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Adaptation to continuous perturbation of balance: Progressive reduction of postural muscle activity with invariant or increasing oscillations of the center of mass depending on perturbation frequency and vision conditions

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36 **Abstract**

37

38 We investigated the adaptation of balancing behavior during a continuous, predictable perturbation
39 of stance consisting of 3-min backward and forward horizontal sinusoidal oscillations of the support
40 base. Two visual conditions (eyes-open, EO; eyes-closed, EC) and two oscillation frequencies (LF,
41 0.2 Hz; HF, 0.6 Hz) were used. Center of Mass (CoM) and Center of Pressure (CoP) oscillations
42 and EMG of Soleus (Sol) and Tibialis Anterior (TA) were recorded. The time course of each variable
43 was estimated through an exponential model. An adaptation index allowed comparison of the
44 degree of adaptation of different variables. Muscle activity pattern was initially prominent under the
45 more challenging conditions (HF, EC and EO; LF, EC) and diminished progressively to reach a
46 steady state. At HF, the behavior of CoM and CoP was almost invariant. The time-constant of EMG
47 adaptation was shorter for TA than for Sol. With EC, the adaptation index showed a larger decay in
48 the TA than Sol activity at the end of the balancing trial, pointing to a different role of the two
49 muscles in the adaptation process. At LF, CoM and CoP oscillations increased during the balancing
50 trial to match the platform translations. This occurred regardless of the different EMG patterns
51 under EO and EC. Contrary to CoM and CoP, the adaptation of the muscle activities had a similar
52 time-course at both HF and LF, in spite of the two frequencies implying a different number of
53 oscillation cycles. During adaptation, under critical balancing conditions (HF), postural muscle
54 activity is tuned to that sufficient for keeping CoM within narrow limits. On the contrary, at LF, when
55 vision permits, a similar decreasing pattern of muscle activity parallels a progressive increase in
56 CoM oscillation amplitude and the adaptive balancing behavior shifts from the initially reactive
57 behavior to one of passive riding the platform. Adaptive balance control would rely on on-line
58 computation of risk of falling and sensory inflow, while minimizing balance challenge and muscle
59 effort. The results from this study contribute to the understanding of plasticity of the balance control
60 mechanisms under posture-challenging conditions.

61

62 **Keyword:** Motor processes; Adaptation; Vision; Dynamic postural control; EMG

63 **1. Introduction**

64

65 Contrary to common belief, bipedal stance is remarkably stable. Falls never occur during quiet
66 standing, in the absence of autonomous failure (Gupta & Nair, 2008). Likewise, falls rarely if ever
67 occur in able-bodied subjects during everyday activities, even when these imply complex
68 movements. Of course balance can be overthrown by slips or postural perturbations. But, within
69 limits, the body usually reacts with a variety of stabilizing responses that render upright stance a
70 robust attractor (Stirling & Zakythinaki, 2004). As a result, balance is preserved under many
71 challenging conditions. The way the body learns to stand up and walk in the first year or life
72 (Hadders-Algra, 2005) and the capacity of the nervous system for compensating the consequences
73 of lesions (Geurts, de Haart, van Nes, & Duysens, 2005; Lacour, 2006) are the extremes of our
74 day-to-day capacity of coping with new environmental situations, by learning the most efficient
75 ways to adapt to postural challenges and by attaining the goal to minimize effort (Orrell, Eves, &
76 Masters, 2006). The nervous system has the capacity to compensate for failure of some of its
77 central or peripheral components in allowing efficient (albeit not optimal) posture and movement.
78 Ageing has a profound influence on postural adjustments to stance perturbation, especially in the
79 presence of sensory conflicts (Bugnariu & Fung, 2007). Under appropriate conditions, however,
80 subjects are able to recalibrate and adapt to the changes, and improve balance capacity.

81

82 Coordinated control of body segments is a complex aspect of motor behavior, owing to the
83 multitude of degrees of freedom of the controlled system (Johansson & Magnusson, 1991;
84 Johansson, Fransson, & Magnusson, 2009). This is particularly evident during maintenance of
85 equilibrium, where different coordination modes might be employed depending on posture
86 dynamics and sensory feedback. When the implicit requirement is to keep the body and its center
87 of mass within the boundaries of the support surface (Schieppati, Hugon, Grasso, Nardone, &
88 Galante, 1994), subjects are able to select their postural behavior from a repertoire of strategies
89 (Gorgy, Vercher, Coyle, & Franck, 2007; Torres-Oviedo & Ting, 2007), innate or learned through
90 experience. This adaptive selection may imply a time-consuming process based on the internal
91 representation of the body dynamics, taking into account the constraint of the new demand and the
92 relevant sensory inflow.

93

94 Motor adaptation to balance-challenging perturbations occurs with the repetition of successive,
95 separate balancing trials (Bhatt, Wening, & Pai, 2006; Hu & Woollacott, 1994; Keshner, Allum, &
96 Pfaltz, 1987; Ledin et al., 1990-1991; Mummel et al., 1998; Perrin et al., 1998) and can be partly
97 transferred to new perturbation conditions (Bhatt & Pai, 2009). Adaptation of the balancing
98 strategies also occur during a sequence of discrete, repeated trials of support-surface translations,
99 with manipulations of oscillation frequency, amplitude and vision (Buchanan & Horak, 1999;
100 Fujiwara, Kiyota, Maeda, & Horak, 2007; van Ooteghem et al., 2008; van Ooteghem, Frank, &
101 Horak, 2010). Buchanan and Horak (1999) briefly pointed to adaptation in the oscillation of the CoP,
102 which decreased in amplitude with repeated exposures to separate, successive trials at
103 frequencies greater than 0.5 Hz, and observed no difference in the adaptation to such a pattern for
104 different vision conditions. Fujiwara et al. (2007) showed a similar decrease on CoP velocity of
105 repeated oscillation trials of one minute each, separated by short breaks. By using variable-
106 amplitude perturbations of the support base, van Ooteghem et al. (2008, 2009) showed
107 improvement of balance with practice, by shifting from an ankle strategy towards a multi-segmental
108 control strategy, allowing balancing with greater energy efficiency. Under different conditions
109 featuring repetitive linear trunk and head accelerations of seated subjects, Blouin, Descarreaux,
110 Bélanger-Gravel, Simoneau, and Teasdale (2003) found that the neck muscle activity progressively
111 diminished across trials. Dietz, Trippel, Ibrahim, and Berger (1993) described an adaptation
112 process, observed during the administration to standing subjects of variable body accelerations
113 produced by changing the frequency of oscillation of a supporting treadmill. These investigations
114 pointed to the operation of adaptation processes, which occurred regardless of the various trials
115 being randomized or segments of perturbations being repeated within a series of variable cycles.
116
117 The present investigation was based on the assumption that a prolonged postural disturbance,
118 challenging the balance control mechanisms by *continuous* and *predictable* oscillations of the
119 support surface, would be an appropriate tool for investigating the characteristics of the time-
120 varying continuous adaptation process of balancing behavior. This type of postural disturbance
121 produces, under steady-state conditions, different balancing strategies depending on vision and
122 frequency of oscillation (Buchanan & Horak, 1999; Cappa et al., 2008; Corna, Tarantola, Nardone,
123 Giordano, & Schieppati, 1999), which are largely controlled by anticipatory mechanisms (Dietz et

124 al., 1993; Fujiwara, Toyama, Asai, & Yamashina, 1990; Fujiwara et al., 2007; Horak & Nashner,
125 1986; Schieppati, Giordano, & Nardone, 2002).

126

127 Clearly, the steady-state must be reached after some time from the onset of the cyclic perturbation.

128 However, the within-trial trend in the kinematic balancing pattern associated with the continuous
129 effort of equilibrium maintenance has never been systematically examined. By the same token, no
130 information exists as to the pattern of EMG activity throughout a prolonged perturbation. This would
131 have relevance for understanding the time constraints necessary for optimizing the balancing
132 behavior and counteracting the risk of falling. It would also give a template against which to
133 evaluate possible sensori-motor disorders in postural steadiness and in the compliance with
134 balance-perturbing conditions (e.g., Morton & Bastian, 2004).

135

136 In order to gain further insight into the adaptation to repeated postural perturbations, we examined
137 in detail the features and the time-course of the changes in dynamic, kinematic and EMG variables
138 during balancing on a continuously backwards and forwards translating platform. We hypothesized
139 that the adaptation strategy would imply keeping the body's center of mass within safe limits by
140 appropriately modifying both body kinematics and postural muscle effort, and that a relation existed
141 between these changes (Peterka, 2002; Schieppati et al., 2002; Scholz et al., 2007). We also
142 hypothesized that adaptation was affected by the visual condition and by the frequency of platform
143 translation.

