



**QUEEN'S
UNIVERSITY
BELFAST**

Slowed sensory reweighting and postural illusions in older adults: the moving platform illusion

Craig, C., & Dumas, M. (2019). Slowed sensory reweighting and postural illusions in older adults: the moving platform illusion. *Journal of Neurophysiology*, 121, 690–700. <https://doi.org/10.1152/jn.00389.2018>

Published in:
Journal of Neurophysiology

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

Publisher rights
Copyright 2019 American Physiological Society. This work is made available online in accordance with the publisher's policies. Please refer to any applicable terms of use of the publisher.

General rights
Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy
The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

Open Access
This research has been made openly available by Queen's academics and its Open Research team. We would love to hear how access to this research benefits you. – Share your feedback with us: <http://go.qub.ac.uk/oa-feedback>

1

2

3

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

6

7 Chesney E. Craig^{1,2} and Michail Dumas¹

8

9 ¹ School of Psychology, Queen's University Belfast, Belfast, Antrim, UK, BT7 1NN

10 ² Research Centre for Musculoskeletal Science and Sports Medicine, Department of Exercise and Sport Science,
11 Manchester Metropolitan University, Crewe, Cheshire, UK, CW1 5DU

12

13

14 Author Contributions. Both authors (CC, MD) contributed to the study conceptualisation,
15 design, data analysis, data interpretation and writing of the manuscript. CC carried out the
16 data collection and wrote the initial draft.

17

18

19 Corresponding author: Chesney Craig

20 Research Centre for Musculoskeletal Science and Sports Medicine, Department of Exercise
21 and Sport Science, Manchester Metropolitan University, Crewe, Cheshire, United Kingdom

22 E: c.craig@mmu.ac.uk

23

24

25

26

Abstract

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

47 *New and Noteworthy:* This is the first paper to show that postural sway after-effects
48 witnessed in older adults after platform stabilization may be due to a perceptual illusion of
49 platform movement. Surprisingly, in both experiments presented it took older adults five
50 times longer than young adults to perceive platform stabilization. This supports a hypothesis

51 of less efficient sensory reintegration in this age group, which may delay the formation of an
52 accurate postural percept.

53

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

55

56

Introduction

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

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

84 Based on this evidence, it could be argued that the delayed sway reduction during the
85 reinstatement of a stable support reflects a conservative response by the postural control
86 system. This response is utilized to preserve CNS resources during transient conditions when
87 there is less postural threat (Jeka *et al.*, 2008), compared with transient conditions with higher

88 threat, such as when sway reference is introduced. This evidence is in line with research in
89 young adults which showed that sensory reweighting is faster when an unstable, threatening
90 environment is introduced but slower when a less threatening environment is restored (Jeka *et*
91 *al.*, 2008; Polastri *et al.*, 2012; Assländer & Peterka, 2014; Logan *et al.*, 2014). However, our
92 recent work demonstrated that the postural after-effects witnessed during platform
93 stabilization were accompanied by prolonged use of muscle co-contraction in older adults,
94 which suggests that this sensory transition posed considerable postural threat to this age
95 group (Craig *et al.*, 2017). This could have important real-life implications, as it suggests that
96 everyday sensory transitions, such as stepping off public transport, could pose considerable
97 postural instability and increased fall risk to older adults.

98 Overall, inefficient sensory reweighting may contribute to increased falls risk, as
99 during sensory transitions older adults will experience prolonged instability until sensory
100 reweighting has been accomplished. Accordingly, evidence supports that sensory reweighting
101 is particularly inefficient in fall-prone older adults, compared to healthy older adults (Jeka *et*
102 *al.*, 2010; Pasma *et al.*, 2015). This link between deficient sensory reweighting and balance
103 impairment is in line with a study that examined which parameters could best detect unstable
104 older adults at risk of *multiple* falls (Soto-Varela *et al.*, 2015). The authors found that the two
105 best predictors were: mean scores on the Sensory Organization Test, which assesses sensory
106 reweighting abilities, and directional control scores on the Limits of Stability test, which
107 assesses ability to control the center of gravity (CoG). These variables may contribute to the
108 leading cause of falls in older adults which is incorrect weight shifting (Robinovitch *et al.*,
109 2013), as sensory reweighting determines an accurate postural percept and directional control
110 determines the ability to efficiently adjust the CoG.

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

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

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

145 **Experimental Procedures**

146 **Participants**

147 ***Experiment 1***

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

151 = .08). Twelve healthy young, twelve healthy older and fourteen fall-prone older adults
152 volunteered to participate in the study. Participants were excluded based on any medical
153 history or recent medication use that could impair postural performance. For example,
154 participants were automatically excluded if they gave a confirmatory response to any of the
155 following; use of orthopedic shoes, previous stroke, Parkinson's disease, hip/knee
156 replacement, use of tricyclic antidepressants or sleep tranquilizers. Inclusion criteria for both
157 older groups also included, scoring 25+ on the *Mini-Mental State Examination (MMSE)* and
158 being classified as independent according to the *Katz Basic Activities of Daily Living* test
159 (Katz *et al.*, 1963) and the *Instrumental Activities of Daily Living Scale* (Lawton & Brody,
160 1969). Failure to meet the MMSE inclusion criteria, missing motion tracking data (gaps
161 >500ms) and extreme outliers resulted in a final sample of 11 young, 11 healthy older and 11
162 fall-prone older adults. The demographic information from the retained participants are listed
163 in Table 1.

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

171

172

173

174

175

176

177

178

179

180 Table 1.

181 *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)*

182

183 *Note.* Values represent mean values, with standard deviations in parentheses. BBS = Berg
 184 balance scale; BMI = body mass index; MMSE = Mini Mental State Examination; ADL =
 185 Katz Basic Activities of Daily Living; IADL = Instrumental Activities of Daily Living;
 186 RAPA = Rapid Assessment of Physical Activity.

187 * $p < .05$.

