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Slowed Sensory Reweighting and Postural Illusions in Older Adults: The Moving Platform Illusion

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Abstract

We investigated whether postural after-effects witnessed during transitions from a moving to stable support are accompanied by a delayed perception of platform stabilization in older adults, in two experiments. In Experiment 1, postural sway and muscle co-contraction were assessed in eleven healthy young, eleven healthy older and eleven fall-prone older adults during blind-folded stance on a fixed platform, followed by a sway-referenced platform then followed by a fixed platform again. The sway-referenced platform was more compliant for young adults to induce similar levels of postural sway in both age groups. Participants were asked to press a button whenever they perceived that the platform had stopped moving. Both older groups showed significantly larger and longer postural sway after-effects during platform stabilization compared to young adults, which were pronounced in fall-prone older adults. In both older groups elevated muscle co-contraction after-effect was also witnessed. Importantly, these after-effects were accompanied by an illusory perception of prolonged platform movement. Following this, Experiment 2 examined whether this illusory perception was a robust age-effect or an experimental confound due to greater surface compliance in young adults, which could create a larger perceptual discrepancy between moving and stable conditions. Despite exposure to the same surface compliance levels during sway-reference, the perceptual illusion was maintained in Experiment 2 in a new group of fourteen healthy older adults, compared to eleven young adults. In both studies, older adults took five times longer than young adults to perceive platform stabilization. This supports that sensory reweighting is inefficient in older adults.

New and Noteworthy: This is the first paper to show that postural sway after-effects witnessed in older adults after platform stabilization may be due to a perceptual illusion of platform movement. Surprisingly, in both experiments presented it took older adults five times longer than young adults to perceive platform stabilization. This supports a hypothesis of less efficient sensory reintegration in this age group, which may delay the formation of an accurate postural percept.

Keywords: aging, falls, postural control, sensory integration, perception

Introduction

Postural control is a complex sensorimotor process that requires coordination between multiple peripheral and central components of the nervous system (Horak *et al.*, 1989; Horak & Macpherson, 1996). A fundamental component of this process is the efficient and adaptive integration of sensory signals, including visual, vestibular and somatosensory signals, in order to form an accurate percept of the current postural state. Adaptive sensory integration is achieved through a process known as sensory reweighting, whereby the importance (weighting) of a sensory channel is determined by its relative reliability in the current context (Ernst & Banks, 2002; Peterka & Loughlin, 2004). For example, when moving from well-lit to dark conditions, visual information must be relied upon less and somatosensory and vestibular information is up-weighted to maintain postural control. However, a plethora of research now indicates that this process is subject to age-related slowing (Teasdale & Simoneau, 2001; Dickin *et al.*, 2006; O'Connor *et al.*, 2008; Doumas & Krampe, 2010; Jeka *et al.*, 2010; Eikema *et al.*, 2012, 2013; Craig *et al.*, 2017).

Prolonged sensory reweighting has been demonstrated in older adults during the manipulation of both visual (O'Connor *et al.*, 2008; Jeka *et al.*, 2010; Eikema *et al.*, 2012) and proprioceptive stimuli (Teasdale & Simoneau, 2001; Doumas & Krampe, 2010; Eikema *et al.*, 2013). For example, Jeka et al. (2010) demonstrated prolonged high postural gains in response to high amplitude visual stimuli in healthy and fall-prone older adults, indicative of a delayed ability to reduce reliance on the visual system, despite the considerable postural instability that this induced. On the other hand, Doumas and Krampe (2010) manipulated the accuracy of proprioceptive input using a technique called sway-referencing, in which the support surface rotates about the ankle joint in proportion to the participant's body sway. They found that in the absence of vision, when sway-referencing was introduced no age differences in the speed of adaptation were shown. However, when a stable platform was restored significantly greater and longer postural after-effects were observed in older, compared with young adults (Doumas & Krampe, 2010; Craig et al. 2017), suggesting difficulties in reintegrating veridical proprioceptive information when it is re-introduced.

Based on this evidence, it could be argued that the delayed sway reduction during the reinstatement of a stable support reflects a conservative response by the postural control system. This response is utilized to preserve CNS resources during transient conditions when there is less postural threat (Jeka *et al.*, 2008), compared with transient conditions with higher threat, such as when sway reference is introduced. This evidence is in line with research in young adults which showed that sensory reweighting is faster when an unstable, threatening environment is introduced but slower when a less threatening environment is restored (Jeka *et al.*, 2008; Polastri *et al.*, 2012; Assländer & Peterka, 2014; Logan *et al.*, 2014). However, our recent work demonstrated that the postural after-effects witnessed during platform stabilization were accompanied by prolonged use of muscle co-contraction in older adults, which suggests that this sensory transition posed considerable postural threat to this age group (Craig *et al.*, 2017). This could have important real-life implications, as it suggests that everyday sensory transitions, such as stepping off public transport, could pose considerable postural instability and increased fall risk to older adults.

Overall, inefficient sensory reweighting may contribute to increased falls risk, as during sensory transitions older adults will experience prolonged instability until sensory reweighting has been accomplished. Accordingly, evidence supports that sensory reweighting is particularly inefficient in fall-prone older adults, compared to healthy older adults (Jeka *et al.*, 2010; Pasma *et al.*, 2015). This link between deficient sensory reweighting and balance impairment is in line with a study that examined which parameters could best detect unstable older adults at risk of *multiple* falls (Soto-Varela *et al.*, 2015). The authors found that the two best predictors were: mean scores on the Sensory Organization Test, which assesses sensory reweighting abilities, and directional control scores on the Limits of Stability test, which assesses ability to control the center of gravity (CoG). These variables may contribute to the leading cause of falls in older adults which is incorrect weight shifting (Robinovitch et al., 2013), as sensory reweighting determines an accurate postural percept and directional control determines the ability to efficiently adjust the CoG.

The current paper aimed to examine how postural after-effects during reinstatement of a stable support may differ in healthy and fall-prone older adults, compared to young adults. Importantly, considering the suggestion that slower sensory reweighting can reflect a conservative response during conditions of reduced postural threat (Jeka *et al.*, 2008; Polastri *et al.*, 2012; Assländer & Peterka, 2014; Logan *et al.*, 2014), we aimed to assess whether older adults recognized whenever the platform had stabilized and consequently perceived less postural threat. We postulated that if postural after-effects were due to a deficit in sensory reweighting in older adults, then these after-effects would be accompanied by a delayed perception of platform stability, due to the delayed formation of an accurate postural percept.