144

145 Whether vision modulates postural adaptation is still an open issue. Under dissimilar balancing
146 conditions (quiet standing), forward shift of center of foot pressure and reduction of body sway are
147 the counterparts of the increased balance capacity as a consequence of learning (Tarantola,
148 Nardone, Tacchini, & Schieppati, 1997). Notably, however, a decrease in body oscillation with trial
149 repetition only occurred when vision was not available (Tarantola et al., 1997), suggesting that
150 vision selects the optimal balancing strategy, hardly requiring further adjustments with trial
151 repetition. Others have shown that the stance-perturbing effect of a non-predictable pseudo-
152 random vibration of the calf muscles was larger without than with vision, as was the rate of
153 attenuation of these effects (Patel, Gomez, Lush, & Fransson, 2009). Vision seems instead not to
154 affect the development of adaptation of successive stabilizing responses to cyclic tilts of the

155 support surface (Keshner et al., 1987). Possibly, vision calibrates the fine postural adjustments
156 occurring during quiet stance (Schieppati et al., 1994), while abrupt head displacements during
157 stance perturbations make vision unreliable for postural adjustments. Therefore, we also addressed
158 the effect of vision on adaptation: contrary to the above proposition, we would expect visual
159 information to be able to speed up and improve the adaptation process. Availability or suppression
160 of vision can and does in fact readily change the pattern of balancing on a continuously oscillating
161 support surface even when the change in visual condition occurs at the time steady-state behavior
162 is attained (De Nunzio, Nardone, Schieppati, 2007; De Nunzio & Schieppati, 2007).

163
164 We also compared the spatio-temporal features of the presumed adaptation process between
165 'demanding' and 'easy' conditions, in the assumption that spatio-temporal features of adaptation
166 would be modulated by task difficulty. Two frequencies of platform translations were used, as low
167 (LF) and high (HF) platform translation frequencies produce a different balancing behavior under
168 steady-state condition. At HF, when the perturbations are more challenging, CoM oscillations are
169 narrow. At LF, CoM oscillates like the platform and CoP back and forth oscillations are smaller than
170 at HF, featuring a 'passive' riding of the platform by the body (Buchanan & Horak, 1999; Corna et
171 al., 1999). Is riding 'passive' from the beginning at LF, and are the CoM oscillations small from the
172 beginning at HF, or are these features the outcome of an adaptation process? Further, the same
173 duration of the balancing trial at the two frequencies (therefore a different number of oscillation
174 cycles within the same time-period), would allow to conjecture about the potential contribution to
175 adaptation of the amount of repeated perturbing events or of the time elapsed from the beginning of
176 the postural challenge.

177 **2. Methods**

178

179 *2.1. Subjects*

180

181 Ten healthy subjects volunteered to participate in the study (8 females and 2 males, mean age $27 \pm$
182 5.4 *SD*). All subjects gave written informed consent according to the Declaration of Helsinki and the
183 guidelines of the local ethics committee. All subjects were naïve to the experimental procedures.

184

185 *2.2. Procedure*

186

187 Subjects rode a mobile platform (Lomazzi & Co., Italy), periodically translating in the antero-
188 posterior (A-P) direction on the horizontal plane in a sinusoidal fashion, along the subjects' sagittal
189 plane. Two different visual conditions (eyes closed, EC; eyes open, EO) and translation frequencies
190 were imposed (high frequency, HF, 0.6 Hz; low frequency, LF, 0.2 Hz) by an ad-hoc software (e-TT,
191 Italy). The amplitude of platform translation was 10 cm for all conditions.

192

193 Subjects stood on the platform in a natural position (feet spaced about 10 cm), with the arms by
194 their side, and kept their head in the primary position. After one short-lasting tryout for familiarizing
195 with the platform, the experiment was started. Subjects were instructed to rest with both feet on the
196 platform and not to make steps in reaction to the perturbations unless necessary to avoid falls. The
197 protocol consisted of 4 trials for each subject, presented in the same experimental session: two
198 trials at HF and two at LF oscillation frequency, each frequency comprising one EC and one EO
199 trial. The trials were randomized across subjects. No more trials per condition per participant were
200 included, in order to prevent specific memories of previous adaptations. Each trial lasted 5 min. It
201 was made of three consecutive parts: subjects stood quietly on the still platform for 1 min; then, the
202 platform translation started and subjects balanced on the platform for 3 min; finally, the platform
203 stopped and subject returned to quiet stance and stood on the still platform for another 1 min. The
204 same visual condition was maintained throughout each trial. The trial did not start until the subjects
205 indicated they were ready to begin. Subjects were aware of the onset of the acquisition, but no
206 warning was given as to the onset or termination of the platform translation cycles within the

207 acquisition epoch. The four trials with different vision and frequency conditions were separated by a
208 time-interval from 1 to several minutes during which subjects were free to move.

209

210 *2.3. Data recording*

211

212 Kinematic data were acquired by means an optoelectronic device (BTS, Italy). Twenty reflective
213 markers were placed bilaterally on the following body landmarks for CoM computation: vertex and
214 lateral head, forehead, acromion, L5, anterior superior iliac spine, greater trochanter, lateral
215 condyle, lateral malleolus, metatarsal distal phalanx, calcaneum. The markers' position in space
216 was recorded by eight cameras at a sampling frequency of 100 Hz and sent to a PC for off line
217 analysis. Kinetic data were acquired by means a pair of sensorized insoles (Pedar Mobile system,
218 Novel, Germany) that measured the plantar pressure distribution and the center of pressure
219 position (CoP) of each foot. These data were sampled at 100 Hz frequency and transmitted to the
220 PC by using Bluetooth technology. Muscle activity was recorded by using a telemetric system
221 (TelEMG, BTS, Italy). The surface electrodes were placed on the belly of the Soleus (Sol) and
222 Tibialis Anterior (TA) muscle of the right side of the body. EMG signals were preamplified (5000x),
223 band-pass filtered (10-600 Hz) and sampled at 1000 Hz.

224

225 *2.4. Data analysis*

226

227 *2.4.1. Standing before the beginning of the platform translation*

228

229 The anthropometric data of each subject were collected and the position in space of the body's
230 center of mass (CoM) computed from the marker traces by means of a custom-made software. For
231 each trial, the mean A-P position of CoM during the first quiet-stance period was computed. In
232 order to average the data from different subjects, the position of the CoM was referred to the
233 position of the malleolus' marker (CoM A-P position minus malleolus A-P position). The standard
234 deviation (SD) of the CoM position was an estimate of the oscillation amplitude around its mean
235 position during the same period. To compute the net A-P CoP instantaneous position from the
236 insole data, home-made software was implemented, based on the formula below

237

$$CoP_{net} = CoP_l \frac{F_l}{F_l + F_r} + CoP_r \frac{F_r}{F_r + F_l}$$

238

239

240 (where F , vertical force; l , left foot; r , right foot). Then, CoP position and oscillation were quantified
241 by the same procedure used for CoM. Each pre-processed EMG trace of TA and Sol muscles, for
242 every subject and trial, was rectified and filtered with a low pass Butterworth filter with a cut-off
243 frequency of 50 Hz to obtain the EMG envelope. The data collected during quiet stance allowed to
244 verify that the initial body postural conditions (body oscillation and orientation in space) of each trial
245 were the same, in order to legitimate the comparison between the data collected during the
246 balancing trials performed under different frequency and vision conditions.