188

189 *Experiment 2*

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

198

199

200

201 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)*

202

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

205

206 **Apparatus and tasks**207 ***Experiment 1***

208 *Postural assessment.* The postural adaptation task was assessed using the Smart
 209 Balance Master (NeuroCom International, Inc., Clackamas, OR, USA). This device consists
 210 of an 18" x 18" dual force plate which records vertical forces at a sampling frequency of
 211 100Hz. The platform was sway-referenced using a servo-controlled motor which introduced
 212 platform tilts in the sagittal plane about the ankle joint axis in proportion to the participant's
 213 expected CoM sway angle (Nashner *et al.*, 1982). The mechanical compliance of the platform
 214 was determined by the pre-selected gain level. In line with Craig, Calvert and Doumas
 215 (2017), the current experiment utilized a gain level of 1.0 for older and fall-prone older adults
 216 and 1.6 for young adults. At a gain level of 1.0, the platform tilts 1° for every 1° of CoP sway.
 217 Whereas, at a gain factor of 1.6, platform tilt is 1.6 times greater than AP CoP sway, thus
 218 inducing greater postural sway (Clark & Riley, 2007). Similarly, to our previous studies, this
 219 manipulation was utilized in order to induce similar levels of postural sway in both age
 220 groups. A blindfold and a non-restrictive safety harness were worn throughout the postural
 221 adaptation task. Participants held a wireless mouse with their dominant hand throughout this
 222 task and were asked to click on the mouse button when the platform stopped moving.

223 *Motion capture.* Body kinematics were assessed during the postural adaptation task
 224 using a Codamotion CX1 sensor unit (Charnwood Dynamics Ltd., Rothley, Leicestershire,
 225 UK). This is an active marker system that utilizes infrared light-emitting diodes (ILEDs) to

226 capture motion data across three dimensions. The marker set-up (Figure 1) consisted of: 2
227 platform markers, one on the fixed section of the platform and one in front of it on the
228 posterior right corner of the moving support surface, and 4 body landmark markers, which
229 were placed at the C7 vertebra (neck level), L5 vertebra (hip level), right popliteal fossa
230 (knee level) and right superior calcaneus (ankle level). The CX1 unit was placed behind the
231 participant at a distance of approximately 2-metres from the fixed platform ILED. Motion
232 capture data were collected at a sampling rate of 100Hz.

233

234 [Insert Figure 1 here]

235

236 *EMG recordings.* Co-contraction of the tibialis anterior (TA) and the gastrocnemius
237 medialis (GM) and soleus (SOL) muscles of the dominant leg were assessed using surface
238 electromyography (EMG) during postural assessment. Disposable Ag-AgCl electrodes
239 (Cleartrace, CONMED, Utica, NY, USA) with an inter-electrode distance of 3cm were
240 attached vertically along the muscle belly of the TA, GM and SOL and a ground electrode
241 was placed on the patella. The EMG signal was pre-amplified at a gain of 2000 using a
242 differential amplifier (EMG100C, Biopac Systems, Inc., Santa Barbara, CA). The signal was
243 sampled at 2 kHz and was initially band-pass filtered at 10-500 Hz. Following this, EMG
244 data were normalized in relation to the maximum values recorded during three maximum
245 voluntary contractions (MVCs) from the TA, SOL and GM.

246 ***Experiment 2***

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

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

256

257 **Procedure**

258 ***Experiment 1***

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

269 The session continued with the postural adaptation task (Figure 2). Participants were
270 given two 1-min practice trials (one with eyes open, the other with eyes closed) during which
271 the platform was sway-referenced at the gain set for that age group (1.0 for older and 1.6 for
272 young participants). Subsequently, the experimental task comprised three phases: (1) a stable
273 2-min baseline phase, (2) a 3-min sway-referenced adaptation phase and (3) a stable 3-min
274 reintegration phase, all of which were performed blindfolded. Postural adaptation was
275 assessed in the range of minutes, rather than in short trials lasting up to a minute which is
276 typical in most postural control studies, on the basis of our previous work (Doumas &
277 Krampe, 2010). That study, using a long period of adaptation (18 min) showed that the
278 largest amount of adaptation to the sway referenced environment occurred after 3 minutes
279 and that after-effects lasted 1 min for young and over 2 minutes for older adults. In a
280 subsequent study, age differences in the after-effect were present even with a 3 min
281 adaptation phase (Craig *et al.*, 2017). The same durations were used in the present study.

282 Participants were instructed to stand as still as possible with their arms by their side.
283 They were warned 10 seconds before the sway-referenced phase was about to commence but
284 were *not* told whenever sway-referencing had stopped. Instead, participants were asked to
285 press a wireless mouse button whenever they believed the platform had stopped moving.
286 EMG activity from the dominant leg TA, SOL and GM muscles was recorded to assess co-
287 contraction levels during each phase of the postural task. Motion tracking was recorded as a

288 measure of AP path length and to explore the postural strategies employed. Participants wore
 289 a safety harness that did not restrict movement during all postural assessment.

290

291 [Insert Figure 2 here]

292 ***Experiment 2***

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

295

296 **Data analysis**

297 ***Experiment 1***

298 Preliminary data analysis was carried out using custom-written Matlab software. Gaps
 299 (<500ms) in the motion tracking data from each marker were interpolated using a cubic
 300 spline routine in Matlab (Warnica *et al.*, 2014). Data from each marker were low-pass filtered
 301 at 4Hz using a 4th order dual-pass Butterworth filter.

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

311 *Equation 1*

$$CCI(N) = \text{avg} \left(\frac{EMG_{\text{low}_i}}{EMG_{\text{high}_i}} \right) (EMG_{\text{low}_i} + EMG_{\text{high}_i})$$

312 N is the selected time window, EMG_{low} is the lower EMG value from the selected
 313 muscle pair (TA/GM or TA/SOL) at the i th data point and EMG_{high} is the higher EMG value
 314 at the i th data point. CCI was initially calculated for 1-s time windows (N), which included

315 4000 data points (i) in each, for the duration of each postural assessment block. For each i th
316 point, the ratio of the low over the high value from each muscle pair was calculated and then
317 multiplied by the sum of both values. In line with our previous paper (Craig *et al.*, 2016), the
318 mean CCI value of these products was calculated, rather than the overall sum. The 1-s mean
319 CCI values were then used to assess the overall mean CCI value for each 30s of the overall
320 data acquisition block. CCI analyses demonstrated a similar pattern of CCI across postural
321 phases in both muscle groups, however, the TA and GM pair showed larger CCI values,
322 therefore only the results from this muscle pair are reported.