In line with our previous study (Craig *et al.*, 2017), Experiment 1 assessed postural sway and muscle co-contraction during blindfolded adaptation to an age-matched sway-referenced support surface, followed by reinstatement of a stable support, in healthy older, fall-prone older and young adults. We predicted that both older groups would show a larger and longer postural after-effect once the stable platform was restored, compared to young adults, despite showing similar levels of postural sway during adaptation to sway-referencing. In addition, we predicted that this would be accompanied by higher muscle co-contraction in older groups and that both postural and muscular after effects would be exaggerated in fall-prone older adults. Perception of platform stability was assessed using a button-press measure during the reintegration phase, which participants were instructed to press whenever they perceived that the platform had stopped moving. We predicted that both older groups would be slower to perceive a stable platform than young adults, and this would be pronounced in fall-prone older adults.

Experiment 2 was conducted as a follow-up to Experiment 1 to investigate whether group differences in the perception of a stable support were a result of the age-matched sway-referencing protocol. In Experiment 1, young adults were exposed to a higher sway-referencing gain setting (Young gain = 1.6, Older gain = 1), in order to ensure similar postural sway levels during the adaptation phase, similar to our previous research (Craig *et al.*, 2017). However, this could create a larger perceptual discrepancy between the moving and stable platform, which could result in a quicker perception of stability in young adults. Consequently, Experiment 2 utilised the same gain setting in both young and older adults (Gain = 1) in order to replicate age differences in the aftereffect and to assess whether the perceptual illusion was a robust age difference or an experimental confound. We predicted that a perceptual delay would remain in older adults during the reintegration phase, which would strengthen the argument for an age-related deficit in sensory reweighting.

Experimental Procedures

Participants

Experiment 1

Based on the data from Craig, Calvert and Doumas (2017), a statistical power analysis indicated that a sample of N= 10 should be sufficient to replicate the postural after-effects witnessed whenever a previously sway-referenced platform is stabilized (alpha = .05, power

= .08). Twelve healthy young, twelve healthy older and fourteen fall-prone older adults volunteered to participate in the study. Participants were excluded based on any medical history or recent medication use that could impair postural performance. For example, participants were automatically excluded if they gave a confirmatory response to any of the following; use of orthopedic shoes, previous stroke, Parkinson's disease, hip/knee replacement, use of tricyclic antidepressants or sleep tranquilizers. Inclusion criteria for both older groups also included, scoring 25+ on the *Mini-Mental State Examination (MMSE)* and being classified as independent according to the *Katz Basic Activities of Daily Living* test (Katz *et al.*, 1963) and the *Instrumental Activities of Daily Living Scale* (Lawton & Brody, 1969). Failure to meet the MMSE inclusion criteria, missing motion tracking data (gaps >500ms) and extreme outliers resulted in a final sample of 11 young, 11 healthy older and 11 fall-prone older adults. The demographic information from the retained participants are listed in Table 1.

Older adults were classified as 'fall-prone' if they reported any incidence of falls in the last year or if they scored ≤ 46 on the Berg Balance Scale (BBS; Berg, 1989). This cut-off score was recommended by Lajoie and Gallagher (2004) and has been utilized in other studies examining sensory reweighting deficits in fall-prone older adults (Jeka *et al.*, 2010). Older adults also completed the *Rapid Assessment of Physical Activity* (RAPA; Topolski et al., 2006). Written informed consent was obtained from all participants and the study was approved by the School of Psychology, Queen's University Belfast Ethics Committee.

Table 1.

Experiment 1 Participant Characteristics

Measure	Young (*N*=11)	Healthy older (*N*=11)	Fall-prone (*N*=11)
Age (yrs)	24.18 (4.24)	72.09 (5.50)	72.09 (5.39)
Sex(male, female)	2, 9	1, 10	2, 9
Height (cm)	166.27 (10.19)	162 (11.2)	166.27 (4.98)
Weight (kg)	62 (10.95)	59.27 (11.64)	71.27(13.40)*
BMI	22.30 (2.06)	22.48 (2.16)	25.70 (4.08)*
MMSE	N/A	29.18 (1.25)	28.82 (1.54)
ADL	N/A	8 (0)	8 (0)
IADL	N/A	8 (0)	8 (0)
RAPA	N/A	5.82 (1.25)	5.27 (1.27)
BBS	N/A	54.82 (2.09)	44.55 (11.17)*

Note. Values represent mean values, with standard deviations in parentheses. BBS = Berg balance scale; 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.

* $p < .05$.

Experiment 2

Participants were recruited according to the same medical inclusion criteria utilized in Experiment 1. In this case, only older adults with no history of falls within the last year were recruited. Fifteen older adults and thirteen young adults volunteered for the study, however, following exclusion of a faulty button press and extreme outliers (>2 SD) fourteen older adults and eleven young adults were retained. The demographic information from the retained sample can be found in Table 2. Written informed consent was obtained from all participants and the study was approved by the School of Psychology, Queen's University Belfast Ethics Committee.

Table 2. *Experiment 2 Participant Characteristics*

Measure	Young (*N*=11)	Healthy older (*N*=14)
Age (yrs)	23.36 (2.62)	72.57 (5.14)
Sex(male, female)	2, 9	2, 12
Height (cm)	169.27 (9.12)	163.71 (9.18)
Weight (kg)	64.1 (9.47)	67.43 (11.39)
BMI	22.37 (2.44)	25.05 (2.92)*

Note. Values represent mean values, with standard deviations in parentheses. BMI = body mass index. * $p < .05$.

Apparatus and tasks

Experiment 1

Postural assessment. The postural adaptation task was assessed using the Smart Balance Master (NeuroCom International, Inc., Clackamas, OR, USA). This device consists of an 18” x 18” dual force plate which records vertical forces at a sampling frequency of 100Hz. The platform was sway-referenced using a servo-controlled motor which introduced platform tilts in the sagittal plane about the ankle joint axis in proportion to the participant’s expected CoM sway angle (Nashner *et al.*, 1982). The mechanical compliance of the platform was determined by the pre-selected gain level. In line with Craig, Calvert and Doumas (2017), the current experiment utilized a gain level of 1.0 for older and fall-prone older adults and 1.6 for young adults. At a gain level of 1.0, the platform tilts 1^{o} for every 1^{o} of CoP sway. Whereas, at a gain factor of 1.6, platform tilt is 1.6 times greater than AP CoP sway, thus inducing greater postural sway (Clark & Riley, 2007). Similarly, to our previous studies, this manipulation was utilized in order to induce similar levels of postural sway in both age groups. A blindfold and a non-restrictive safety harness were worn throughout the postural adaptation task. Participants held a wireless mouse with their dominant hand throughout this task and were asked to click on the mouse button when the platform stopped moving.

Motion capture. Body kinematics were assessed during the postural adaptation task using a Codamotion CX1 sensor unit (Charnwood Dynamics Ltd., Rothley, Leicestershire, UK). This is an active marker system that utilizes infrared light-emitting diodes (ILEDs) to capture motion data across three dimensions. The marker set-up (Figure 1) consisted of: 2 platform markers, one on the fixed section of the platform and one in front of it on the posterior right corner of the moving support surface, and 4 body landmark markers, which were placed at the C7 vertebra (neck level), L5 vertebra (hip level), right popliteal fossa (knee level) and right superior calcaneus (ankle level). The CX1 unit was placed behind the participant at a distance of approximately 2-metres from the fixed platform ILED. Motion capture data were collected at a sampling rate of 100Hz.