247

248 *2.4.2. Pattern of adaptation during the oscillation period*

249

250 The peak-to-peak (P-P) CoM and CoP A-P oscillations were computed for each platform translation
251 cycle. This was the difference between the relative minimum and the subsequent relative maximum
252 value within each cycle. CoM and CoP peak-to-peak oscillations and the EMG activity have been
253 interpolated with an exponential function ($y = A + B e^{-t/\tau}$), which has often been considered
254 appropriate for descriptive assessment of learning or adaptation over time (Franklin, Osu, Burdet,
255 Kawato, & Milner, 2003; Heathcote, Brown, & Mewhort, 2000; Mazur & Hastie, 1978; Newell,
256 Mayer-Kress, Hong, & Liu, 2009). The A, B and τ parameters were computed by using the
257 minimum sum squared algorithm. This was achieved with the iterative conjugate gradient method
258 of the Excel Solver utility (see Sozzi, Monti, De Nunzio, Do, & Schieppati, 2011). These parameters
259 gave an estimation of the variable values at the beginning of the trial (the intercept value with the
260 ordinate at time zero, equal to A+B) and at the steady state (the asymptotic value, A), and of the
261 time-decay of the function (the time constant, τ). Since the first oscillation cycle contains a large
262 EMG response connected to the complex reflex response elicited by the abrupt, unexpected onset
263 of the platform displacement (see Allum, Tang, Carpenter, Oude Nijhuis, & Bloem, 2011; Oude
264 Nijhuis, Allum, Valls-Sole, Overeem, & Bloem, 2010), and since such response is of a different
265 nature than the following EMG activity (reflex vs. anticipatory) (see Siegmund, Blouin, & Inglis,
266 2008), for all variables the interpolation procedure has been performed on the entire duration of the
267 oscillation period except for the time interval corresponding to the duration of the first cycle. This
268 procedure is exemplified in Fig. 1 for the EMG envelope. A possible limitation of this analysis

269 depends on our fitting of the variable profiles with a single best-fit exponential curve, instead of
270 using a set of exponential curves, each characterized by its time constant (Franklin et al., 2003),
271 which would allow determining if the postural adaptation process is a set of co-existing distinct
272 processes that evolve with different time scales (Newell et al., 2009).

273

274 *2.4.3. The adaptation index*

275

276 For the P-P of CoM and CoP oscillations and for the EMG envelope, an arbitrary adaptation index
277 was also computed in order to allow comparison in the adaptation behavior between variables of
278 different nature. This index highlights the difference between the initial value of the variable and the
279 value attained at the end of the perturbation period (EMG activity or oscillation amplitudes of kinetic
280 and kinematic measures), in order to give an estimation of the entity of the change due to the
281 continuous repetition of the perturbing stimulus. This was defined as the value of the fitted
282 exponential curve at time $t = 180$ s, divided by the value at time zero (intercept value, $A+B$). An
283 index < 1 indicated that the variable value was smaller at the end than at the onset of the balancing
284 trial; vice versa for an index > 1 .

285

286 *2.5. Statistical analysis*

287

288 *2.5.1. Standing before the beginning of the platform translation*

289

290 The TA and Sol EMG data were analysed separately with 2-way ANOVA (within frequency and
291 vision condition). The CoM and CoP mean positions were analysed with 3-way ANOVA (within
292 variable, frequency and vision condition). The frequency condition was added to the ANOVA design,
293 even if these data were collected before platform translation, in order to check the consistency of
294 the initial setting across the stance periods belonging to all subsequent balancing periods. The
295 same ANOVA design was used to compare the mean CoM and CoP traces.

296

297 *2.5.2. Pattern of adaptation during the oscillation period*

298

299 Three-way ANOVA was computed to compare the τ value of each EMG, kinematic and kinetic
300 variables under the different frequency and vision conditions. For the intercept values, a 2-way
301 ANOVA (frequency and vision) was computed for TA and Sol, separately. The same analysis was
302 performed for the asymptotic values. The intercept values of the exponential curve fitting CoM and
303 CoP P-P oscillations were compared with a 3-way ANOVA (variables, frequency and vision
304 condition). A similar analysis was performed for the asymptotic values.

305

306 The adaptation indexes for all EMG, kinematic and kinetic variables were compared by a 3-way
307 ANOVA (within variables, frequency and vision). When the results of the ANOVA were significant (p
308 $< .05$), the Newman-Keuls post-hoc test was run. The software package Statistica (StatSoft, USA)
309 was used.

310

311

312 **3. Results**

313

314 *3.1. Standing before the beginning of the platform translation*

315

316 All data referring to this initial period are summarized in Table 1. Before the onset of the platform
317 translations, the Sol showed a tonic activity revealing the postural function of the muscle; the
318 activity of the TA was irregular, as normally observed during quiet stance. As expected, ANOVA
319 (within frequency and vision) on the TA mean area showed no significant differences between
320 frequency and vision conditions. Similar results were obtained for the mean area of Sol activity.
321 CoM and CoP mean positions showed no differences between frequency and vision conditions.
322 Conversely, the SD of the CoP was always significantly greater than that of CoM (see Table 1).
323 Vision affected the amplitude of the CoM and CoP oscillations. With EC the oscillations of both
324 variables were significantly larger than that with EO (see Table 1), as repeatedly shown (e.g.,
325 Seigle, Ramdani, & Bernard, 2009).

326

327 *3.2. Pattern of adaptation during the oscillation period*

328

329 *3.2.1. The effects of frequency and vision*

330

331 Fig. 2 gives examples of the traces of TA and Sol EMG (panels A-B and C-D), CoM (panels E-F)
332 and CoP displacements (G-H), while balancing on the translating platform at 0.6 Hz (HF, left
333 column) and 0.2 Hz (LF, right column) with EC. The traces of the malleolus marker, corresponding
334 to the platform displacement, are also depicted (I-L). TA activity shows an exponential trend,
335 regardless of the frequency condition. The strong initial activation rapidly decreases to reach a
336 steady state value. Sol activity also shows an exponential trend, but its time decay is slower than
337 that of TA. CoM oscillations remain roughly the same at HF; at LF, an increase of the oscillations
338 from the onset to the end of the trial period is evident. Further, CoM oscillations are larger at LF
339 than HF. CoP oscillations show an opposite behavior, being larger at HF than LF.

340

341 During the initial cycles of the oscillation period, both muscles were strongly activated, but this
342 activation progressively diminished to reach a steady state. The evolution in time of the EMG
343 activity and of the peak-to-peak (P-P) oscillations of CoM and CoP has been described by fitting
344 the data with an exponential model (see Methods). Then, the mean coefficients defining the curves
345 were considered in order to assess possible differences in the pattern of change of the different
346 variables.

347

348 The mean intercept values of TA (Fig. 3, upper panel) showed differences between visual
349 conditions, $F(1, 9) = 15.77, p < .05$. Regardless of the frequency, the initial activity of TA was higher
350 with EC than EO ($p < .05$). Sol showed no differences between frequency, $F(1, 9) = 1.17, p > .1$,
351 and vision conditions, $F(1, 9) = 3.6, p > .1$. CoM and CoP P-P oscillations (Fig. 3, upper panel)
352 showed differences between variables, $F(1, 9) = 131.28, p < .0005$, and frequency conditions, $F(1,$
353 $9) = 19.07, p < .005$; the interaction between variables and frequency was significant, $F(1, 9) =$
354 $26.65, p < .0005$. The initial oscillation of the CoP was always greater than that of CoM ($p < .05$, all
355 comparisons, except for EO 0.2 Hz, $p > .1$). CoP values were affected by both vision and frequency.
356 CoP oscillations were greater EC than EO ($p < .05$, all comparisons), and greater at HF than at LF
357 ($p < .005$ for all comparisons). Conversely, the CoM oscillations remained roughly the same
358 independently of frequency and vision ($p > .5$ for all comparisons).

359

360 The mean asymptotic values of TA activity (Fig. 3, middle panels) were different between frequency,
361 $F(1, 9) = 29.61, p < .005$, and vision conditions, $F(1, 9) = 23.83, p < .001$, and higher at HF than LF,
362 but significantly so only for EC ($p < .005$). Vision affected the asymptotic value of TA only at HF
363 (higher EC than EO) ($p < .005$, all comparisons). The asymptotic value of Sol was not affected by
364 frequency and vision (frequency: $F(1, 9) = 0.48, p > .5$; vision: $F(1, 9) = 0.42, p > .5$). The analysis
365 on the mean asymptotic values of CoM and CoP P-P oscillations showed differences between the
366 two variables, $F(1, 9) = 169.30, p < .0001$; the interaction between variables and frequency was
367 significant, $F(1, 9) = 67.87, p < .0001$. The asymptotic values of CoP P-P oscillation were always
368 greater than those of CoM ($p < .005$, for all comparisons).