323 AP path length of the hip marker and CCI were calculated in 30s windows for the
324 three phases. This window duration was chosen because it represents a typical duration of a
325 postural control trial in the literature, it is also sufficiently long to capture approximately
326 three full cycles of body movement during sway referencing (body movement frequency:
327 0.1Hz; Peterka & Loughlin, 2004; Doumas & Krampe, 2010) and because it allowed us to
328 plot and statistically analyze AP path length and CCI in the same manner. In a further
329 analysis AP path length for baseline and reintegration was calculated in 10s windows. This
330 calculation was used in order to increase our temporal resolution and to identify a more exact
331 time point in the reintegration phase in which sway returned to baseline levels and to
332 compare this point with the button-press. The 10s window at which each participant's AP
333 path length returned to baseline was determined as the first 10s reintegration time window
334 which was within one standard deviation of the baseline mean. The difference between this
335 return to baseline time and the time at which participants perceived that the platform was
336 stable (button press time) was then compared.

337 *Statistical analysis.* An outlier analysis was initially performed on each measure,
338 which identified outliers that fell two standard deviations beyond the group mean. Outliers
339 that were only present in one time window were normalized to the group mean, however,
340 participants who showed several outliers were excluded from the experiment. In line with
341 Craig *et al.* (2017), differences in AP path length and CCI within each phase were assessed
342 using two-way mixed-design ANOVAs with age as between- and time window (per 30s) as
343 within-subject factors. Differences in AP path length and CCI during the sensory transitions
344 were assessed using mixed-design ANOVAs, which compared the baseline mean to the mean
345 of the adaptation and reintegration phase in both age groups. Paired samples t-tests were run
346 to examine whether there were significant differences between the exact 10s window that

347 each group's AP path length returned to baseline and the time of their button press to indicate
348 when they perceived the platforms return to stability. In ANOVAs in which sphericity was
349 violated a Greenhouse-Geisser correction was applied. Predicted effects and/or interactions
350 were explored further with simple effects analyses and unexpected effects were explored
351 further using Bonferroni post hoc tests.

352 *Experiment 2*

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

355

356

Results

357 **EXPERIMENT 1**

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

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

366 **ADAPTATION.** Exposure to a sway-referenced support instilled a large increase in
367 AP path length of the hip marker in all groups, as shown in Figure 3A. A mixed-design
368 ANOVA, which compared the mean AP path length during adaptation to the mean during
369 baseline, confirmed that AP path length was significantly higher during the adaptation phase,
370 $F(1,30) = 161.88, p < .001, \eta_p^2 = .84$. There was no difference between groups or interaction
371 between group and condition. Analysis of AP path length throughout the adaptation phase,
372 also found no overall effect of group, mirroring our previous findings that increasing the gain
373 setting for young adults can remove any age differences in postural sway. AP path length
374 decreased over time as shown by a main effect of window, $F(3.56,106.81) = 13.47, p =$
375 $.001, \eta_p^2 = .31$. Bonferroni pairwise comparisons indicated that AP path length showed

376 successive decline between windows A1 and 2 ($p < .001$). There was no interaction between
377 time window and group in the adaptation phase.

378 REINTEGRATION. The restoration of a stable support surface resulted in clear
379 postural after effects, which were larger in older adults, especially fall-prone older adults
380 (Figure 3A). The significance of these after-effects was confirmed using a mixed-design
381 ANOVA, which compared the mean AP path length of the hip marker during reintegration
382 with the mean of the 4 baseline windows (B1-B4). Results showed that AP path length was
383 significantly higher during reintegration, $F(1,30) = 51.14, p < .001, \eta_p^2 = .63$. More
384 importantly, a group by phase interaction, $F(1,30) = 7.77, p = .002, \eta_p^2 = .34$, suggested older
385 and fall prone older adults may show a greater AP path length increase compared with young
386 adults. Paired samples t-tests with an alpha level corrected for multiple comparisons to 0.017,
387 showed that both older adult groups showed significantly higher AP path length during
388 reintegration (Healthy: $t(10) = 4.97, p = .001$; Fall-prone: $t(10) = 5.62, p < .001$), but this
389 increase was not shown in young adults. The duration of any significant after-effects were
390 examined using paired samples t-tests comparing each 30s reintegration window with the
391 mean of the baseline windows, with an alpha level corrected for multiple comparisons to
392 0.008. Tests showed that for young adults the after-effect was only significantly different
393 from baseline in the first 30s (R1), $t(10) = 3.71, p = .004$. However, for both older groups, the
394 after-effect was significant for up to 60 s (window R2) (Healthy: $t(10) = 8.24 - 3.40, p \leq$
395 $.001-.007$; Fall-prone: $t(10) = 7.27 - 3.38, p \leq .001-.007$). Between window R2 and R4 there
396 was also a slight increase in path length for the healthy older group, resulting in an additional
397 difference between baseline and window 4, $t(10) = 3.99, p = .003$.

398 Analysis of AP path length of the hip marker throughout the reintegration phase was
399 performed to assess whether the observed pattern of results (Figure 3A) showing that fall
400 prone older adults exhibit the largest after-effect was statistically reliable. Results showed a
401 main effect of group within the reintegration phase, $F(2,30) = 4.01, p = .03, \eta_p^2 = .21$, which
402 varied across 30s time windows, as shown by a significant time window by group interaction,
403 $F(5,150) = 8.91, p < .001, \eta_p^2 = .37$. Simple effects analyses demonstrated that there was a
404 significant difference between fall-prone and young adults for windows R1 and R2, (winR1:
405 $F(1,20) = 16.11, p = .001$; winR2: $F(1,20) = 4.35, p = .03$), whereby fall-prone older adults
406 showed a larger after-effect compared to young adults (Figure 3A). Additionally, fall-prone
407 older adults also showed a larger after-effect than healthy older adults during window R1,

408 $F(1,20) = 7.33, p = .01$, and healthy older adults showed a larger after-effect than young
409 adults during this window, $F(1,20) = 5.74, p = .01$. AP path length declined over time as
410 shown by a main effect of window, $F(2.23,66.79) = 77.02, p = .001, \eta_p^2 = .72$. Bonferroni
411 pairwise comparisons revealed that all groups only showed a significant decrease in path
412 length between successive windows from R1 to R2, (Young: $p = .04$; Healthy: $p = .001$; Fall-
413 prone: $p < .001$).