[Insert Figure 1 here]

EMG recordings. Co-contraction of the tibialis anterior (TA) and the gastrocnemius medialis (GM) and soleus (SOL) muscles of the dominant leg were assessed using surface electromyography (EMG) during postural assessment. Disposable Ag-AgCl electrodes (Cleartrace, CONMED, Utica, NY, USA) with an inter-electrode distance of 3cm were attached vertically along the muscle belly of the TA, GM and SOL and a ground electrode was placed on the patella. 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 sampled at 2 kHz and was initially band-pass filtered at 10-500 Hz. Following this, EMG data were normalized in relation to the maximum values recorded during three maximum voluntary contractions (MVCs) from the TA, SOL and GM.

Experiment 2

The postural assessment task from Experiment 1 was exactly replicated in Experiment 2, however, the gain setting for young adults was adjusted to 1.0, to match that of the older group. This modification allowed us to examine if any perceptual differences between age groups in Experiment 1 were merely a result of a lower gain setting. EMG signals were not recorded in Experiment 2, as the focus was on the perceptual effects.

Additionally, the push button apparatus was upgraded in Experiment 2 to include a hand-held push button, which was sampled at 100Hz. The push button signal was recorded through a Micro1401-3 data acquisition device using Signal v7 software (Cambridge Electronic Design Ltd., Cambridge, UK).

Procedure

Experiment 1

For older participants, the experiment commenced with the completion of a number of short tests, including the RAPA, MMSE and BBS. Following this, the session continued for older adults, and commenced for young adults with the recording of three maximum voluntary contractions (MVCs) of the TA, SOL and GM muscles, the largest of which would then be used to normalize the EMG recordings. TA MVCs were assessed during seated maximal isometric dorsiflexions of the ankle, with the knee flexed at 90º. SOL MVCs were assessed similarly during seated isometric plantarflexions of the ankle. During both TA and GM MVCs, the participants were instructed to flex the foot to full range of motion of the ankle joint. GM MVCs were assessed during standing single-leg heel raises (Nelson-Wong *et al.*, 2012a).

The session continued with the postural adaptation task (Figure 2). Participants were given two 1-min practice trials (one with eyes open, the other with eyes closed) during which the platform was sway-referenced at the gain set for that age group (1.0 for older and 1.6 for young participants). Subsequently, the experimental task comprised three phases: (1) a stable 2-min baseline phase, (2) a 3-min sway-referenced adaptation phase and (3) a stable 3-min reintegration phase, all of which were performed blindfolded. Postural adaptation was assessed in the range of minutes, rather than in short trials lasting up to a minute which is typical in most postural control studies, on the basis of our previous work (Doumas & Krampe, 2010). That study, using a long period of adaptation (18 min) showed that the largest amount of adaptation to the sway referenced environment occurred after 3 minutes and that after-effects lasted 1min for young and over 2 minutes for older adults. In a subsequent study, age differences in the after-effect were present even with a 3 min adaptation phase (Craig *et al.*, 2017). The same durations were used in the present study.

Participants were instructed to stand as still as possible with their arms by their side. They were warned 10 seconds before the sway-referenced phase was about to commence but were *not* told whenever sway-referencing had stopped. Instead, participants were asked to press a wireless mouse button whenever they believed the platform had stopped moving. EMG activity from the dominant leg TA, SOL and GM muscles was recorded to assess co-contraction levels during each phase of the postural task. Motion tracking was recorded as a measure of AP path length and to explore the postural strategies employed. Participants wore a safety harness that did not restrict movement during all postural assessment.

[Insert Figure 2 here]

Experiment 2

The postural adaptation task procedure from Experiment 1 (Figure 2), detailed above, was exactly replicated in Experiment 2.

Data analysis

Experiment 1

Preliminary data analysis was carried out using custom-written Matlab software. Gaps (<500ms) in the motion tracking data from each marker were interpolated using a cubic spline routine in Matlab (Warnica *et al.*, 2014). Data from each marker were low-pass filtered at 4Hz using a 4th order dual-pass Butterworth filter.

In terms of the EMG data, raw EMG data were full-wave rectified and linear envelopes were created using a 5th order Butterworth dual-pass filter with a cut-off frequency of 4 Hz. The data from the postural trials were then normalized as a percentage of each participant's peak MRs. Co-contraction indices (CCI) were calculated between the tibialis anterior (TA) and the gastrocnemius medialis (GM) and additionally between the TA and the soleus (SOL), using the equation described below (Equation 1). This equation was chosen as it permits the calculation of CCI without the identification of agonist and antagonist muscle pairs (Lewek *et al.*, 2004; Nelson-Wong *et al.*, 2012), which can be difficult during static postural control.

Equation 1

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

N is the selected time window, EMG_{low} is the lower EMG value from the selected muscle pair (TA/GM or TA/SOL) at the *i*th data point and EMG_{high} is the higher EMG value at the *i*th 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. 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. In line with our previous paper (Craig *et al.*, 2016),the mean CCI value of these products was calculated, rather than the overall sum. 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. CCI analyses demonstrated a similar pattern of CCI across postural phases in both muscle groups, however, the TA and GM pair showed larger CCI values, therefore only the results from this muscle pair are reported.

AP path length of the hip marker and CCI were calculated in 30s windows for the three phases. This window duration was chosen because it represents a typical duration of a postural control trial in the literature, it is also sufficiently long to capture approximately three full cycles of body movement during sway referencing (body movement frequency: 0.1Hz; Peterka & Loughlin, 2004; Doumas & Krampe, 2010) and because it allowed us to plot and statistically analyze AP path length and CCI in the same manner. In a further analysis AP path length for baseline and reintegration was calculated in 10s windows. This calculation was used in order to increase our temporal resolution and to identify a more exact time point in the reintegration phase in which sway returned to baseline levels and to compare this point with the button-press. The 10s window at which each participant's AP path length returned to baseline was determined as the first 10s reintegration time window which was within one standard deviation of the baseline mean. The difference between this return to baseline time and the time at which participants perceived that the platform was stable (button press time) was then compared.