369

370 The bottom panels of Fig. 3 show the mean time-constants (τ). These were different between
371 recorded variables, $F(3, 27) = 20.41, p < .0001$) but not between frequency and vision conditions
372 (frequency: $F(1, 9) = 0.92, p > .3$; vision: $F(1, 9) = 3.51, p > .1$). There were interactions between
373 variables and frequency, $F(3, 27) = 10.71, p < .0001$, variables and vision, $F(3, 27) = 4.48, p$
374 $< .01$, and frequency and vision, $F(1, 9) = 6.94, p < .05$. For each frequency and visual condition, τ
375 was always greater for Sol than TA ($p < .05$, for all comparisons). During the more challenging
376 condition (HF EC), TA activity reached the steady state very quickly, and its τ value was shorter
377 than that of CoM P-P oscillations ($p < .05$), which decayed slowly. This latter τ was in turn very
378 similar to that of Sol ($p > .5$). The time decay of CoM was similar to that of CoP P-P oscillations
379 under each frequency and visual condition ($p > .5$, for all comparisons). With EC, the oscillation
380 frequency had significant effects only for the kinematic and kinetic variables ($p < .05$), while no
381 differences between frequency conditions were found for muscle activities ($p > .5$). At LF EC, τ of
382 CoM and of CoP P-P oscillations was lower than of HF. Conversely, with EO, frequency had a
383 significant effect for all variables ($p < .05$, for all comparisons): frequency led to opposite behavior
384 of muscle activity and kinematics or kinetic variables: passing from HF to LF, τ increased for both
385 muscles, but decreased for CoM and CoP.

386

387 The general pattern of time-varying changes can be appreciated in Fig. 4 for all variables. The plots
388 show the exponential curves of the EMG activity and CoM and CoP P-P oscillations, computed by
389 using the mean coefficients (τ , A and B) obtained from the curves fitted to the data recorded during
390 each trial of each subject. From this synthetic representation, it emerges that different patterns of

391 muscle activity are associated with different patterns of kinematic and kinetic behaviors. For
392 example, an initially large and rapidly decaying TA activity together with a moderate and slowly
393 decaying Sol activity produce an almost invariant behavior of CoM and CoP (black lines for 0.6 Hz).
394 TA and Sol behaviors similar to the above produce instead a very different pattern in both CoM and
395 CoP at 0.2 Hz (black lines): under this condition, CoM and CoP oscillations increase during the trial.
396 On the other hand, at 0.2 EO (grey lines), the very low and constant activity of TA is associated with
397 an increase in CoM: notably, in this case, Sol activity is also low and stable.

398

399 3.2.2. The 'adaptation index'

400

401 The adaptation index was calculated for EMG, kinematic and kinetic data to allow comparison of
402 the behaviors of variables of different nature. At HF, TA and Sol indexes were much smaller than
403 one, indicating a reduction in EMG activity at the end of the balancing period, for both visual
404 conditions (Fig. 5). The reduction was smaller for Sol than TA, and more evident at EC than EO.
405 Similar results were found for LF. Note that the index is not representative of the overall level of
406 muscle activity, but only of its relative decay. The index for CoM was close to one at HF, for both
407 EC and EO. Regardless of vision, this index was significantly higher than 1 at LF, indicating that
408 CoM P-P oscillations increased as the trial evolved. Similar values were found for the CoP P-P
409 index. The indexes of all variables entered the same ANOVA design, in order to assess potential
410 differences under different vision and frequency conditions. There were differences between
411 variables, $F(3, 27) = 81.93$, $p < .0001$, and between frequency conditions, $F(1, 9) = 5.33$, $p < .05$.
412 Interestingly, not all variables exhibited an adaptation. For instance, the index of TA activity was
413 small at HF and LF, while the Sol index pointed to decaying activity only in the most challenging
414 condition (HF EC). CoP and CoM P-P indexes showed adaptation at 0.2 Hz, in the opposite sense
415 (see the right and left panels of Fig. 5). There was an interaction between variables and frequency
416 ($F(3,27) = 5.11$, $p < .005$) and an interaction between variables, frequency and vision, $F(3, 27) =$
417 3.71 , $p < .05$. Frequency had a significant effect only for CoM and CoP P-P indexes, both EO and
418 EC ($p < .0005$ for both comparisons).

419 **4. Discussion**

420

421 Balance training leads to changes in the performance of a task (Anderson, 1980; Diener, Dichgans,
422 Bootz, & Bacher, 1984) and improves static and dynamic balance (DiStefano, Clark, & Padua,
423 2009). The CNS is malleable and flexible and adapts to practice and experience (Hall, Brauer,
424 Horak, & Hodges, 2010; Hu & Woollacott, 1994; Ledin et al., 1991). Adaptation mainly consists in
425 the definition of a new motor strategy that appears to be the most appropriate in terms of task-
426 variable control and energy expenditure minimization (Ting & McKay, 2007). Part of this process
427 consists in a gradual shift from feed-back to feed-forward rules (Dietz et al., 1993). With repeated
428 perturbations, the CNS builds new or updates existing internal models to enhance feed-forward
429 control (Bhatt et al., 2006; Bhushan & Shadmehr, 1999; De Nunzio, Nardone, & Schieppati, 2005;
430 Kawato & Gomi, 1992; Pavol & Pai, 2002).

431

432 Dynamic perturbations of balance have been previously used by various laboratories and the
433 balancing pattern described in detail (Buchanan & Horak, 1999; Corna et al., 1999; Schmid,
434 Nardone, De Nunzio, Schmid, & Schieppati, 2007). However, the balancing patterns have been
435 analyzed mainly under steady-state condition (Buchanan & Horak, 1999; Dietz et al., 1993;
436 Schieppati et al., 2002; Schmid et al., 2008). Dietz et al. (1993) pointed to a relatively quick
437 adaptation to a change in acceleration of subjects (which were already 'adapted' to smaller or to
438 faster continuous displacements of the treadmill upon which they stood). The adaptation was
439 studied within four cycles (corresponding to a time period of about 15 s). Both TA and calf muscle
440 activity and body center of mass featured this process: the forces acting on the body were
441 minimized, as a manifestation of the take-over of a feed-forward control as opposed to the outcome
442 of a reflex chain.

443

444 The present study investigated the adaptation phenomenon that occurs on passing from quiet
445 stance to a continuous balance perturbation consisting in prolonged back and forth horizontal
446 translations of a platform upon which subjects stand. In particular, we investigated the features and
447 the time-course of the adaptation that ensues in the postural muscles' activity and body balancing
448 pattern during a 3-min period of continuous, predictable, sinusoidal oscillation, and the modulation

449 in this adaptation depending on visual condition (eyes-open, EO; eyes-closed, EC) and frequency
450 (LF, 0.2 Hz; HF, 0.6 Hz) of platform translations.

451

452 4.1. General features of adaptation

453

454 When our naïve subjects were presented with platform perturbations, we observed a clear-cut
455 adaptation, consisting in a progressive reduction of the initially very prominent leg muscle activities
456 (Fig. 2). This occurred in the face of a remarkably unvaried kinematics of the CoM cyclic
457 displacements (Fig. 2). The entity of the variation has been represented by the value of the
458 adaptation index. For example, at high oscillation frequency without vision, the EMG activity of the
459 TA muscle was reduced at the end of the perturbation period to about 40% of the initial value.
460 Under the same condition, the CoM and CoP antero-posterior oscillation hardly changed at the end
461 of the perturbation period (Fig. 5). Vision, as well as oscillation frequency, affected the adaptation
462 process. Frequency mainly affected the time course of the kinematic and kinetic variables, as
463 shown by the values of the time-constant (τ , see the bottom panels of Fig. 3, and Fig. 4), and vision
464 mainly affected the level of the muscle activity (see the upper and middle panels of Fig. 3).

465

466 It appears that, when the subject is not familiar with the perturbation, and the latter is particularly
467 challenging (HF, EC and EO; LF, EC), aim of the CNS is to keep the CoM within limits even at the
468 cost of a remarkable dissipation of energy, witnessed by the large TA and Sol activation (Fig. 3,
469 upper panels). This parallels the initially large CoP oscillations. As soon as the CNS estimates the
470 degree and type of balance challenge, muscle activity diminishes. It seems that the balance control
471 mechanism is effective in restricting the CoM oscillations from the beginning, but this goal is
472 achieved in a more efficient way during the adaptation process (see also, in a different context,
473 Bachmann, Müller, van Hedel, & Dietz, 2008). These findings are in line with the idea of an optimal
474 trade-off between the opposing demands of achieving a task-level performance goal versus
475 minimizing energy expenditure (Körding, 2007; Lockhart & Ting, 2007; Shadmehr & Krakauer, 2008;
476 Ting & McKay, 2007; Todorov & Jordan, 2002). On the other hand, when the postural system is
477 only slightly perturbed, for example when the platform translates at LF EO, no major activation of
478 the two postural muscles occurs, even at the beginning of the trial. As expected, since the CoP
479 displacements reflect the balance-controlling muscle activity (Nardone & Schieppati, 1988), the

