

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 more challenging conditions (HF, EC and EO; LF, EC) and diminished progressively to reach a 45 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 under EO and EC. Contrary to CoM and CoP, the adaptation of the muscle activities had a similar 51 52 time-course at both HF and LF, in spite of the two frequencies implying a different number of oscillation cycles. During adaptation, under critical balancing conditions (HF), postural muscle 53 activity is tuned to that sufficient for keeping CoM within narrow limits. On the contrary, at LF, when 54 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

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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 & Zakynthinaki, 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, subjects are able to recalibrate and adapt to the changes, and improve balance capacity. 80

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; Johansson, Fransson, & Magnusson, 2009). This is particularly evident during maintenance of 84 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 trough 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.

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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, & Horak, 2010). Buchanan and Horak (1999) briefly pointed to adaptation in the oscillation of the CoP, 101 102 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 diminished across trials. Dietz, Trippel, Ibrahim, and Berger (1993) described an adaptation 111 112 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

The present investigation was based on the assumption that a prolonged postural disturbance,
challenging the balance control mechanisms by *continuous* and *predictable* oscillations of the
support surface, would be an appropriate tool for investigating the characteristics of the timevarying continuous adaptation process of balancing behavior. This type of postural disturbance
produces, under steady-state conditions, different balancing strategies depending on vision and
frequency of oscillation (Buchanan & Horak, 1999; Cappa et al., 2008; Corna, Tarantola, Nardone,
Giordano, & Schieppati, 1999), which are largely controlled by anticipatory mechanisms (Dietz et

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- 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-motors 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

Whether vision modulates postural adaptation is still an open issue. Under dissimilar balancing 145 146 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 attenuation of these effects (Patel, Gomez, Lush, & Fransson, 2009). Vision seems instead not to 153 154 affect the development of adaptation of successive stabilizing responses to cyclic tilts of the

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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 We also compared the spatio-temporal features of the presumed adaptation process between 164 165 '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	6
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

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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 optoeletronic 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	(TeIEMG, 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	

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

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238	
239	
240	(where F, vertical force; I, 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	6
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 $ au$ 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

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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, $F(1, 9) = 131.28$, $p < .0005$, and frequency conditions, $F(1, 9) = 131.28$, $p < .0005$, and frequency conditions, $F(1, 9) = 131.28$, $p < .0005$, and frequency conditions, $F(1, 9) = 131.28$, $p < .0005$, and frequency conditions, $F(1, 9) = 131.28$, $p < .0005$, and frequency conditions, $F(1, 9) = 131.28$, $p < .0005$, and frequency conditions, $F(1, 9) = 131.28$, $p < .0005$, and frequency conditions, $F(1, 9) = 131.28$, $p < .0005$, and frequency conditions, $F(1, 9) = 131.28$, $p < .0005$, and frequency conditions, $F(1, 9) = 131.28$, $p < .0005$, and frequency conditions, $F(1, 9) = 131.28$, $p < .0005$, and $F(1, 9) = 131.28$, $p < .0005$, and $F(1, 9) = 131.28$, $p < .0005$, and $F(1, 9) = 131.28$, $p < .0005$, and $F(1, 9) = 131.28$, $p < .0005$, and $F(1, 9) = 131.28$, $p < .0005$, $P < .000$
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).

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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 that 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 < .01, and frequency and vision, F(1, 9) = 6.94, p < .05. For each frequency and visual condition, τ 374 375 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 than that of CoM P-P oscillations (p < .05), which decayed slowly. This latter τ was in turn very 377 378 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 differences between frequency conditions were found for muscle activities (p > .5). At LF EC, τ of 381 382 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, au increased for both 385 muscles, but decreased for CoM and CoP.

386

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

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

398

3.2.2. The 'adaptation index'

399 400

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 condition (HF EC). CoP and CoM P-P indexes showed adaptation at 0.2 Hz, in the opposite sense 414 415 (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).

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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 consists in a gradual shift from feed-back to feed-forward rules (Dietz et al., 1993). With repeated 427 428 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

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

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in this adaptation depending on visual condition (eyes-open, EO; eyes-closed, EC) and frequency
(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

It appears that, when the subject is not familiar with the perturbation, and the latter is particularly 466 467 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; Shadmer & 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

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- 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

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

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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	6
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,

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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,

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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 are 598 comparable with those recoded under the respective steady state conditions (Buchanan & Horak, 599 1999; Corna et al., 1999). 600 601 602 5. Conclusion

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The adaptive behavior of the postural control under dynamic conditions, which emerges from our data collected while standing on a continuously moving platform, is not stereotyped and univocal. Under challenging conditions, represented by fast balance-challenging oscillations of the support base, the amplitude of CoM oscillations remains invariant in spite of EMG reduction. During slow platform translations, a similar reduction in muscle activity parallels a progressive increase in the CoM cyclic displacement; under this condition, the modulation of the command to the muscles 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 continuous balance perturbations. Contrary to the wealth of papers on the adaptation of arm 613 614 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

Such a protocol can be administered within a relatively short period of time, and recording of
kinematic, kinetic and EMG activities can be simplified by accepting reasonable approximations, in
order to test balancing capacities in the elderly or in patients with movement disorders. The same
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).
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640	
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642	
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Schmid et al., Manuscript # HMS-D-10-00159 R1, 2nd revised version, January 14th, 2011 840 **Figure legends** 841 842 843 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 Fig. 2. Traces of TA and Sol EMG activity (panels A-B and C-D), CoM (panels E-F) and CoP 849 850 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. 854 855 Fig. 3. The histograms show the intercept (top panels), asymptotic (middle panels) and time-856 constant value (bottom panels), obtained by fitting the data of TA and Sol EMG activity and of CoM 857 858 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 exponential equation $y = A + B e^{-t/\tau}$ the mean values of the parameters A, B and τ . Each mean 866 867 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.

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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 $y = A + B e^{-t/r}$ 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	6						
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.						

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		0.6 Hz		0.2 Hz		Between	Between	Between CoM
		EC	EO	EC	EO	frequency F(1.9) =	vision F(1.9) =	and CoP F(1.9) =
	TA area	380.61 ±	367.48 ±	346.94 ±	333.35 ±	3.23, <i>p</i> > .5	0.2, p > .5	
	(µvoit) Sol area	255.46 914.43 ±	251.75 903.58 ±	262.64 911.74 ±	257.57 910.12 ±	0.01 p > 5	0.01 n > 5	
	(uVolt) CoM	308.57 3 86 ± 0.96	356.97 3 54 ± 0 74	362.96 3.64 ± 0.89	317.98 3.65 ± 0.82	0.01, <i>p</i> > .0	0.01, p > .0	
	position (cm) CoP position (cm)	3.66 ± 0.96 3.58 ± 0.74	3.54 ± 0.74 3.18 ± 0.83	3.64 ± 0.69 3.32 ± 0.59	3.65 ± 0.82 3.49 ± 0.76	0.02, <i>p</i> > .5	0.33, <i>p</i> > .1	0.69, <i>p</i> > .1
	CoM SD (cm)	0.55 ± 0.11	0.45 ± 0.09	0.57 ± 0.22	0.45 ± 0.15	0.003. p > .5	20.02, p	42.13, p
	CoP SD (cm)	0.81 ± 0.18	0.62 ± 0.23	0.76 ± 0.15	0.63 ± 0.09		< .001	< .0001
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