Statistical analysis. An outlier analysis was initially performed on each measure, which identified outliers that fell two standard deviations beyond the group mean. Outliers that were only present in one time window were normalized to the group mean, however, participants who showed several outliers were excluded from the experiment. In line with Craig et al. (2017), differences in AP path length and CCI within each phase were assessed using two-way mixed-design ANOVAs with age as between- and time window (per 30s) as within-subject factors. Differences in AP path length and CCI during the sensory transitions were assessed using mixed-design ANOVAs, which compared the baseline mean to the mean of the adaptation and reintegration phase in both age groups. Paired samples t-tests were run to examine whether there were significant differences between the exact 10s window that each group's AP path length returned to baseline and the time of their button press to indicate when they perceived the platforms return to stability. In ANOVAs in which sphericity was violated a Greenhouse-Geisser correction was applied. Predicted effects and/or interactions were explored further with simple effects analyses and unexpected effects were explored further using Bonferroni post hoc tests.

Experiment 2

The data from Experiment 2 was pre-processed and statistically analysed according to the same protocol specified for motion tracking data from Experiment 1.

Results

EXPERIMENT 1

Anterior-posterior (AP) path length of the hip marker

BASELINE. Figure 3A illustrates the mean AP path length of the hip marker across each 30s for each of the three postural phases in young, healthy older and fall-prone older adults. A mixed-design ANOVA showed no overall group differences (p= .21) in the baseline phase, but there was a change in AP path length over time as shown by a main effect of window $F(3,90)$= 6.42, p= .001, η_p^2 = .18. Bonferroni pairwise comparisons demonstrated an increase in path length from window B3 to window B4 (p< .001). There was no significant interaction (p=.86).

ADAPTATION. Exposure to a sway-referenced support instilled a large increase in AP path length of the hip marker in all groups, as shown in Figure 3A. A mixed-design ANOVA, which compared the mean AP path length during adaptation to the mean during baseline, confirmed that AP path length was significantly higher during the adaptation phase, $F(1,30)$ = 161.88, p< .001, η_p^2 = .84. There was no difference between groups or interaction between group and condition. Analysis of AP path length throughout the adaptation phase, also found no overall effect of group, mirroring our previous findings that increasing the gain setting for young adults can remove any age differences in postural sway. AP path length decreased over time as shown by a main effect of window, $F(3.56,106.81)$= 13.47, p= .001, η_p^2 = .31. Bonferroni pairwise comparisons indicated that AP path length showed successive decline between windows A1 and 2 ($p< .001$). There was no interaction between time window and group in the adaptation phase.

REINTEGRATION. The restoration of a stable support surface resulted in clear postural after effects, which were larger in older adults, especially fall-prone older adults (Figure 3A). The significance of these after-effects was confirmed using a mixed-design ANOVA, which compared the mean AP path length of the hip marker during reintegration with the mean of the 4 baseline windows (B1-B4). Results showed that AP path length was significantly higher during reintegration, $F(1,30) = 51.14$, $p< .001$, $\eta_p^2 = .63$. More importantly, a group by phase interaction, $F(1,30) = 7.77$, $p= .002$, $\eta_p^2 = .34$, suggested older and fall prone older adults may show a greater AP path length increase compared with young adults. Paired samples t-tests with an alpha level corrected for multiple comparisons to 0.017, showed that both older adult groups showed significantly higher AP path length during reintegration (Healthy: $t(10) = 4.97$, $p= .001$; Fall-prone: $t(10) = 5.62$, $p< .001$), but this increase was not shown in young adults. The duration of any significant after-effects were examined using paired samples t-tests comparing each 30s reintegration window with the mean of the baseline windows, with an alpha level corrected for multiple comparisons to 0.008. Tests showed that for young adults the after-effect was only significantly different from baseline in the first 30s (R1), $t(10) = 3.71$, $p= .004$. However, for both older groups, the after-effect was significant for up to 60 s (window R2) (Healthy: $t(10) = 8.24$- 3.40, $p<=$ .001-.007; Fall-prone: $t(10) = 7.27$- 3.38, $p<=$ .001-.007). Between window R2 and R4 there was also a slight increase in path length for the healthy older group, resulting in an additional difference between baseline and window 4, $t(10) = 3.99$, $p= .003$.

Analysis of AP path length of the hip marker throughout the reintegration phase was performed to assess whether the observed pattern of results (Figure 3A) showing that fall prone older adults exhibit the largest after-effect was statistically reliable. Results showed a main effect of group within the reintegration phase, $F(2,30) = 4.01$, $p= .03$, $\eta_p^2 = .21$, which varied across 30s time windows, as shown by a significant time window by group interaction, $F(5,150) = 8.91$, $p<.001$, $\eta_p^2 = .37$. Simple effects analyses demonstrated that there was a significant difference between fall-prone and young adults for windows R1 and R2, (winR1: $F(1,20) = 16.11$, $p= .001$; winR2: $F(1,20) = 4.35$, $p= .03$), whereby fall-prone older adults showed a larger after-effect compared to young adults (Figure 3A). Additionally, fall-prone older adults also showed a larger after-effect than healthy older adults during window R1,

$F(1,20) = 7.33$, $p = .01$, and healthy older adults showed a larger after-effect than young adults during this window, $F(1,20) = 5.74$, $p = .01$. AP path length declined over time as shown by a main effect of window, $F(2.23,66.79) = 77.02$, $p = .001$, $\eta_p^2 = .72$. Bonferroni pairwise comparisons revealed that all groups only showed a significant decrease in path length between successive windows from R1 to R2, (Young: $p = .04$; Healthy: $p = .001$; Fall-prone: $p < .001$).

[Insert Figure 3 here]

Muscle co-contraction (CCI)

BASELINE. Figure 3B illustrates the mean CCI values for the GM and TA across each 30s for each of the three postural phases in young, healthy older and fall-prone older adults. The mixed-design ANOVA revealed no significant effects of group or time window during baseline and no group by time window interaction.

ADAPTATION. During exposure to a sway-referenced support, all groups showed an increase in CCI levels, however, this was particularly pronounced in fall-prone older adults (Figure 3B). A mixed-design ANOVA comparing the adaptation mean to the baseline mean confirmed that CCI levels were higher during the adaptation phase, $F(1,30) = 34.34$, $p < .001$, $\eta_p^2 = .53$. However, there was no difference between groups or interaction between group and condition. Analysis of CCI levels across the adaptation phase showed that the effect of group approached significance ($p = .050$) and CCI declined over time, $F(3.12,93.70) = 6.84$, $p < .001$, $\eta_p^2 = .19$. Bonferroni pairwise comparisons indicated that the change in CCI levels was gradual, as there were no significant differences between successive windows, however, window A1 was significantly higher than all windows apart from A2, ($p = .001$-$.03$). There was no group by time window interaction.