480 CoP oscillations were initially smaller than under the more challenging conditions (Fig. 3, upper
481 panels).

482

483 *4.2. Adaptation of Sol and TA activity*

484

485 In our hands, the continuous oscillations (with constant characteristics of amplitude and frequency
486 from the beginning to the end of the trial) induced an adaptation phenomenon that started from the
487 beginning of the perturbations and followed an exponential law. Under challenging conditions (HF,
488 EC and EO; LF EC), the muscle activity, particularly for TA, showed a progressive reduction from
489 an initial massive activity until a steady-state value, definitely smaller than that at the beginning of
490 trial (Figs. 4 and 5). The mean time constant of this process was not much different across
491 perturbation conditions, amounting for TA to about 70 s on average, so that TA activity reached the
492 steady state roughly at the end of the perturbation period. The time constant of the Sol adaptation
493 was again not different across perturbation conditions, but it was clearly longer than that of TA,
494 amounting to about 400 s on average. Therefore, Sol activity diminished much more slowly, without
495 reaching the steady state value by the end of the oscillation period. On the other hand, the similar
496 time constants within each muscle across LF and HF, in spite of the different overall amount of
497 EMG activity at the two frequencies, signifies that the adaptation process does not depend on the
498 number of oscillation cycles or on the level of muscle activity, but rather on the time elapsed from
499 the beginning of the perturbation. On the basis of the present data, it seems that such adaptation
500 process should in fact take into account not only the number of perturbing cycles but also the body
501 reactions to these continuous displacements, and this would be a time-consuming process. Such
502 supposition needs confirmation by testing different, higher perturbation frequencies and different
503 perturbation amplitudes.

504

505 It is reasonable to assume that the dichotomy between TA and Sol behavior may be due to their
506 different role in the postural control. TA operates the necessary corrections to maintain the CoM
507 within the support base, while Sol mainly counteracts gravity allowing upright posture. In passing,
508 changes in visual condition during a steady-state balancing behavior on the translating platform
509 also produced larger changes in muscle activity for TA than Sol (De Nunzio & Schieppati, 2007).
510 Under challenging conditions and during the initial oscillation cycles, when the characteristics of the

511 perturbations are not yet known, both muscles contribute strongly to the initial fall-preventing
512 responses by producing a considerable effort. An 'optimization' process is progressively activated,
513 whereby TA activity rapidly diminishes whilst Sol activity is reduced until the level necessary and
514 sufficient for keeping the body upright. The Sol EMG does not further diminish below the level
515 observed under quite stance. Notably, the large initial muscle activities must nonetheless be finely
516 coordinated, likely by in-built, largely reflex mechanisms, whereby the CoM is kept within restricted
517 limits from the beginning.

518

519 *4.3. The effect of vision*

520

521 The time-course of adaptation in muscle activity is affected by vision only at LF. At HF vision has a
522 minor effect: the mean time constants describing the exponential trend of the muscle activity were
523 in fact not different for either muscle under the two visual conditions. Vision *per se* should therefore
524 not be held responsible for a 'better' or 'quicker' adaptation of postural muscle activity. Conversely,
525 vision would provide the CNS useful information to allow balancing with minimal muscle activity,
526 particularly in the TA, independently of the oscillation frequency. A similar effect of vision on the
527 level of muscle activity has been previously shown by Dietz et al. (1993), who found a generally
528 higher EMG activity with EC than EO. This effect was more evident in the TA than calf muscle
529 responses to the changes in treadmill acceleration. However, no specific influence of vision was
530 found on the rate of attenuation of muscle activity.

531

532 *4.4. CoM and CoP behavior, and its relationship with the EMG changes*

533

534 Previous studies (Alexandrov, Frolov, & Massion, 1998; Crenna, Frigo, Massion, & Pedotti, 1987;
535 Oddsson, 1988; Oddsson & Thortensson, 1986) have shown that during forward and backward
536 trunk bending movements, the CoM is efficiently regulated with respect to the base of support. The
537 idea that CoM is the stabilised reference for posture and movement coordination (Massion, 1992)
538 has been put forward by other authors investigating a range of whole body movements with
539 changing the configuration of the support base (Mouchnino, Aurenty, Massion, & Pedotti, 1992,
540 Nardone & Schieppati, 1988), with different moving segments (Bouisset & Zattara, 1981; Eng,
541 Winter, MacKinnon, & Patla, 1992) or during altered environmental conditions (Horstmann & Dietz,

542 1990; Mouchnino et al., 1996). During dynamic tasks, the CNS controls the CoM trajectory more
543 precisely than individual joint angles (Scholz & Schöner, 1999), suggesting that successful balance
544 control depends on having accurate knowledge of the entire body configuration in space, as well as
545 of the location of the CoM.

546

547 At high frequency, our findings show that no exponential trend, similar to that visible in the EMG
548 activity, is obvious in the mean oscillations of CoM, EC and EO. In the face of the large and fairly
549 rapid changes in the TA EMG pattern, no parallel changes characterise the CoM oscillation, which
550 remains almost constant in amplitude (Figs. 4 and 5). This is evidence that different patterns of
551 muscle activity can be successful in accurately controlling CoM and keeping it in a safe position
552 (compare the adaptation indexes in Fig. 5). Vision does not affect the pattern of CoM displacement,
553 either. Therefore, CoM represents an invariant variable of this adaptation process. Conversely, CoP
554 oscillations, which control the CoM oscillations, do change their amplitude depending on visual
555 conditions. With EO, both the initial oscillation amplitude and the asymptotic value of CoP are
556 smaller with respect to EC, in parallel with the EMG activity (Fig. 3). Nevertheless, vision did not
557 greatly modify the time course of this process (Fig. 3, bottom left panel).

558

559 Different conclusions can be inferred for the LF condition. From the onset to the end of the trial, the
560 amplitude of CoM and CoP displacement increases to reach the amplitude of the platform
561 translation at steady state (Figs. 4 and 5). Note that, at the beginning of the LF platform translation,
562 the amplitude of the CoM oscillations in the very first cycles is equal to that observed at the very
563 beginning of the HF platform translations (see Fig. 3, upper right panel). The CoM starts to move
564 with relatively small oscillations, which then *increase* successively in an exponential way, at the
565 same time as subjects learn to cope with the slow platform translations. A similar behavior is
566 exhibited by the CoP. At LF, the boundaries within which CoM can oscillate safely may not be
567 immediately estimated. As the perturbation continues, less and less effort is made for keeping body
568 oscillations within restricted limits, and EMG gradually diminish in this LF condition while CoM
569 gradually increases. The adaptation process would now consist in developing the more economical
570 mode to passively follow the platform displacement. Therefore, not only it is possible to note a
571 variation in CoM behavior, but this event is accompanied by a reduction the TA muscle, which is
572 evident only at EC because at EO TA activity is very small from the beginning. On the other hand,

573 Sol activity does not contribute to this process. At LF, for both EC and EO, Sol almost exclusively
574 plays the role of postural muscle leaving to TA the control of the dynamic body stabilization.
575 Perhaps, the CNS selects the mechanisms subserving adaptation by computing the risk that the
576 equilibrium is challenged beyond a certain threshold (Tjernström, Fransson, & Magnusson, 2005;
577 Ishizaki, Pyykkö, Aalto, & Starck, 1991). Fujiwara and al. (2007) noted that the subjects, who were
578 more unsteady in the first of five trials, had a greater need for adaptability of postural control.
579
580 A noteworthy point of this adaptation process is that the time constant that shapes the increase in
581 oscillation amplitude of kinematic and kinetic variables is similar to that of the decrease of TA EMG
582 at HF EC and EO and LF EC, conditions in which the muscular adaptation process is clearly visible.
583 This would mean that the time course of the adaptation is not different with respect to the nature of
584 the controlled variable: a single temporal law controls the variables directly involved in the
585 adaptation process. This is in keeping with the view that the kinematics of the balancing body (the
586 controlled variable in the balancing process) is strictly associated with the activity of the recorded
587 leg muscles, which are the muscles directly opposing the ground reaction force (the controlling
588 variable). No time-dependent changes in the CoM oscillation are instead obvious under HF
589 condition, in spite of a clearly diminishing muscle activity. Under this condition, the initial oscillation
590 of the CoM would be the 'default' value, probably a 'safe' value weighted based on our
591 anthropometric variables and the more frequently encountered day-to-day perturbations (the same
592 value of oscillation amplitude exhibited at the onset of the adaptation process during LF condition).
593 The absence of a reduction in oscillation at HF may be connected with the already small enough
594 'default' value. On the other hand, an increase in oscillation such as that observed under LF would
595 have been detrimental to balance, because it would produce a large displacement velocity, which
596 would require stronger forces to keep it from falling at reaching the anterior or posterior turning
597 points of the platform. As expected, the asymptotic values of body oscillations at HF and LF are
598 comparable with those recorded under the respective steady state conditions (Buchanan & Horak,
599 1999; Corna et al., 1999).