414

415 [Insert Figure 3 here]

416

417

418 **Muscle co-contraction (CCI)**

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

423 **ADAPTATION.** During exposure to a sway-referenced support, all groups showed an
424 increase in CCI levels, however, this was particularly pronounced in fall-prone older adults
425 (Figure 3B). A mixed-design ANOVA comparing the adaptation mean to the baseline mean
426 confirmed that CCI levels were higher during the adaptation phase, $F(1,30) = 34.34, p < .001,$
427 $\eta_p^2 = .53$. However, there was no difference between groups or interaction between group and
428 condition. Analysis of CCI levels across the adaptation phase showed that the effect of group
429 approached significance ($p = .050$) and CCI declined over time, $F(3.12,93.70) = 6.84, p <$
430 $.001, \eta_p^2 = .19$. Bonferroni pairwise comparisons indicated that the change in CCI levels was
431 gradual, as there were no significant differences between successive windows, however,
432 window A1 was significantly higher than all windows apart from A2, ($p = .001-.03$). There
433 was no group by time window interaction.

434 **REINTEGRATION.** During the restoration of a stable support surface, each group
435 showed a peak in CCI levels during the first 30s window (R1), which was larger in fall-prone
436 older adults (Figure 3B). Similarly to the AP path length analysis, a mixed-design ANOVA
437 comparing the mean of the reintegration phase to the baseline mean was used to examine the

438 significance of this CCI after-effect. The analysis confirmed that CCI levels were greater
439 during the reintegration phase, $F(1,30) = 9.22, p = .005, \eta_p^2 = .24$. Additionally, the test found
440 a significant effect of group, $F(1,30) = 3.40, p = .047, \eta_p^2 = .19$, which Bonferroni pairwise
441 comparisons showed was due to larger CCI levels in fall-prone older adults compared to
442 young adults ($p = .03$). The duration of the CCI after-effect for each group was assessed using
443 paired samples t-tests comparing each 30s reintegration window with the mean of the
444 baseline windows, with an alpha level corrected for multiple comparisons to 0.008. These
445 tests demonstrated that young adults showed no significant CCI after-effect for any window.
446 However, both healthy older and fall-prone older adults show a significant after-effect in the
447 first 30s window (Healthy: $t(10) = 3.29, p = .008$; Fall-prone: $t(10) = 3.56, p = .005$).

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

455 **Perception of platform stability and postural after-effects**

456 Two-tailed independent samples t-tests, with an alpha value corrected for multiple
457 comparisons to 0.016, were used to explore whether there were significant age differences in
458 the time at which each group perceived that the platform had stabilized at the start of the
459 reintegration phase (Figure 4). Both older groups pressed the push button significantly later
460 than the young group (healthy vs. young: $t(20) = 3.03, p = .007$; fall-prone vs. young:
461 $t(12.89) = 4.27, p = .001$) and there were no differences in the perception of platform stability
462 between the two older adult groups.

463 Paired samples t-tests were also used to examine differences between the time
464 window at which the postural after-effect returned to baseline and the time at which the
465 participants perceived that the platform had stopped moving, for each group (Figure 4). Only
466 young adults showed a difference between the two latencies, namely they perceived the
467 reinstatement of a stable platform earlier than postural sway returned to baseline levels $t(10)$
468 $= 2.95, p = .02$. (Figure 4). However, for both older groups the time at which they perceived

469 the reinstatement of a stable platform was similar to the time that postural sway returned to
470 baseline levels. Albeit not significant, it is instructive to note that healthy older adults' sway
471 returned to baseline before they perceived the return to stability a few seconds later, whereas
472 for fall-prone older adults they perceived the stable platform ~14s before their sway returned
473 to baseline. Additionally, it should be noted that one fall-prone older adult never pressed the
474 push-button, as they failed to recognise that the platform had stopped moving throughout the
475 duration of the reintegration phase. This participant's time was normalized to the group
476 mean. No participant pressed the push-button before the platform had stabilized.

477 [Insert Figure 4 here]

478

479 **EXPERIMENT 2**

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

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

489 **ADAPTATION.** In line with Experiment 1, exposure to a sway-referenced support
490 instilled a large increase in AP path length of the hip marker in both groups, as witnessed in
491 Figure 5A. A mixed-design ANOVA, which compared the mean AP path length during
492 adaptation to the mean during baseline, confirmed that AP path length was significantly
493 higher during the adaptation phase, $F(1,23) = 107.85, p < .001, \eta_p^2 = .82$. In this case, there
494 was also a significant difference between groups, $F(1,23) = 13.02, p = .001, \eta_p^2 = .36$, which
495 suggested that the age difference witnessed at baseline was maintained in the adaptation
496 phase. There was no significant interaction ($p = .24$). Analysis of AP path length throughout
497 the adaptation phase, also showed a significant difference between groups, $F(1,23) = 6.95, p =$
498 $.015, \eta_p^2 = .23$, and a significant change across time windows, $F(5,115) = 4.98, p < .001, \eta_p^2 =$
499 $.18$. There was also a significant interaction between group and time window, $F(5,115) =$

500 2.75, $p = .02$, $\eta_p^2 = .11$. Examination of the effect of time window in each group individually
501 showed that young participants did not show a significant reduction in AP path length over
502 time ($p = .72$), whereas older adults did show an effect of time window, $F(5,65) = 7.31$, $p <$
503 $.001$, $\eta_p^2 = .36$. Bonferroni pairwise comparisons showed that AP path length showed
504 successive decline between windows A1 and 2 ($p = .03$) for older adults. In addition,
505 independent samples t-tests with an alpha level corrected for multiple comparisons to 0.008,
506 showed that the older adult group showed significantly higher AP path length compared to
507 young adults during the first adaptation window only ($t(23) = 3.09$, $p = .005$).

508 REINTEGRATION. In line with Experiment 1, restoration of a stable support surface
509 resulted in clear postural after effects, which were larger in older adults (Figure 5B). This was
510 confirmed using a mixed-design ANOVA, which compared the mean AP path length of the
511 hip marker during the reintegration phase with the mean during baseline (B_M). Results
512 showed that AP path length was significantly higher during reintegration, $F(1,23) = 40.22$, $p <$
513 $.001$, $\eta_p^2 = .64$, and there was a significant group difference, $F(1,23) = 27.62$, $p <$
514 $.001$, $\eta_p^2 = .55$. Additionally, a group by phase interaction, $F(1,23) = 11.49$, $p = .003$, $\eta_p^2 = .33$, suggested
515 that the after effect may differ between age groups. The duration of the after-effect for each
516 group was assessed using paired samples t-tests comparing each 30s reintegration window
517 with the baseline mean (Figure 5B), with an alpha level corrected for multiple comparisons to
518 0.008. In younger adults, AP path length was only significantly higher than baseline during
519 the first 30s reintegration window ($t(10) = 4.51$, $p = .001$). However, in parallel to Experiment
520 1, the after-effect was significant for up to 60s (R2) in older adults ($t(10) = 7.05$ - 4.14, $p \leq$
521 $.001$).