REINTEGRATION. During the restoration of a stable support surface, each group showed a peak in CCI levels during the first 30s window (R1), which was larger in fall-prone older adults (Figure 3B). Similarly to the AP path length analysis, a mixed-design ANOVA comparing the mean of the reintegration phase to the baseline mean was used to examine the significance of this CCI after-effect. The analysis confirmed that CCI levels were greater during the reintegration phase, $F(1,30) = 9.22$, $p = .005$, $\eta_p^2 = .24$. Additionally, the test found a significant effect of group, $F(1,30) = 3.40$, $p = .047$, $\eta_p^2 = .19$, which Bonferroni pairwise comparisons showed was due to larger CCI levels in fall-prone older adults compared to young adults ($p = .03$). The duration of the CCI after-effect for each group was assessed using paired samples t-tests comparing each 30s reintegration window with the mean of the baseline windows, with an alpha level corrected for multiple comparisons to 0.008. These tests demonstrated that young adults showed no significant CCI after-effect for any window. However, both healthy older and fall-prone older adults show a significant after-effect in the first 30s window (Healthy: $t(10) = 3.29$, $p = .008$; Fall-prone: $t(10) = 3.56$, $p = .005$).

Analysis of CCI levels throughout the reintegration phase also showed group differences, $F(1,30) = 3.48$, $p = .04$, $\eta_p^2 = .19$. Bonferroni pairwise comparisons revealed that this was due to significantly greater CCI values in fall-prone older adults compared to young adults (p= .04). Similarly to the adaptation phase, CCI levels declined over the reintegration phase as shown by a main effect of window $F(2.04,61.10) = 5.08$, $p = .009$, $\eta_p^2 = .15$. Bonferroni pairwise comparisons demonstrated that this effect of time was due to a decrease in CCI from window R1 to R2 ($p = .002$). There was no group by time window interaction.

Perception of platform stability and postural after-effects

Two-tailed independent samples t-tests, with an alpha value corrected for multiple comparisons to 0.016, were used to explore whether there were significant age differences in the time at which each group perceived that the platform had stabilized at the start of the reintegration phase (Figure 4). Both older groups pressed the push button significantly later than the young group (healthy vs. young: $t(20) = 3.03$, $p = .007$; fall-prone vs. young: $t(12.89) = 4.27$, $p = .001$) and there were no differences in the perception of platform stability between the two older adult groups.

Paired samples t-tests were also used to examine differences between the time window at which the postural after-effect returned to baseline and the time at which the participants perceived that the platform had stopped moving, for each group (Figure 4). Only young adults showed a difference between the two latencies, namely they perceived the reinstatement of a stable platform earlier than postural sway returned to baseline levels $t(10) = 2.95$, $p = .02$. (Figure 4). However, for both older groups the time at which they perceived the reinstatement of a stable platform was similar to the time that postural sway returned to baseline levels. Albeit not significant, it is instructive to note that healthy older adults' sway returned to baseline before they perceived the return to stability a few seconds later, whereas for fall-prone older adults they perceived the stable platform ~14s before their sway returned to baseline. Additionally, it should be noted that one fall-prone older adult never pressed the push-button, as they failed to recognise that the platform had stopped moving throughout the duration of the reintegration phase. This participant's time was normalized to the group mean. No participant pressed the push-button before the platform had stabilized.

[Insert Figure 4 here]

EXPERIMENT 2

Anterior-posterior (AP) path length of the hip marker

BASELINE. Figure 5A illustrates the mean AP path length of the hip marker across each 30s for each of the three postural phases in young and healthy older adults. A mixed-design ANOVA showed an overall group difference, $F(1,23) = 18.40, p < .001,\ \eta_p^2 = .44$, whereby older adults showed a larger AP path length ($M = 162.2 \pm 53.27$cm) compared to young adults ($M = 101.85 \pm 23.21$cm). In addition, there was a change in AP path length over time as shown by a main effect of window $F(3,69) = 3.65$, $p = .017$, $\eta_p^2 = .14$. However, Bonferroni pairwise comparisons found no significant difference between windows. There was no significant interaction ($p=.42$).

ADAPTATION. In line with Experiment 1, exposure to a sway-referenced support instilled a large increase in AP path length of the hip marker in both groups, as witnessed in Figure 5A. A mixed-design ANOVA, which compared the mean AP path length during adaptation to the mean during baseline, confirmed that AP path length was significantly higher during the adaptation phase, $F(1,23) = 107.85$, $p < .001$, $\eta_p^2 = .82$. In this case, there was also a significant difference between groups, $F(1,23) = 13.02$, $p = .001$, $\eta_p^2 = .36$, which suggested that the age difference witnessed at baseline was maintained in the adaptation phase. There was no significant interaction ($p = .24$). Analysis of AP path length throughout the adaptation phase, also showed a significant difference between groups, $F(1,23) = 6.95$, $p = .015$, $\eta_p^2 = .23$, and a significant change across time windows, $F(5,115) = 4.98$, $p < .001$, $\eta_p^2 = .18$. There was also a significant interaction between group and time window, $F(5,115) =$

2.75, p= .02, η_p^2 = .11. Examination of the effect of time window in each group individually showed that young participants did not show a significant reduction in AP path length over time (p = .72), whereas older adults did show an effect of time window, F(5,65) = 7.31, p< .001, η_p^2 = .36. Bonferroni pairwise comparisons showed that AP path length showed successive decline between windows A1 and 2 (p= .03) for older adults. In addition, independent samples t-tests with an alpha level corrected for multiple comparisons to 0.008, showed that the older adult group showed significantly higher AP path length compared to young adults during the first adaptation window only (*t*(23) = 3.09, p= .005).

REINTEGRATION. In line with Experiment 1, restoration of a stable support surface resulted in clear postural after effects, which were larger in older adults (Figure 5B). This was confirmed using a mixed-design ANOVA, which compared the mean AP path length of the hip marker during the reintegration phase with the mean during baseline (B_M). Results showed that AP path length was significantly higher during reintegration, F(1,23) = 40.22, p< .001, η_p^2 = .64, and there was a significant group difference, F(1,23) = 27.62, p< .001, η_p^2 = .55. Additionally, a group by phase interaction, F(1,23) = 11.49, p= .003 , η_p^2 = .33, suggested that the after effect may differ between age groups. The duration of the after-effect for each group was assessed using paired samples t-tests comparing each 30s reintegration window with the baseline mean (Figure 5B), with an alpha level corrected for multiple comparisons to 0.008. In younger adults, AP path length was only significantly higher than baseline during the first 30s reintegration window (*t*(10) = 4.51, p= .001). However, in parallel to Experiment 1, the after-effect was significant for up to 60s (R2) in older adults (*t*(10) = 7.05- 4.14, p≤ .001).