600

601

602

5. Conclusion

603

604 The adaptive behavior of the postural control under dynamic conditions, which emerges from our
605 data collected while standing on a continuously moving platform, is not stereotyped and univocal.
606 Under challenging conditions, represented by fast balance-challenging oscillations of the support
607 base, the amplitude of CoM oscillations remains invariant in spite of EMG reduction. During slow
608 platform translations, a similar reduction in muscle activity parallels a progressive increase in the
609 CoM cyclic displacement; under this condition, the modulation of the command to the muscles
610 controlling balance accompanies the shift from active to 'passive' displacement of the body.

611
612 These findings expand the current knowledge on the mechanisms subserving adaptation to
613 continuous balance perturbations. Contrary to the wealth of papers on the adaptation of arm
614 reaching movements, few studies have dealt with the problem of adaptation of the whole body to
615 perturbation. Presence, extent and time-course of the adaptation process have been addressed
616 mostly as a secondary part of a main investigation, or during time-intervals limited to few cycles of
617 perturbation. Otherwise, aspecific adaptation modes have been described when continuous
618 perturbations have been used. In other studies, the perturbations were separate, and the interval
619 between perturbations must surely have affected the reported adaptation rates. Our use of a
620 prolonged continuous perturbation, at different frequencies and sensory conditions, allows to focus
621 on the time-course of an adaptation process evolving during the continuous administration of the
622 perturbation, in addition to establishing the different modes of adaptive interactions between
623 kinematics and muscle activity depending on mechanical constraints and vision. Possibly, as
624 suggested earlier, the adaptation described here relies on a central process receiving and
625 integrating a number of afferent inputs without being wholly dependent on any one for its function.
626 Processing of this information may continuously update the internal model of the moving body,
627 allowing shifting the postural control from a feedback to a feed-forward mode. Our next aim will be
628 to assess, by ad-hoc experiments, the persistence in time and the dependence on sensory
629 information of this adapted state.

630
631 Such a protocol can be administered within a relatively short period of time, and recording of
632 kinematic, kinetic and EMG activities can be simplified by accepting reasonable approximations, in
633 order to test balancing capacities in the elderly or in patients with movement disorders. The same
634 protocol can be adjusted to train balancing capacities and reduce the likelihood of falls in

635 populations at risk. The challenge would be to provide evidence about the efficacy of specific
636 training approaches facilitating people reaching an optimal level of balance control in daily life
637 (Nardone, Godi, Artuso, & Schieppati, 2010; Schubert et al., 2008; Pai, Bhatt, Wang, Espy, & Pavol
638 2010).

639

640

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642

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646

647

648 **References**

649

650 Alexandrov, A., Frolov, A., & Massion, J. (1998). Axial synergies during human upper trunk bending.
651 *Experimental Brain Research*, 118, 210-220.

652 Allum, J. H. J., Tang, K.-S., Carpenter, M. G., Oude Nijhuis, L. B., & Bloem, B. R. (2010). Review of
653 first trial responses in balance control: Influence of vestibular loss and Parkinson's disease.
654 *Human Movement Science*.

655 Anderson, J. R. (1980). *Cognitive skills and their acquisition*. Hillsdale, NJ: Erlbaum.

656 Bachmann, V., Müller, R., van Hedel, H. J., & Dietz, V. (2008). Vertical perturbations of human gait:
657 Organisation and adaptation of leg muscle responses. *Experimental Brain Research*, 186, 123-
658 130.

659 Bhatt, T., Wening, J. D., & Pai, Y. C. (2006). Adaptive control of gait stability in reducing slip-related
660 backward loss of balance. *Experimental Brain Research*, 170, 61-73.

661 Bhatt, T., & Pai, Y. C. (2009). Generalization of gait adaptation for fall prevention: From moveable
662 platform to slippery floor. *Journal of Neurophysiology*, 101, 948-957.

663 Bhushan, N., & Shadmehr, R. (1999). Computational nature of human adaptive control during
664 learning of reaching movements in force fields. *Biological Cybernetics*, 81, 39-60.

- 665 Blouin, J.S., Descarreaux, M., Bélanger-Gravel, A., Simoneau, M., & Teasdale, N. (2003).
666 Attenuation of human neck muscle activity following repeated imposed trunk-forward linear
667 acceleration. *Experimental Brain Research*, 150, 458-464.
- 668 Bouisset, S., & Zattara, M. (1981). A sequence of postural movements precedes voluntary
669 movement. *Neuroscience Letters*, 22, 263-270.
- 670 Buchanan, J. J., & Horak, F. B. (1999). Emergence of postural patterns as a function of vision and
671 translation frequency. *Journal of Neurophysiology*, 81, 2325-2339.
- 672 Bugnariu, N., & Fung, J. (2007). Aging and selective sensorimotor strategies in the regulation of
673 upright balance. *Journal of Neuroengineering & Rehabilitation*, 4, 19.
- 674 Cappa, P., Patanè, F., Rossi, S., Tetrarca, M., Castelli, E., & Berthoz, A. (2008). Effect of changing
675 visual condition and frequency of horizontal oscillations on postural balance of standing healthy
676 subjects. *Gait & Posture*, 28, 615-26.
- 677 Corna, S., Tarantola, J., Nardone, A., Giordano, A., & Schieppati, M. (1999). Standing on a
678 continuously moving platform: Is body inertia counteracted or exploited? *Experimental Brain
679 Research*, 124, 331-341.
- 680 Crenna, P., Frigo, C., Massion, J., & Pedotti, A. (1987). Forward and backward axial synergies in
681 man. *Experimental Brain Research*, 65, 538-548.
- 682 De Nunzio, A. M., Nardone, A., & Schieppati, M. (2005). Head stabilization on a continuously
683 oscillating platform: The effect of a proprioceptive disturbance on the balancing strategy.
684 *Experimental Brain Research*, 165, 261-272.
- 685 De Nunzio, A. M., Nardone, A., Schieppati, M. (2007). The control of equilibrium in Parkinson's
686 disease patients: Delayed adaptation of balancing strategy to shifts in sensory set during a
687 dynamic task. *Brain Research Bulletin*, 74, 258-270.
- 688 De Nunzio, A. M., & Schieppati, M. (2007). Time to reconfigure balancing behaviour in man:
689 Changing visual condition while riding a continuously moving platform. *Experimental Brain
690 Research*, 178, 18-36.
- 691 Diener, H. C., Dichgans, J., Bootz, F., & Bacher, M. (1984). Early stabilization of human posture
692 after a sudden disturbance: Influence of rate and amplitude of displacement. *Experimental Brain
693 Research*, 56, 126-134.

- 694 Dietz, V., Trippel, M., Ibrahim, I. K., & Berger, W. (1993). Human stance on a sinusoidally
695 translating platform: Balance control by feedforward and feedback mechanisms. *Experimental*
696 *Brain Research*, *93*, 352-362.
- 697 DiStefano, L. J., Clark, M. A., & Padua, D. A. (2009). Evidence supporting balance training in
698 healthy individuals: A systemic review. *Journal of Strength and Conditioning Research*, *23*,
699 2718-2731.
- 700 Eng, J. J., Winter, D. A., MacKinnon, C. D., & Patla, A. E. (1992). Interaction of the reactive
701 movements and centre of mass displacement for postural control during voluntary arm
702 movements. *Neuroscience Research Communications*, *11*, 73-80.
- 703 Franklin, D. W., Osu, R., Burdet, E., Kawato, M., & Milner, T. E. (2003). Adaptation to stable and
704 unstable dynamics achieved by combined impedance control and inverse dynamics model.
705 *Journal of Neurophysiology*, *90*, 3270-3282.
- 706 Fujiwara, K., Toyama, H., Asai, H., & Yamashina, T. (1990). Development of adaptability of postural
707 control during floor vibration. In: Brandt, T., Paulus, W., Bles, W., & Dieterich, M. (Eds),
708 *Disorders of Posture and Gait*. (pp. 185-189). New York: Georg Thieme Verlag.
- 709 Fujiwara, K., Kiyota, T., Maeda, K., & Horak, F. B. (2007). Postural control adaptability to floor
710 oscillation in the elderly. *Journal of Physiological Anthropology*, *26*, 485-493.
- 711 Geurts, A. C., de Haart, M., van Nes I. J., & Duysens, J. (2005). A review of standing balance
712 recovery from stroke. *Gait & Posture*, *22*, 267-281.
- 713 Gorgy, O., Vercher, J. L., Coyle, T., & Franck, B. (2007). Coordination of upper and lower body
714 during balance recovery following a support translation. *Perception & Motor Skills*, *105*, 715-32.
- 715 Gupta, D., & Nair, M. D. (2008). Neurogenic orthostatic hypotension: Chasing "the fall".
716 *Postgraduate Medical Journal*, *84*, 6-14.
- 717 Hadders-Algra, M. (2005). Development of postural control during the first 18 months of life. *Neural*
718 *Plasticity*, *12*, 99-108.
- 719 Hall, L. M., Brauer, S., Horak, F., & Hodges, P. W. (2010). Adaptive changes in anticipatory postural
720 adjustments with novel and familiar postural supports. *Journal of Neurophysiology*, *103*, 968-
721 976.
- 722 Heathcote, A., Brown, S., & Mewhort, D. J. (2000). The power law repealed: The case for an
723 exponential law of practice. *Psychonomic Bulletin & Review*, *7*, 185-207.

