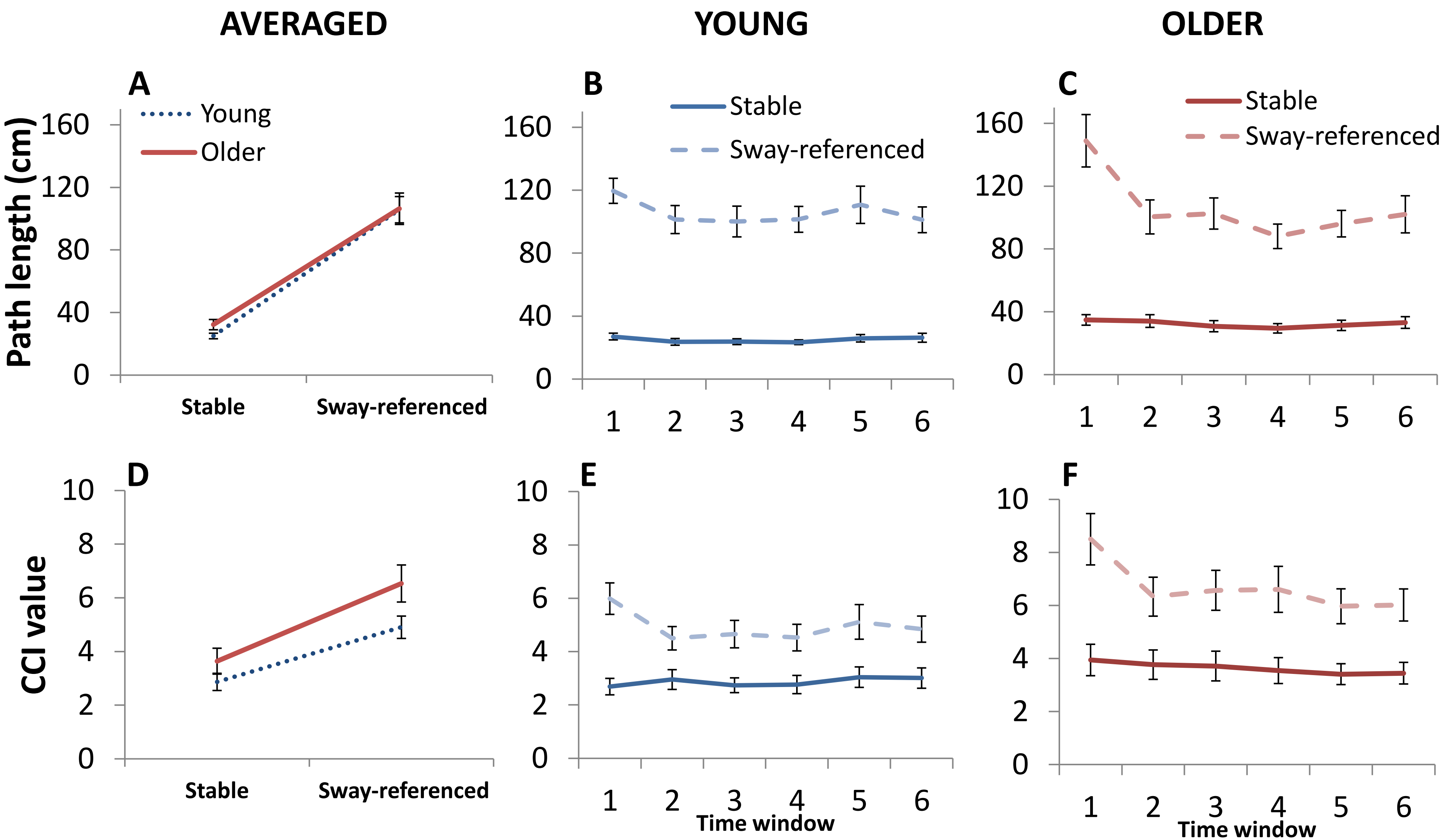
(A) mean AP path length (cm) and AP path length across 30s time windows for **(B)** young and **(C)** older adults and **(D)** mean co-contraction index (CCI) and CCI across 30s time windows for **(E)** young and **(F)** older adults, for the two conditions.

Fig 4.

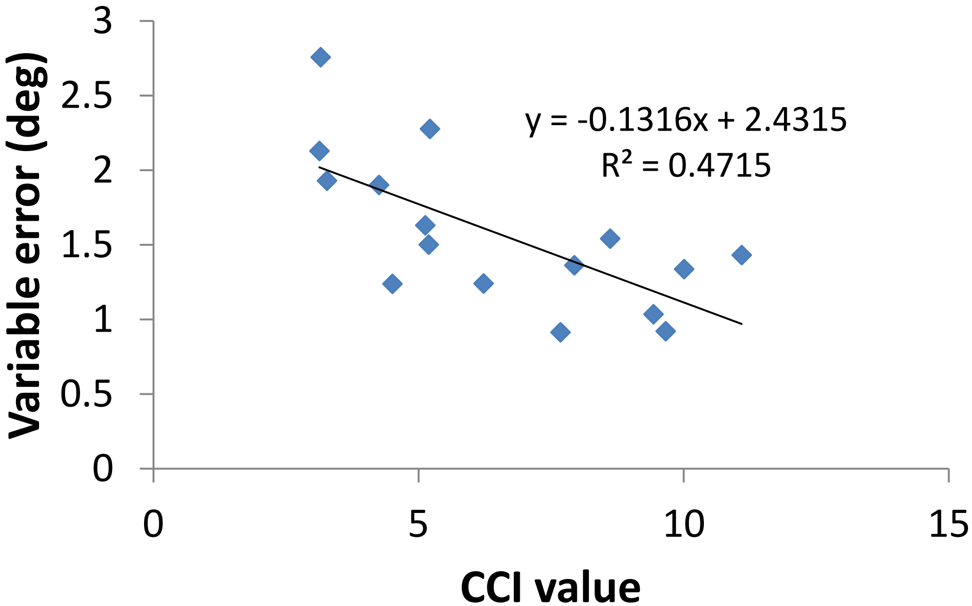
Cross plot showing the correlation between variable error during the active proprioceptive task and CCI during sway-referencing in older adults.




A
Absolute error (deg)
5
4
3
2
1
0
Young
Older
B
Variable error (deg)
2.5
2
1.5
1
0.5
0
10deg
15deg
Young
Older



AVERAGED
YOUNG
OLDER
A
Young
Older
Path length (cm)
160
120
80
40
0
Stable
Sway-referenced
B
Stable
Sway-referenced
1
2
3
4
5
6
C
D
CCI value
10
8
6
4
2
0
E
Time window
F


Variable error (deg)
3
2.5
2
1.5
1
0.5
0
0
5
10
15
CCI value
y = -0.1316x + 2.4315
R² = 0.4715

Highlights

- We assessed lower limb muscle activity during equivalent postural sway in young and older adults.
- Despite age-equivalent postural sway, older adults still showed higher muscle co-contraction.
- Older adults with *better* proprioceptive acuity showed more co-contraction.
- Although co-contraction may be an age-specific strategy, its use varies between older adults.
- Future work should explore whether different postural strategies may account for this variation.