Analysis of AP path length of the hip marker throughout the reintegration phase was performed to assess whether age differences occurred across different time windows. The analysis found an overall group difference, F(1,23) = 28.75, p< .001, η_p^2 = .56, and change in path length across time windows, F(5,115) = 36.01, p< .001, η_p^2 = .61. In addition, there was a significant interaction between age group and time window, F(5,115) = 5.56, p< .001, η_p^2 = .20. Examination of the effect of time window in each group individually showed that both groups showed a significant reduction in AP path length over time (Young: F(1.71,25.60) = 17.30, p< .001, η_p^2 = .63; Older: F(1.97, 25.60) = 26.34, p< .001, η_p^2 = .67). Bonferroni pairwise comparisons showed that only older adults showed an immediate significant decline in path length between windows 1 and 2 (p < .001), whereas in young adults decline was more gradual, with a significant reduction from window 1 shown from window 3 onwards ($p = .007$-$.02$). In addition, independent samples t-tests with an alpha level corrected for multiple comparisons to 0.008, showed that the older adult group showed significantly higher AP path length compared to young adults across all reintegration time windows ($p \leq .003$).

[Insert Figure 5 here]

Perception of platform stability and postural after-effects

A two-tailed independent samples t-test was used to investigate whether there was a significant age difference in the time at which each group perceived that the platform had stabilized at the start of the reintegration phase (Figure 6). In line with Experiment 1, the older adults pressed the push button significantly later than the young group ($t(14.53) = 6.06$, $p < .001$). On average, older adults pressed the push button over 5x later than young adults ($M_{Young} = 5.18 \pm 2.66$s, $M_{Older} = 26.63 \pm 12.86$s).

Paired samples t-tests were used to examine whether there was a significant difference between the time at which AP path length returned to baseline levels and the time at which each group perceived that the platform had stopped moving. Only young adults showed a significant difference between these latencies ($t(9) = 5.73$, $p < .001$), in which they perceived the reinstatement of a stable platform earlier than postural sway returned to baseline levels (Figure 6).

[Insert Figure 6 here]

Discussion

The current paper had two key aims; (1) to investigate whether postural sway and muscle co-contraction after-effects during the restoration of a stable support differed in healthy and fall-prone older adults, and (2) to examine whether such after-effects were accompanied by a delayed perception of platform stabilisation, in support of the argument of an age-related slowing of sensory reweighting. In line with our previous findings, in Experiment 1 we found that both older groups showed significantly larger and longer postural after-effects when a stable platform was reinstated and proprioceptive information was reintegrated, compared to young adults (Doumas & Krampe, 2010; Craig *et al.*, 2017). As predicted, this postural after-effect was also significantly larger in the fall-prone group, compared to the healthy older adults, suggesting that this transition may instill additional instability in this group. Additionally, in both older groups, after-effects were also witnessed in terms of muscle co-contraction. More importantly, we demonstrated that these after-effects were accompanied by a delayed perception that the platform had stopped moving, as it took both older groups five times longer than the young group to detect this change.

Despite absent visual feedback, young adults recognized that the platform had stopped moving in ~8 seconds. In contrast, both older groups took on average ~40 seconds to recognize that the platform had stabilized. Considering the magnitude of these latencies, these age differences cannot be explained by age-related delays in reaction time, which typically occur on the scale of milliseconds (Fozard *et al.*, 1994). Additionally, this cannot be explained by the level of postural sway prior to platform stabilisation, as our gain manipulation during sway-referencing successfully induced similar levels of sway in young and older groups during the adaptation phase. Despite this, the fact that young adults were standing on a more compliant surface (gain = 1.6) compared with older adults (gain = 1), could suggest that the perceptual illusion may be an experimental confound, whereby young adults experienced a larger perceptual discrepancy between the moving and stable platform, which resulted in a quicker perception of stability. Consequently, the aim of Experiment 2 was to examine whether the perceptual illusion would be replicated following postural adaptation to the same gain setting (gain = 1) in both young and older adults.

In support of our hypothesis, the perceptual illusion was maintained in Experiment 2, in which a healthy older sample once more took five times longer than the young group to detect platform stabilization, despite postural adaptation to the same gain setting (gain = 1). Additionally, Experiment 2 successfully replicated other key findings of Experiment 1, namely the similar adaptation rates between age groups and the larger and longer aftereffects for older adults in the 30s reintegration phase analysis. However, some secondary differences were shown between the two experiments with older adults showing larger baseline postural sway compared with young adults, which has also been shown in one of our previous studies (Doumas & Krampe, 2010). Older adults also showed lower group variability in both the perceptual delay and the return to baseline in Experiment 2 compared with Experiment 1 (see error bars in Figures 6 and 4 respectively) suggesting that the older group in Experiment 2 was inherently more homogeneous. Regardless of these secondary differences between experiments, the replication of a fivefold delay in the time to detect platform stabilization in older adults supports that the perceptual illusion is a robust age-specific effect. This finding, in combination with the age-related postural sway after-effects witnessed in both studies, provides compelling evidence that sensory reweighting is deficient when attempting to reintegrate veridical proprioceptive information. The duration of this perceptual illusion of continued movement is striking, as it implies that the previously noted age-related delays in sensory reweighting (O'Connor *et al.*, 2008; Doumas & Krampe, 2010; Jeka *et al.*, 2010; Eikema *et al.*, 2012, 2013) could have significant perceptual consequences in real life. For example, everyday sensory transitions, such as, stepping off recently moving transport (especially in dark conditions) could pose a considerable fall risk to an older person.

Age-related Deficits in Sensory Reweighting

The age-related postural sway after-effects shown in the present paper are observed after prolonged adaptation to a sway-referenced surface. When standing on this surface, proprioceptive information about body sway is inaccurate and as a result the weight assigned to proprioception is reduced (Peterka & Loughlin, 2004). At the same time the weight for the accurate, vestibular input increases and gradually sway is reduced over the 3 minutes of adaptation. However, when the stable surface is restored the initial weights also have to be restored. Restoration of the two weights is much slower in older adults (Doumas & Krampe, 2010; Craig *et al.*, 2017) and in the present Experiment 1 in fall-prone older adults, and this slowing is reflected in the age-related postural sway after-effect. Our findings suggest that this slow sensory reweighting in older adults results in the delayed formation of an accurate postural percept. Previous research had suggested that postural after-effects during platform stabilization could be due to a conservative strategy to preserve CNS resources dedicated to postural control during transient conditions of reduced postural threat (Jeka *et al.*, 2008). However, our finding of a continued perception that the platform is moving (Experiment 1 & 2) and prolonged muscle co-contraction in older adults (Experiment 1), suggests that considerable postural threat is still experienced during this transition. Rather, slowed sensory reweighting in older adults results in the delayed formation of an accurate postural percept, which is associated with prolonged postural sway until sensory reweighting is completed, which may instil a postural illusion in this age group that the platform is still moving.