- 724 Horak, F. B., & Nashner, L. M. (1986). Central programming of postural movements: Adaptation to
725 altered support-surface configurations. *Journal of Neurophysiology*, *55*, 1369-1381.
- 726 Horstmann, G. A., & Dietz, V. (1990). A basic posture control mechanism: The stabilization of the
727 centre of gravity. *Electroencephalography and Clinical Neurophysiology*, *76*, 165-176.
- 728 Hu, M. H., & Woollacott, M. H. (1994). Multisensory training of standing balance in older adults: I.
729 Postural stability and one-leg stance balance. *Journal of Gerontology*, *49*, M52-M61.
- 730 Ishizaki, H., Pyykkö, I., Aalto, H., & Starck, J. (1991). Repeatability and effect of instruction of body
731 sway. *Acta Otolaryngologica Supplementum*, *481*, 589-592.
- 732 Johansson, R., & Magnusson, M. (1991). Human postural dynamics. *Critical Reviews of*
733 *Biomedical Engineering*, *18*, 413-437.
- 734 Johansson, R., Fransson, P. A., & Magnusson, M. (2009) Optimal coordination and control of
735 posture and movements. *Journal de Physiologie (Paris)*, *103*, 159-177.
- 736 Kawato, M., & Gomi, H. (1992). A computational model of four regions of the cerebellum based on
737 feedback-error learning. *Biological Cybernetics*, *68*, 95-103.
- 738 Keshner, E. A., Allum, J. H., & Pfaltz, C. R. (1987). Postural coactivation and adaptation in the sway
739 stabilizing responses of normals and patients with bilateral vestibular deficit. *Experimental Brain*
740 *Research*, *69*, 77-92.
- 741 Körding, K. (2007). Decision theory: What "should" the nervous system do? *Science*, *318*, 606-610.
- 742 Lacour, M. (2006). Restoration of vestibular function: Basic aspects and practical advances for
743 rehabilitation. *Current Medical Research and Opinion*, *22*, 1651-1659.
- 744 Ledin, T., Kronhed, A. C., Möller, C., Möller, M., Odqvist, L. M., & Olsson, B. (1990-1991). Effects of
745 balance training in elderly evaluated by clinical tests and dynamic posturography. *Journal of*
746 *Vestibular Research*, *1*, 129-138.
- 747 Lockhart, D. B., & Ting, L. H. (2007). Optimal sensorimotor transformations for balance. *Nature*
748 *Neuroscience*, *10*, 1329-1336.
- 749 Massion, J. (1992). Movement, posture and equilibrium: Interaction and coordination. *Progress in*
750 *Neurobiology*, *38*, 35-56.
- 751 Mazur, J. E., & Hastie, R. (1978). Learning as accumulation: A re-examination of the learning curve.
752 *Psychological Bulletin*, *85*, 1256-1274.
- 753 Morton, S. M., & Bastian, A. J. (2004). Cerebellar control of balance and locomotion. *Neuroscientist*,
754 *10*, 247-59.

- 755 Mouchnino, L., Aurenty, R., Massion, J., & Pedotti, A. (1992). Coordination between equilibrium and
756 head-trunk orientation during leg movement: A new strategy build up by training. *Journal of*
757 *Neurophysiology*, 67, 1587-1598.
- 758 Mouchnino, L., Cincera, M., Fabre, J. C., Assaiante, C., Amblard, B., Pedotti, A., & Massion J.
759 (1996). Is the regulation of the center of mass maintained during leg movement under
760 microgravity conditions? *Journal of Neurophysiology*, 76, 1212-1223.
- 761 Mummel, P., Timmann, D., Krause, U. W., Boering, D., Thilmann, A. F., Diener, H. C., & Horak, F. B.
762 (1998). Postural responses to changing task conditions in patients with cerebellar lesions.
763 *Journal of Neurology Neurosurgery Psychiatry*, 65, 734-742.
- 764 Nardone, A., & Schieppati, M. (1988). Postural adjustments associated with voluntary contraction of
765 leg muscles in standing man. *Experimental Brain Research*, 69, 469-480.
- 766 Nardone, A., Godi, M., Artuso, A., & Schieppati, M. (2010). Balance rehabilitation by moving
767 platform and exercises in patients with neuropathy or vestibular deficit. *Archives of Physical*
768 *Medicine and Rehabilitation* 91, 1869-1877.
- 769 Newell, K. M., Mayer-Kress, G., Hong, S. L., & Liu, Y. T. (2009). Adaptation and learning:
770 Characteristic time scales of performance dynamics. *Human Movement Science*, 28, 655-687.
- 771 Oddsson, L. (1988). Co-ordination of a simple voluntary multi-joint movement with postural
772 demands: Trunk extension in standing man. *Acta Physiologica Scandinavica*, 134, 109-118.
- 773 Oddsson, L., & Thorstensson, A. (1986). Fast voluntary trunk flexion movements in standing:
774 Primary movements and associated postural adjustments. *Acta Physiologica Scandinavica*, 128,
775 341-349.
- 776 Orrell, A. J., Eves, F. F., & Masters, R. S. (2006). Implicit motor learning of a balancing task. *Gait &*
777 *Posture*, 23, 9-16.
- 778 Oude Nijhuis, L. B., Allum, J. H., Valls-Sole, J., Overeem, S., & Bloem, B. R. (2010). First trial
779 postural reactions to unexpected balance disturbances: A comparison with the acoustic startle
780 reaction. *Journal of Neurophysiology*, 104, 2704-2712.
- 781 Pai, Y. C., Bhatt, T., Wang, E., Espy, D., & Pavol, M. J. (2010). Inoculation against falls: Rapid
782 adaptation by young and older adults to slips during daily activities. *Archives of Physical*
783 *Medicine and Rehabilitation*, 91, 452-459.

- 784 Patel, M., Gomez, S., Lush, D., & Fransson, P. A. (2009). Adaptation and vision change the
785 relationship between muscle activity of the lower limbs and body movement during human
786 balance perturbations. *Clinical Neurophysiology*, *120*, 601-609.
- 787 Pavol, M. J., & Pai, Y. C. (2002). Feedforward adaptations are used to compensate for a potential
788 loss of balance. *Experimental Brain Research*, *145*, 528-538.
- 789 Perrin, P., Schneider, D., Deviterne, D., Perrot, C., & Constantinescu, L. (1998). Training improves
790 the adaptation to changing visual conditions in maintaining human posture control in a test of
791 sinusoidal oscillation of the support. *Neuroscience Letters*, *245*, 155-158.
- 792 Peterka, R. J. (2002). Sensorimotor integration in human postural control. *Journal of*
793 *Neurophysiology*, *88*, 1097-1118.
- 794 Schieppati, M., Giordano, A., & Nardone, A. (2002). Variability in a dynamic postural task attests
795 ample flexibility in balance control mechanisms. *Experimental Brain Research*, *144*, 200-210.
- 796 Schieppati, M., Hugon, M., Grasso, M., Nardone, A., & Galante, M. (1994). The limits of equilibrium
797 in young and elderly normal subjects and in parkinsonians. *Electroencephalography and Clinical*
798 *Neurophysiology*, *93*, 286-298.
- 799 Schmid, M., Casabianca, L., Bottaro, A., & Schieppati M. (2008). Graded changes in balancing
800 behavior as a function of visual acuity. *Neuroscience*, *153*, 1079-1091.
- 801 Schmid, M., Nardone, A., De Nunzio, A. M, Schmid, M., & Schieppati, M. (2007). Equilibrium during
802 static and dynamic tasks in blind subjects: No evidence of cross-modal plasticity. *Brain*, *130*,
803 2097-2107.
- 804 Scholz, J. P., & Schöner, G. (1999). The uncontrolled manifold concept: Identifying control variables
805 for a functional task. *Experimental Brain Research*, *126*, 289-306.
- 806 Scholz, J. P., Schöner, G., Hsu, W. L., Jeka, J. J., Horak, F. B., & Martin, V. (2007). Motor
807 equivalent control of the center of mass in response to support surface perturbations.
808 *Experimental Brain Research*, *180*, 163-179.
- 809 Schubert, M., Beck, S., Taube, W., Amtage, F., Faist, M., & Gruber, M. (2008). Balance training and
810 ballistic strength training are associated with task-specific corticospinal adaptations. *European*
811 *Journal Neuroscience*, *27*, 2007-2018.
- 812 Seigle, B., Ramdani, S., & Bernard, P. L. (2009). Dynamical structure of center of pressure
813 fluctuations in elderly people. *Gait and Posture*, *30*, 223-226.