522 Analysis of AP path length of the hip marker throughout the reintegration phase was
523 performed to assess whether age differences occurred across different time windows. The
524 analysis found an overall group difference, $F(1,23) = 28.75$, $p <$
525 $.001$, $\eta_p^2 = .56$, and change in
526 path length across time windows, $F(5,115) = 36.01$, $p <$
527 $.001$, $\eta_p^2 = .61$. In addition, there was
528 a significant interaction between age group and time window, $F(5,115) = 5.56$, $p <$
529 $.001$, $\eta_p^2 = .20$. Examination of the effect of time window in each group individually showed that both
530 groups showed a significant reduction in AP path length over time (Young: $F(1.71,25.60) =$
531 17.30 , $p <$
529 $.001$, $\eta_p^2 = .63$; Older: $F(1.97, 25.60) = 26.34$, $p <$
530 $.001$, $\eta_p^2 = .67$). Bonferroni
531 pairwise comparisons showed that only older adults showed an immediate significant decline
in path length between windows 1 and 2 ($p <$
531 $.001$), whereas in young adults decline was

532 more gradual, with a significant reduction from window 1 shown from window 3 onwards
533 ($p = .007-.02$). In addition, independent samples t-tests with an alpha level corrected for
534 multiple comparisons to 0.008, showed that the older adult group showed significantly higher
535 AP path length compared to young adults across all reintegration time windows ($p \leq .003$).

536 [Insert Figure 5 here]

537

538 **Perception of platform stability and postural after-effects**

539 A two-tailed independent samples t-test was used to investigate whether there was a
540 significant age difference in the time at which each group perceived that the platform had
541 stabilized at the start of the reintegration phase (Figure 6). In line with Experiment 1, the
542 older adults pressed the push button significantly later than the young group ($t(14.53) = 6.06$,
543 $p < .001$). On average, older adults pressed the push button over 5x later than young adults
544 ($M_{Young} = 5.18 \pm 2.66s$, $M_{Older} = 26.63 \pm 12.86s$).

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

551 [Insert Figure 6 here]

552

553 **Discussion**

554 The current paper had two key aims; (1) to investigate whether postural sway and
555 muscle co-contraction after-effects during the restoration of a stable support differed in
556 healthy and fall-prone older adults, and (2) to examine whether such after-effects were
557 accompanied by a delayed perception of platform stabilisation, in support of the argument of
558 an age-related slowing of sensory reweighting. In line with our previous findings, in
559 Experiment 1 we found that both older groups showed significantly larger and longer postural
560 after-effects when a stable platform was reinstated and proprioceptive information was
561 reintegrated, compared to young adults (Domas & Krampe, 2010; Craig *et al.*, 2017). As

562 predicted, this postural after-effect was also significantly larger in the fall-prone group,
563 compared to the healthy older adults, suggesting that this transition may instill additional
564 instability in this group. Additionally, in both older groups, after-effects were also witnessed
565 in terms of muscle co-contraction. More importantly, we demonstrated that these after-effects
566 were accompanied by a delayed perception that the platform had stopped moving, as it took
567 both older groups five times longer than the young group to detect this change.

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

582 In support of our hypothesis, the perceptual illusion was maintained in Experiment 2,
583 in which a healthy older sample once more took five times longer than the young group to
584 detect platform stabilization, despite postural adaptation to the same gain setting (gain = 1).
585 Additionally, Experiment 2 successfully replicated other key findings of Experiment 1,
586 namely the similar adaptation rates between age groups and the larger and longer aftereffects
587 for older adults in the 30s reintegration phase analysis. However, some secondary differences
588 were shown between the two experiments with older adults showing larger baseline postural
589 sway compared with young adults, which has also been shown in one of our previous studies
590 (Doumas & Krampe, 2010). Older adults also showed lower group variability in both the
591 perceptual delay and the return to baseline in Experiment 2 compared with Experiment 1 (see
592 error bars in Figures 6 and 4 respectively) suggesting that the older group in Experiment 2
593 was inherently more homogeneous. Regardless of these secondary differences between

594 experiments, the replication of a fivefold delay in the time to detect platform stabilization in
595 older adults supports that the perceptual illusion is a robust age-specific effect. This finding,
596 in combination with the age-related postural sway after-effects witnessed in both studies,
597 provides compelling evidence that sensory reweighting is deficient when attempting to
598 reintegrate veridical proprioceptive information. The duration of this perceptual illusion of
599 continued movement is striking, as it implies that the previously noted age-related delays in
600 sensory reweighting (O'Connor *et al.*, 2008; Doumas & Krampe, 2010; Jeka *et al.*, 2010;
601 Eikema *et al.*, 2012, 2013) could have significant perceptual consequences in real life. For
602 example, everyday sensory transitions, such as, stepping off recently moving transport
603 (especially in dark conditions) could pose a considerable fall risk to an older person.

604 **Age-related Deficits in Sensory Reweighting**

605 The age-related postural sway after-effects shown in the present paper are observed
606 after prolonged adaptation to a sway-referenced surface. When standing on this surface,
607 proprioceptive information about body sway is inaccurate and as a result the weight assigned
608 to proprioception is reduced (Peterka & Loughlin, 2004). At the same time the weight for the
609 accurate, vestibular input increases and gradually sway is reduced over the 3 minutes of
610 adaptation. However, when the stable surface is restored the initial weights also have to be
611 restored. Restoration of the two weights is much slower in older adults (Doumas & Krampe,
612 2010; Craig *et al.*, 2017) and in the present Experiment 1 in fall-prone older adults, and this
613 slowing is reflected in the age-related postural sway after-effect. Our findings suggest that
614 this slow sensory reweighting in older adults results in the delayed formation of an accurate
615 postural percept. Previous research had suggested that postural after-effects during platform
616 stabilization could be due to a conservative strategy to preserve CNS resources dedicated to
617 postural control during transient conditions of reduced postural threat (Jeka *et al.*, 2008).
618 However, our finding of a continued perception that the platform is moving (Experiment 1 &
619 2) and prolonged muscle co-contraction in older adults (Experiment 1), suggests that
620 considerable postural threat is still experienced during this transition. Rather, slowed sensory
621 reweighting in older adults results in the delayed formation of an accurate postural percept,
622 which is associated with prolonged postural sway until sensory reweighting is completed,
623 which may instil a postural illusion in this age group that the platform is still moving.