It is interesting to note in Experiment 1, that whilst fall-prone older adults demonstrated a significantly larger postural sway after-effect compared to healthy older adults, there was no significant difference in the time at which these groups perceived platform stabilisation. This could suggest that sensory reweighting delays are similar in both groups but the body's ability to compensate for this is impaired in fall-prone older adults. In support of this, fall-prone older adults showed similar postural sway in the first 30s of the reintegration phase to that shown during the first 30s of sway-referencing, suggesting that this transition resulted in considerable postural instability in this group. Furthermore, the extent of fall-prone older adults' reliance on co-contraction during the reintegration phase was noteworthy, as whilst their postural sway levels gradually reached the same values as young adults', their CCI remained higher than young adults' throughout the reintegration phase. This is important, because if used excessively, muscle co-contraction is likely to be maladaptive, as literature shows that co-contraction can increase postural sway (Laughton *et al.*, 2003; Reynolds, 2010; Nagai *et al.*, 2011; Warnica *et al.*, 2014) and has been associated with increased falls risk (Ho & Bendrups, 2002; Nelson-Wong *et al.*, 2012). This increased falls risk could be due to increased lower limb rigidity and impeded adaptive reactions to postural perturbations (Tucker *et al.*, 2008) or reduced proprioceptive input from active muscle spindles, compared to passive muscle spindles (Wise *et al.*, 1998; Proske & Gandevia, 2012).

Muscle Co-contraction

This pattern of increased reliance on muscle co-contraction in fall-prone older adults was shown throughout each postural phase in Experiment 1 but only reached significance during reintegration, whenever postural sway also showed a significant age difference. The literature suggests that muscle co-contraction is witnessed in response to increased challenge to postural stability (Chambers & Cham, 2007; Cenciarini *et al.*, 2010; Warnica *et al.*, 2014) and is generally higher in those with poorer postural control ability (Nagai *et al.*, 2011, 2016). It is thought that muscle co-contraction is used as ankle stiffening strategy to minimize postural sway (Baratta *et al.*, 1988; Hortobágyi & Devita, 2000; Benjuya *et al.*, 2004; Engelhart *et al.*, 2015). In support of this, we found that all groups showed increased muscle co-contraction when exposed to increased postural sway due to a sway-referenced support. However, in contrast to our previous findings (Craig et al., 2016, 2017) and other literature (Nagai *et al.*, 2011, 2013), we did not find significant age differences in muscle co-contraction throughout all phases. This is likely due to the stratification of older adults into 'healthy' and 'fall-prone' groups in the current study, which was not done in the previous literature. Nagai et al (2011, 2013) reported that high muscle co-contraction was strongly associated with poorer postural performance in older adults. In light of which, they proposed that muscle co-contraction use could be utilised as a predictor of postural impairment (Nagai *et al.*, 2013). Consequently, our current results may not be surprising and could support the use of muscle co-contraction as an indicator of balance impairment and potential falls risk.

Study Limitations and Future Directions

This argument of increased reliance on muscle co-contraction in fall-prone older adults would be strengthened if Experiment 1 found significantly higher muscle co-contraction in the fall-prone group during the postural adaptation phase. However, high variability in CCI in this group resulted in this measure failing to reach significance. This variability may be due to problems defining fall-prone individuals. In order to understand fall incidents it is important to study postural control in fall-prone older adults. However, a limitation of this work is that there is no clear, formal and generally accepted way of categorizing older adults as fall-prone. Experiment 1 utilized the same definition as that used by Jeka et al. (2010) in another study examining sensory reweighting deficits in fall-prone older adults. However, this categorization is problematic because self-reporting of falls can be unreliable and because the BBS, a widely used instrument for the functional assessment of balance has shown limited predictability of actual falls (Lima *et al.*, 2018). The use of more reliable reporting techniques, such as, third-party recall (e.g. clinician or family member report) or prospective falls diaries may result in a more homogeneous sample. It is likely that such a sample would demonstrate significantly higher CCI levels throughout all postural phases.

Another potential study limitation was the way in which the EMG activity was normalized in Experiment 1. Our calculation of the co-contraction index was based on a well-established method used by many previous studies (Nelson-Wong *et al.*, 2012), however, both this method as well as another commonly used method of calculating muscle co-contraction (Falconer & Winter, 1985) normalize EMG by the MVC. This may not be the most functionally relevant method of normalizing EMG because MVC is calculated outside the postural control task. A more appropriate and functionally relevant method would be to normalize by the baseline EMG before sway referencing was introduced, or even to not normalize at all and to simply multiply the filtered EMG signals of the flexor and extensor muscles (Reynolds, 2010).

In conclusion, the current dual-experiment paper provided compelling evidence that postural after-effects witnessed during stabilization of a previously sway-referenced support are accompanied by a perceptual illusion that the platform is still moving in older adults. This corroborates previous findings that sensory reweighting is delayed in this age group, resulting in a delayed formation of an accurate postural percept. Interestingly, in Experiment 1, despite showing a larger postural sway after-effect, fall-prone older adults did not show prolonged perceptual delays compared to healthy older adults. This could suggest that sensory reweighting delays are similar in these groups but the way the body compensates for these delays differs. An example of this may be witnessed in the fall-prone group's excessive use of muscle co-contraction during the reinstatement of the stable support. Excessive use of muscle co-contraction may be a physiological marker for fall-risk in older adults. Future research should examine differences in how muscle co-contraction is implemented in healthy and fall-prone older adults.

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Data accessibility

The original Excel data files for each measure have been made available via Figshare, DOI: 10.6084/m9.figshare.7448297.

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Figures

Figure 1. Diagram of the postural adaptation task.

The accuracy of proprioceptive information was manipulated using sway-referencing, during which the support surface tilts in proportion to body sway in the AP axis. Postural sway was assessed using infrared Codamotion markers placed at the C7, L5, right popliteal fossa, and right superior calcaneus. Muscle co-contraction (CCI) was assessed using EMG of the dominant TA, SOL and GM.

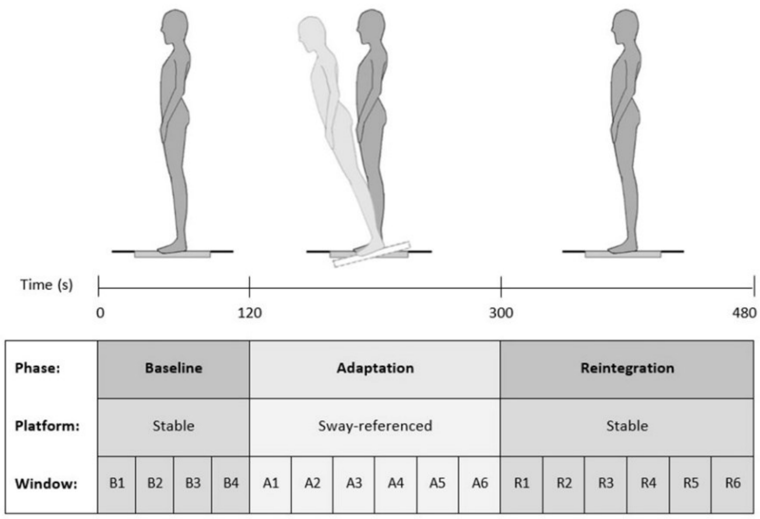

Figure 2. Schematic of experimental procedure.