- 814 Shadmehr, R., & Krakauer, J. W. (2008). A computational neuroanatomy for motor control.
815 *Experimental Brain Research*, 185, 359-381.
- 816 Siegmund, G. P., Blouin, J. S., & Inglis, J. T. (2008). Does startle explain the exaggerated first
817 response to a transient perturbation? *Exercise and Sport Sciences Reviews*, 36, 76-82.
- 818 Sozzi, S., Monti, A., De Nunzio A. M., Do, M. C., & Schieppati, M. (2011). Sensorimotor integration
819 during stance: Time-adaptation of control mechanisms on adding or removing vision. *Human*
820 *Movement Science* [Epub ahead of print] PMID: 20727610.
- 821 Stirling, J. R., & Zakyntinaki, M. S. (2004). Stability and the maintenance of balance following a
822 perturbation from quiet stance. *Chaos*, 14, 96-105.
- 823 Tarantola, J., Nardone, A., Tacchini, E., & Schieppati, M. (1997). Human stance stability improves
824 with the repetition of the task: Effect of foot position and visual condition. *Neuroscience Letters*,
825 228, 75-78.
- 826 Ting, L. H., & McKay, J. L. (2007). Neuromechanics of muscle synergies for posture and movement.
827 *Current Opinion in Neurobiology*, 17, 622-628.
- 828 Tjernström, F., Fransson, P. A., & Magnusson, M. (2005). Improved postural control through
829 repetition and consolidation. *Journal of Vestibular Research*, 15, 31-39.
- 830 Todorov, E., & Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination.
831 *Nature Neuroscience*, 5, 1226-1235.
- 832 Torres-Oviedo, G., & Ting, L. H. (2007). Muscle synergies characterizing human postural responses.
833 *Journal Neurophysiology*, 98, 2144-2156.
- 834 van Ooteghem, K., Frank, J. S., Allard, F., Buchanan, J. J., Oates, A. R., & Horak, F. B. (2008).
835 Compensatory postural adaptations during continuous, variable amplitude perturbations reveal
836 generalized rather than sequence-specific learning. *Experimental Brain Research*, 187, 603-611.
- 837 van Ooteghem, K., Frank, J. S., & Horak, F. B. (2009). Practice-related improvements in posture
838 control differ between young and older adults exposed to continuous, variable amplitude
839 oscillations of the support surface. *Experimental Brain Research*, 199, 185-193.

840 **Figure legends**

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843 Fig. 1. Example of the EMG activity of the TA muscle acquired during the platform translation trial of
844 three minute duration at 0.6 Hz with eyes closed (EC). The trace corresponds to the rectified and
845 filtered muscle activity. The trace has been fitted by an exponential model ($y = A + Be^{-t/\tau}$). The best-
846 fit curve thus obtained is superimposed to the EMG trace (grey line).

847

848

849 Fig. 2. Traces of TA and Sol EMG activity (panels A-B and C-D), CoM (panels E-F) and CoP
850 displacements (panels G-H) of one representative subject while balancing on the translating
851 platform at 0.6 Hz (left column) and 0.2 Hz oscillation frequency (right column). The traces of the
852 malleolus marker are also depicted (panels I-L). All the traces have been recorded during the same
853 trial performed under EC condition.

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855

856 Fig. 3. The histograms show the intercept (top panels), asymptotic (middle panels) and time-
857 constant value (bottom panels), obtained by fitting the data of TA and Sol EMG activity and of CoM
858 and CoP peak-to-peak oscillations. Mean data under the two visual (EO and EC) and frequency
859 (HF, 0.6 Hz and LF, 0.2 Hz) conditions are shown.

860

861

862 Fig. 4. Reconstructed exponential curves fitting the TA and Sol activity profiles (upper panels) and
863 the CoM and CoP peak-to-peak oscillations throughout a perturbation trial (bottom panels), for both
864 vision and frequency conditions. For each panel, the two visual conditions are superimposed (grey
865 lines, EO; black lines, EC). These exponential curves have been computed by inserting in the
866 exponential equation $y = A + B e^{-t/\tau}$ the mean values of the parameters A, B and τ . Each mean
867 value has been obtained by averaging the corresponding values of each subject. These data are
868 detailed in the insets to each plot. Note that the functions intercept the ordinate at A + B.

869

870

871 Fig. 5. Mean adaptation indices of TA and Sol activity and of CoM and CoP peak-to-peak
872 oscillations, for 0.6 Hz and 0.2 Hz, under EC (grey circles) and EO (white circles) conditions. For
873 each subject, the adaptation index has been computed as the ratio between the value of the
874 exponential curve $y = A + B e^{-t/\tau}$ at the end of the platform translation period ($t = 180$ s) divided by
875 the value at time zero. An index close to 1 means that the variable value was similar at the
876 beginning and at the end of the oscillation period. TA and Sol activities were smaller at the end
877 than at the onset of the platform translation period under all perturbation conditions. Conversely,
878 the oscillation amplitudes of CoM and CoP did not vary throughout the perturbation period at 0.6
879 Hz; at 0.2 Hz these variables were larger at the end than that at the onset of the period.

880

881 **Table legend**

882

883 Table 1. Mean values (\pm standard deviations) of the mean area of TA and Sol, position and oscillation
884 amplitude of CoM and CoP during the quiet stance periods preceding the beginning of the platform
885 translations (0.6 and 0.2 Hz). Note that an approximation of the oscillation amplitude is expressed by
886 the standard deviation of the CoM and CoP trace (CoM SD and CoP SD). Both CoM and CoP were
887 referred to the position of the malleolus' marker. The results of the 2-way ANOVA (frequency and vision
888 conditions) are shown for both TA and Sol. The results of the 3-way ANOVA (variable, frequency and
889 vision conditions) for CoM and CoP position and for CoM and CoP SDs are also reported.

890

891

	0.6 Hz		0.2 Hz		Between frequency F(1,9) =	Between vision F(1,9) =	Between CoM and CoP F(1,9) =
	EC	EO	EC	EO			
TA area (μVolt)	380.61 ± 255.46	367.48 ± 251.75	346.94 ± 262.64	333.35 ± 257.57	3.23, <i>p</i> > .5	0.2, <i>p</i> > .5	-----
Sol area (μVolt)	914.43 ± 308.57	903.58 ± 356.97	911.74 ± 362.96	910.12 ± 317.98	0.01, <i>p</i> > .5	0.01, <i>p</i> > .5	-----
CoM position (cm)	3.86 ± 0.96	3.54 ± 0.74	3.64 ± 0.89	3.65 ± 0.82	0.02, <i>p</i> > .5	0.33, <i>p</i> > .1	0.69, <i>p</i> > .1
CoP position (cm)	3.58 ± 0.74	3.18 ± 0.83	3.32 ± 0.59	3.49 ± 0.76			
CoM SD (cm)	0.55 ± 0.11	0.45 ± 0.09	0.57 ± 0.22	0.45 ± 0.15	0.003, <i>p</i> > .5	20.02, <i>p</i> < .001	42.13, <i>p</i> < .0001
CoP SD (cm)	0.81 ± 0.18	0.62 ± 0.23	0.76 ± 0.15	0.63 ± 0.09			

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ACCEPTED MANUSCRIPT