624 It is interesting to note in Experiment 1, that whilst fall-prone older adults
625 demonstrated a significantly larger postural sway after-effect compared to healthy older

626 adults, there was no significant difference in the time at which these groups perceived
627 platform stabilisation. This could suggest that sensory reweighting delays are similar in both
628 groups but the body's ability to compensate for this is impaired in fall-prone older adults. In
629 support of this, fall-prone older adults showed similar postural sway in the first 30s of the
630 reintegration phase to that shown during the first 30s of sway-referencing, suggesting that this
631 transition resulted in considerable postural instability in this group. Furthermore, the extent of
632 fall-prone older adults' reliance on co-contraction during the reintegration phase was
633 noteworthy, as whilst their postural sway levels gradually reached the same values as young
634 adults', their CCI remained higher than young adults' throughout the reintegration phase.
635 This is important, because if used excessively, muscle co-contraction is likely to be
636 maladaptive, as literature shows that co-contraction can increase postural sway (Laughton *et al.*,
637 2003; Reynolds, 2010; Nagai *et al.*, 2011; Warnica *et al.*, 2014) and has been associated
638 with increased falls risk (Ho & Bendrups, 2002; Nelson-Wong *et al.*, 2012). This increased
639 falls risk could be due to increased lower limb rigidity and impeded adaptive reactions to
640 postural perturbations (Tucker *et al.*, 2008) or reduced proprioceptive input from active
641 muscle spindles, compared to passive muscle spindles (Wise *et al.*, 1998; Proske &
642 Gandevia, 2012).

643 **Muscle Co-contraction**

644 This pattern of increased reliance on muscle co-contraction in fall-prone older adults
645 was shown throughout each postural phase in Experiment 1 but only reached significance
646 during reintegration, whenever postural sway also showed a significant age difference. The
647 literature suggests that muscle co-contraction is witnessed in response to increased challenge
648 to postural stability (Chambers & Cham, 2007; Cenciarini *et al.*, 2010; Warnica *et al.*, 2014)
649 and is generally higher in those with poorer postural control ability (Nagai *et al.*, 2011, 2016).
650 It is thought that muscle co-contraction is used as ankle stiffening strategy to minimize
651 postural sway (Baratta *et al.*, 1988; Hortobágyi & Devita, 2000; Benjuya *et al.*, 2004;
652 Engelhart *et al.*, 2015). In support of this, we found that all groups showed increased muscle
653 co-contraction when exposed to increased postural sway due to a sway-referenced support.
654 However, in contrast to our previous findings (Craig *et al.*, 2016, 2017) and other literature
655 (Nagai *et al.*, 2011, 2013), we did not find significant age differences in muscle co-
656 contraction throughout all phases. This is likely due to the stratification of older adults into
657 'healthy' and 'fall-prone' groups in the current study, which was not done in the previous

658 literature. Nagai et al (2011, 2013) reported that high muscle co-contraction was strongly
659 associated with poorer postural performance in older adults. In light of which, they proposed
660 that muscle co-contraction use could be utilised as a predictor of postural impairment (Nagai
661 *et al.*, 2013). Consequently, our current results may not be surprising and could support the
662 use of muscle co-contraction as an indicator of balance impairment and potential falls risk.

663 **Study Limitations and Future Directions**

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

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

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

704

705 **Acknowledgments**

706 The authors wish to thank Nialla Doherty, Glenn Calvert and Rebecca Stevenson for
707 their assistance in data collection during this project.

708 **Grants**

709 This work was supported by a Department of Employment and Learning PhD
710 studentship to C. Craig and a British Academy/Leverhulme Small Research Grant
711 R1067PSY to M. Dumas.

712 **Data accessibility**

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

715

716

- 717 Assländer, L. & Peterka, R.J. (2014) Sensory reweighting dynamics in human postural
718 control. *J. Neurophysiol.*, **111**, 1852–1864.
- 719 Baratta, R., Solomonow, M., Zhou, B.H., Letson, D., Chuinard, R., & D’Ambrosia, R. (1988)
720 Muscular coactivation. The role of the antagonist musculature in maintaining knee
721 stability. *Am. J. Sports Med.*, **16**, 113–122.
- 722 Benjuya, N., Melzer, I., & Kaplanski, J. (2004) Aging-induced shifts from a reliance on
723 sensory input to muscle cocontraction during balanced standing. *journals Gerontol. A,*
724 *Biol. Sci. Med. Sci.*, **59**, 166–171.
- 725 Berg, K., Wood-Dauphinee, S., Williams, J.I., & Gayton, D. (1989) Measuring balance in the
726 elderly: preliminary development of an instrument. *Physiother. Canada*, **41**, 304–311.
- 727 Cenciari, M., Loughlin, P.J., Sparto, P.J., & Redfern, M.S. (2010) Stiffness and damping in
728 postural control increase with age. *IEEE Trans. Biomed. Eng.*, **57**, 267–275.
- 729 Chambers, A.J. & Cham, R. (2007) Slip-related muscle activation patterns in the stance leg
730 during walking. *Gait Posture*, **25**, 565–572.
- 731 Clark, S. & Riley, M.A. (2007) Multisensory information for postural control: sway-
732 referencing gain shapes center of pressure variability and temporal dynamics. *Exp. brain*
733 *Res.*, **176**, 299–310.
- 734 Craig, C.E., Calvert, G.H.M., & Dumas, M. (2017) Effects of the availability of accurate
735 proprioceptive information on older adults’ postural sway and muscle co-contraction.
736 *Eur. J. Neurosci.*, **46**, 2548–2556.
- 737 Craig, C.E., Goble, D.J., & Dumas, M. (2016) Proprioceptive acuity predicts muscle co-
738 contraction of the tibialis anterior and gastrocnemius medialis in older adults’ dynamic
739 postural control. *Neuroscience*, **322**, 251–261.
- 740 Dickin, D.C., Brown, L.A., & Doan, J.B. (2006) Age-dependent differences in the time
741 course of postural control during sensory perturbations. *Aging Clin. Exp. Res.*, **18**, 94–
742 99.
- 743 Dumas, M. & Krampe, R.T. (2010) Adaptation and reintegration of proprioceptive
744 information in young and older adults’ postural control. *J. Neurophysiol.*, **104**, 1969–
745 1977.
- 746 Eikema, D.J.A., Hatzitaki, V., Konstantakos, V., & Papaxanthis, C. (2013) Elderly adults
747 delay proprioceptive reweighting during the anticipation of collision avoidance when
748 standing. *Neuroscience*, **234**, 22–30.
- 749 Eikema, D.J.A., Hatzitaki, V., Tzovaras, D., & Papaxanthis, C. (2012) Age-dependent