Motion capture and EMG data were recorded during a 2-minute stable baseline phase, followed by 3 minutes of adaptation to sway-referencing and finally a 3-minute reintegration phase, in which the platform was stabilized. A push-button measure was used during the reintegration phase to assess the time at which participants perceived that the platform had stabilized.

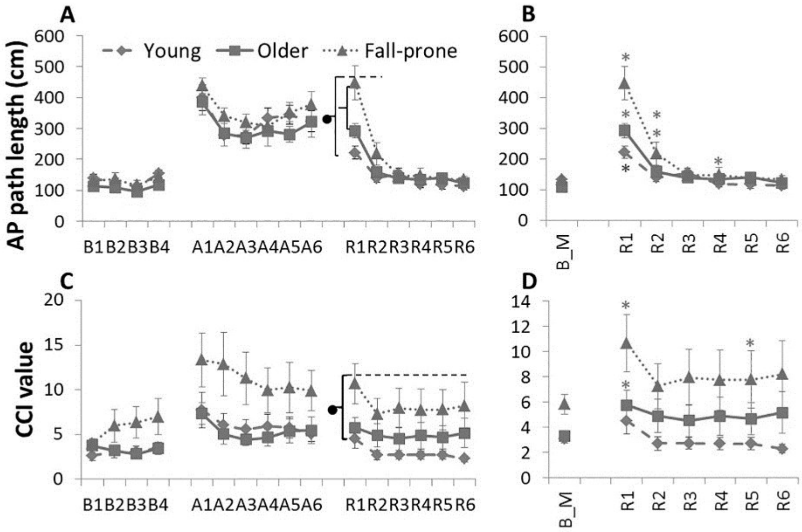

Figure 3. Experiment 1 AP path length from the hip marker and muscle co-contraction (CCI) results. (A) Mean AP path length from the hip marker for each 30s window of each postural phase; baseline (B1-4), adaptation (A1-6) and reintegration (R1-6) for each group. (B) Close up of the mean AP path length for each 30s window of the reintegration phase (R1-6), alongside the overall baseline mean (B_M) for each group. (C) Mean CCI values for the TA and GM, for each 30s window of each postural phase (B1-4, A1-6, R1-6) for each group. (D) Close up of the mean CCI values for each 30s window of the reintegration phase (R1-6), alongside the overall baseline mean (B_M) for each group.

N = 11 per group. Error bars represent the SEM. ● Significant group difference, indicated by simple effects analysis following ANOVA with group as between- and time window (per 30s) as within-subject factors, p< .05. Dashed lines represent the time windows over which this difference remained significant. */*/* Significant difference from baseline mean (B_M), indicated by paired t-tests with alpha level corrected for multiple comparisons, p< .008.

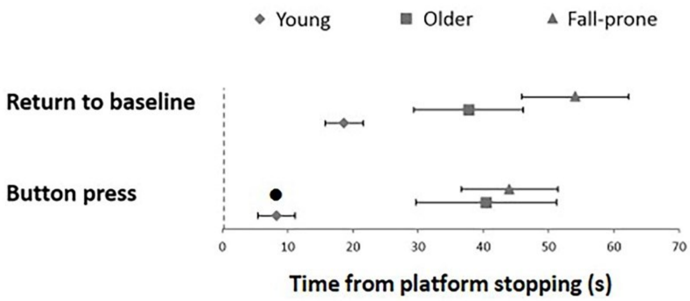

Figure 4. Experiment 1 group averages of the time taken to perceive that the platform had stopped moving (button press) and the time that each group's postural sway returned to baseline levels, compared to when the platform stopped moving (time=0).

N = 11 per group. Error bars represent SEM. ● Significant difference from both other groups, indicated by two-tailed independent samples t-test with alpha level corrected for multiple comparisons, p< .016.

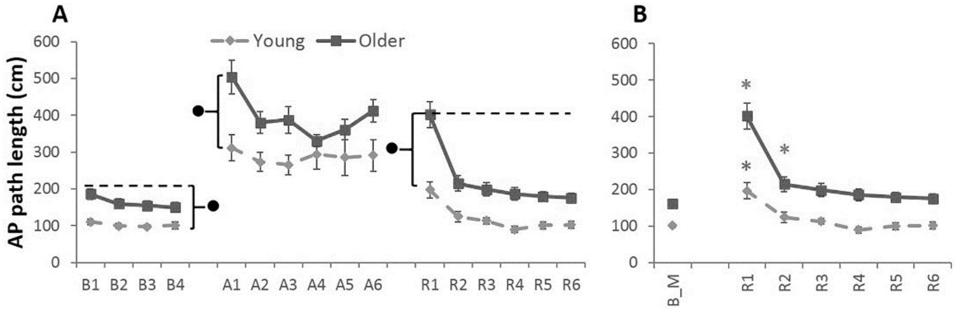

Figure 5. Experiment 2 AP path length from the hip marker results. (A) Mean AP path length from the hip marker for each 30s window of each postural phase; baseline (B1-4), adaptation (A1-6) and reintegration (R1-6) for each group. (B) Close up of the mean AP path length for each 30s window of the reintegration phase (R1-6), alongside the overall baseline mean (B_M) for each group.

N^{Young} = 11, N^{Older} = 14. Error bars represent the SEM. ● Significant group difference, indicated by mixed ANOVA, followed up by independent samples t-test with alpha level corrected for multiple comparisons, p< .008. Dashed lines represent the time windows over which this difference remained significant. */* Significant difference from baseline mean (B_M), indicated by paired t-tests with alpha level corrected for multiple comparisons, p< .008.

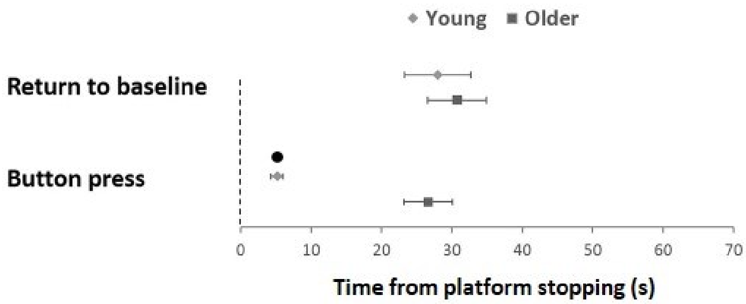

Figure 6. Experiment 2 group averages of the time taken to perceive that the platform had stopped moving (button press) and the time that each group's postural sway returned to baseline levels, compared to when the platform stopped moving (time=0).

$N^{Young} = 11$, $N^{Older} = 14$. Error bars represent SEM. ● Significant difference between groups, indicated by two-tailed independent samples t-test ($p < .001$).