- 750 modulation of sensory reweighting for controlling posture in a dynamic virtual
751 environment. *Age (Omaha)*, **34**, 1381–1392.
- 752 Engelhart, D., Pasma, J.H., H, Schouten, A.C., Aarts, R.G.K.M., Meskers, C.G.M., Maier,
753 A.B., & van der Kooij, H. (2015) Adaptation of multi-joint coordination during standing
754 balance in healthy young and healthy old individuals. *J. Neurophysiol.*, **216**,
755 jn.00030.2015.
- 756 Ernst, M.O. & Banks, M.S. (2002) Humans integrate visual and haptic information in a
757 statistically optimal fashion. *Nature*, **415**, 429–433.
- 758 Falconer, K. & Winter, D.A. (1985) Quantitative assessment of co-contraction at the ankle
759 joint in walking. *Electromyogr. Clin. Neurophysiol.*, **25**, 135–149.
- 760 Fozard, J.L., Vercruyssen, M., Reynolds, S.L., Hancock, P.A., & Quilter, R.E. (1994) Age
761 Differences and Changes in Reaction Time: The Baltimore Longitudinal Study of
762 Aging. *J. Gerontol.* , **49**, P179–P189.
- 763 Ho, C.Y. & Bendrups, A.P. (2002) Ankle reflex stiffness during unperceived perturbation of
764 standing in elderly subjects. *J. Gerontol. A. Biol. Sci. Med. Sci.*, **57**, B344–B350.
- 765 Horak, F.B. & Macpherson, J.. (1996) Postural Orientation and Equilibrium. In Terjung, R.
766 (ed), *Handbook of Physiology. Section 12. Exercise: Regulation and Integration of*
767 *Multiple Systems*. John Wiley & Sons, Inc., Hoboken, NJ, USA, pp. 255–292.
- 768 Horak, F.B., Shupert, C.L., & Mirka, A. (1989) Components of postural dyscontrol in the
769 elderly: a review. *Neurobiol. Aging*, **10**, 727–738.
- 770 Hortobágyi, T. & Devita, P. (2000) Muscle pre- and coactivity during downward stepping are
771 associated with leg stiffness in aging. *J. Electromyogr. Kinesiol.*, **10**, 117–126.
- 772 Jeka, J.J., Allison, L.K., & Kiemel, T. (2010) The dynamics of visual reweighting in healthy
773 and fall-prone older adults. *J. Mot. Behav.*, **42**, 37–41.
- 774 Jeka, J.J., Oie, K.S., & Kiemel, T. (2008) Asymmetric adaptation with functional advantage
775 in human sensorimotor control. *Exp. Brain Res.*, **191**, 453–463.
- 776 Katz, S., Ford, A.B., Moskowitz, R.W., Jackson, B.A., & Jaffe, M.W. (1963) Studies of
777 illness in the aged. The index of ADL: A standardised measure of biological and
778 psychological function. *JAMA*, **185**, 914–919.
- 779 Kurlowicz, L. & Wallace, M. (1999) The Mini Mental State Examination (MMSE). *Director*,
780 **7**, 62.
- 781 Lajoie, Y. & Gallagher, S.. (2004) Predicting falls within the elderly community: comparison
782 of postural sway, reaction time, the Berg balance scale and the Activities-specific

- 783 Balance Confidence (ABC) scale for comparing fallers and non-fallers. *Arch. Gerontol.*
784 *Geriatr.*, **38**, 11–26.
- 785 Laughton, C.A., Slavin, M., Katdare, K., Nolan, L., Bean, J.F., Kerrigan, D.C., Phillips, E.,
786 Lipsitz, L.A., & Collins, J.J. (2003) Aging, muscle activity, and balance control:
787 Physiologic changes associated with balance impairment. *Gait Posture*, **18**, 101–108.
- 788 Lawton, M.P. & Brody, E.M. (1969) Assessment of Older People: Self-Maintaining and
789 Instrumental Activities of Daily Living. *Gerontol.* , **9**, 179–186.
- 790 Lewek, M.D., Rudolph, K.S., & Snyder-Mackler, L. (2004) Control of frontal plane knee
791 laxity during gait in patients with medial compartment knee osteoarthritis. *Osteoarthritis*
792 *Cartilage*, **12**, 745–751.
- 793 Lima, C.A., Ricci, N.A., Nogueira, E.C., & Perracini, M.R. (2018) The Berg Balance Scale
794 as a clinical screening tool to predict fall risk in older adults: a systematic review.
795 *Physiotherapy*,.
- 796 Logan, D., Kiemel, T., & Jeka, J.J. (2014) Asymmetric sensory reweighting in human upright
797 stance. *PLoS One*, **9**, e100418.
- 798 Nagai, K., Okita, Y., Ogaya, S., & Tsuboyama, T. (2016) Effect of higher muscle
799 coactivation on standing postural response to perturbation in older adults. *Aging Clin.*
800 *Exp. Res.*,.
- 801 Nagai, K., Yamada, M., Mori, S., Tanaka, B., Uemura, K., Aoyama, T., Ichihashi, N., &
802 Tsuboyama, T. (2013) Effect of the muscle coactivation during quiet standing on
803 dynamic postural control in older adults. *Arch. Gerontol. Geriatr.*, **56**, 129–133.
- 804 Nagai, K., Yamada, M., Uemura, K., Yamada, Y., Ichihashi, N., & Tsuboyama, T. (2011)
805 Differences in muscle coactivation during postural control between healthy older and
806 young adults. *Arch. Gerontol. Geriatr.*, **53**, 338–343.
- 807 Nashner, L.M., Black, F.O., & Wall, C. (1982) Adaptation to altered support and visual
808 conditions during stance: patients with vestibular deficits. *J. Neurosci.*, **2**, 536–544.
- 809 Nelson-Wong, E., Appell, R., McKay, M., Nawaz, H., Roth, J., Sigler, R., Third, J., &
810 Walker, M. (2012) Increased fall risk is associated with elevated co-contraction about
811 the ankle during static balance challenges in older adults. *Eur. J. Appl. Physiol.*, **112**,
812 1379–1389.
- 813 O'Connor, K.W., Loughlin, P.J., Redfern, M.S., & Sparto, P.J. (2008) Postural adaptations to
814 repeated optic flow stimulation in older adults. *Gait Posture*, **28**, 385–391.
- 815 Pasma, J.H., Engelhart, D., Maier, A.B., Schouten, A.C., van der Kooij, H., & Meskers,

- 816 C.G.M. (2015) Changes in sensory reweighting of proprioceptive information during
817 standing balance with age and disease. *J. Neurophysiol.*, **114**, 3220–3233.
- 818 Peterka, R.J. & Loughlin, P.J. (2004) Dynamic regulation of sensorimotor integration in
819 human postural control. *J. Neurophysiol.*, **91**, 410–423.
- 820 Polastri, P.F., Barela, J.A., Kiemel, T., & Jeka, J.J. (2012) Dynamics of inter-modality re-
821 weighting during human postural control. *Exp. brain Res.*, **223**, 99–108.
- 822 Proske, U. & Gandevia, S.C. (2012) The Proprioceptive Senses: Their Roles in Signaling
823 Body Shape, Body Position and Movement, and Muscle Force. *Physiol Rev*, **92**, 1651–
824 1697.
- 825 Reynolds, R.F. (2010) The ability to voluntarily control sway reflects the difficulty of the
826 standing task. *Gait Posture*, **31**, 78–81.
- 827 Soto-Varela, A., Faraldo-García, A., Rossi-Izquierdo, M., Lirola-Delgado, A., Vaamonde-
828 Sánchez-Andrade, I., del-Río-Valeiras, M., Gayoso-Diz, P., & Santos-Pérez, S. (2015)
829 Can we predict the risk of falls in elderly patients with instability? *Auris Nasus Larynx*,
830 **42**, 8–14.
- 831 Teasdale, N. & Simoneau, M. (2001) Attentional demands for postural control: the effects of
832 aging and sensory reintegration. *Gait Posture*, **14**, 203–210.
- 833 Topolski, T.D., LoGerfo, J., Patrick, D.L., Williams, B., Walwick, J., & Patrick, M.B. (2006)
834 The Rapid Assessment of Physical Activity (RAPA) among older adults. *Prev. Chronic
835 Dis.*, **3**, A118.
- 836 Tucker, M.G., Kavanagh, J.J., Barrett, R.S., & Morrison, S. (2008) Age-related differences in
837 postural reaction time and coordination during voluntary sway movements. *Hum. Mov.
838 Sci.*, **27**, 728–737.
- 839 Warnica, M.J., Weaver, T.B., Prentice, S.D., & Laing, A.C. (2014) The influence of ankle
840 muscle activation on postural sway during quiet stance. *Gait Posture*, **39**, 1115–1121.
- 841 Wise, A.K., Gregory, J.E., & Proske, U. (1998) Detection of movements of the human
842 forearm during and after co-contractions of muscles acting at the elbow joint. *J.
843 Physiol.*, **508**, 325–330.
- 844

845

Figure Captions

846 *Figure 1.* Diagram of the postural adaptation task.

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

851

852 *Figure 2.* Schematic of experimental procedure.

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

857

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

865 $N = 11$ per group. Error bars represent the SEM. ● Significant group difference, indicated by simple
866 effects analysis following ANOVA with group as between- and time window (per 30s) as within-
867 subject factors, $p < .05$. Dashed lines represent the time windows over which this difference remained
868 significant. */** Significant difference from baseline mean (B_M), indicated by paired t-tests with
869 alpha level corrected for multiple comparisons, $p < .008$.

870

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

874 $N = 11$ per group. Error bars represent SEM. ● Significant difference from both other groups,
875 indicated by two-tailed independent samples t-test with alpha level corrected for multiple
876 comparisons, $p < .016$.

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

881 $N^{Young} = 11$, $N^{Older} = 14$. Error bars represent the SEM. ● Significant group difference, indicated by
882 mixed ANOVA, followed up by independent samples t-test with alpha level corrected for multiple
883 comparisons, $p < .008$. Dashed lines represent the time windows over which this difference remained
884 significant. */* Significant difference from baseline mean (B_M), indicated by paired t-tests with
885 alpha level corrected for multiple comparisons, $p < .008$.

886

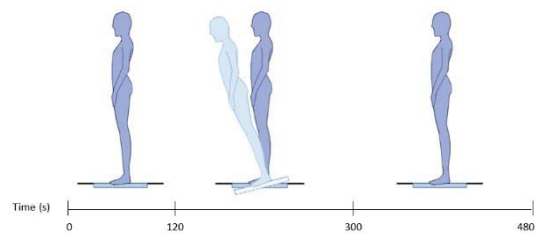
887 *Figure 6.* Experiment 2 group averages of the time taken to perceive that the platform had stopped
888 moving (button press) and the time that each group's postural sway returned to baseline levels,
889 compared to when the platform stopped moving (time=0).

890 $N^{Young} = 11$, $N^{Older} = 14$. Error bars represent SEM. ● Significant difference between groups, indicated
891 by two-tailed independent samples t-test ($p < .001$).

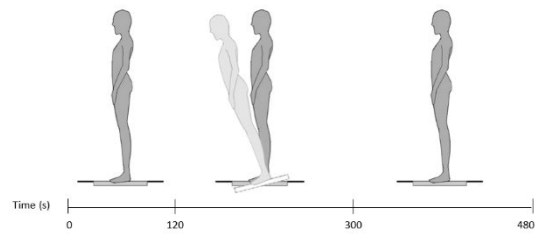
892







Phase:	Baseline				Adaptation						Reintegration					
Platform:	Stable				Sway-referenced						Stable					
Window:	B1	B2	B3	B4	A1	A2	A3	A4	A5	A6	R1	R2	R3	R4	R5	R6



Phase:	Baseline				Adaptation						Reintegration					
Platform:	Stable				Sway-referenced						Stable					
Window:	B1	B2	B3	B4	A1	A2	A3	A4	A5	A6	R1	R2	R3	R4	R5	R6

