

Vibrotactile cuing revisited to reveal a possible challenge to sensorimotor adaptation

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Abstract Motor responses to unexpected external perturbations require the adjustment of the motor commands driving the ongoing activity. Strategies can be learned with practice to compensate for these unpredictable perturbations (e.g., externally induced slips and trips). It has been hypothesized that response improvements reflect the adaptation of motor commands through updates of an internal model. This hypothesis may be nuanced when a pre-existing motor response could be used. In that case, since a relatively adequate response is known, only the timing of the command needs to be determined. If so, then it could be inferred that the timing of movement initiation and the specific sequence of motor commands can be dissociated. Previously, we quantified the benefits of cuing vs. learning on recovery motor responses resulting from a trip induced by the abrupt stop of one side of a split belt treadmill. Trip occurrence was randomized within a series of strides. Two groups of young adults participated to two distinct experiments (learning, cuing). In the learning experiment, trip recovery improved progressively from the 4th to the 8th trial to reach an “adapted response”. In the cuing experiment, trip recovery was immediate (from 1st trial). Expanding from these results, the aim of the present work was to differentiate

the processes underlying the generation of motor compensation strategies in response to an external perturbation under time uncertainty. A supplementary analysis revealed that “cued” responses were kinematically similar to the “adapted response” and remained invariant regardless of cue lead time (250, 500 ms before trip) and application location of the cue (arm, trunk, lower leg). It is posited that all responses (cued and non-cued) are the expression of a pre-existing motor program derived from life experiences. Here, the cue significantly reduces time uncertainty and adaptation consists primarily in resolving time uncertainty based on the trial-by-trial learning of the stochastic property of trip occurrence in order to reduce the response delay. Hence, response time delay and motor program parameters appear to stem from two distinct processes.

Keywords Timing uncertainty · Vibrotactile cuing · Induced trip · Rehabilitation · Fall recovery

Introduction

Motor responses to unexpected external perturbations require the adjustment of the motor program driving the ongoing activity. While walking, a trip or slip triggers a basic modification of the gait program to return the body dynamic equilibrium. Responses to these unpredictable externally generated perturbations have been used to investigate learning compensation strategies through practice (Mansfield et al. 2007; Pai et al. 2010). Uncertainty may concern the timing and pattern of corrective movements. Temporal uncertainty includes the instant at which a perturbation/event will occur as well as timing and duration variations of muscle contractions driving the motor response. Pattern or motor program parameters uncertainty includes the sequence of actions, movement direction, amplitude/force, velocity as a

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function of a context. A number of models based on decision theory employ a Bayesian approach to resolve the spatial and temporal uncertainty of motor behaviors (see Berniker and Körding 2011; Wolpert and Landy 2012 for review). As in many models attempting to predict human movements in the face of indeterminacy caused by degrees of freedom redundancy/abundance (e.g., Kim et al. 2014), these models also assume that the central nervous system minimizes a cost or gain/loss function (e.g., Hudson et al. 2008) to produce an optimal solution, which corresponds to an optimized motor program (Schmidt et al. 1975; Keele 1981).

The hierarchical structure of motor programs and thus the processes associated with motor program selection and motor program parameters, including time control, are still debated (Leuthold and Jentzsch 2009). The cuing or pre-cuing paradigm (Rosenbaum 1980, 1983), latter associated with brain imaging (Riehle 2005), or event-related potentials (Leuthold et al. 2004) have been extensively used to address these issues. The results yielded by this method show that prior information about time and/or pattern (Rosenbaum 1983; Requin et al. 1991; Riehle 2005) allows for a significant reduction in reaction time.

In real life, removing time uncertainty may facilitate the compensation of perturbations compromising the outcome of a movement. For example, balance disruption by an unpredictable trip is a critical hazard, especially in the elderly population (Blake et al. 1988; Alexander et al. 1992; Mathers and Weiss 1998; Schiller et al. 2007). However, in our recent study (Lee et al. 2016) including two experiments with two distinct groups of participants, we compared learning trip recovery from an unpredictable perturbation by trial-by-trial repetition with cuing by application of a brief vibrotactile stimulus to a body segment. Our results demonstrated that on the very first trial with cuing the compensatory/trip recovery response was equivalent to the adapted response obtained after eight learning trials. All responses with vibrotactile cuing were similar regardless of its lead time (250 or 500 ms) and location of application (arm, trunk, lower leg). The cue provided only a warning without specifying any movement parameters. Hence, the aim of the present work is to differentiate the processes underlying the generation of motor compensation strategies in response to an external perturbation under time uncertainty. Here, we report the results of a supplementary analysis that was applied to our previous kinematic recordings to test the hypothesis that when a motor response/motor program/pattern exists then timing only needs to be determined, regardless of the cue location.

Methods

A detailed account of the methods used to collect the current data is provided in Lee et al. (2016). Briefly, Twenty

healthy young adults were randomly assigned to one of two groups of ten (four females, six males). The University of Houston Institutional Review Boards approved the experimental protocol, and informed consent was obtained from each participant. A split belt treadmill was controlled to produce a trip by the abrupt stop (within 100 ms) of one of the belts at the foot loading phase (as defined in Perry 1992) and resume its motion (within 100 ms) after the first heel strike of the non-trip foot. Force plates located underneath each belt measured ground reaction forces, and an algorithm identified all gait events (e.g., heel strike, toe off, gait cycle, and loading phase). Trip occurrence was randomized within a series of strides. Either a 250 or 500 ms vibrotactile stimulation at 250 Hz provided trip warning/cues in one experiment while the other involved trips without any cuing. The cue triggering time was determined using the average time of ten gait cycles prior to the trip (see trial sequence in protocol). Reflective markers were placed on body landmarks to record and quantify body segment movements with a 12-camera Vicon™ motion capture system. Force signals and movement data were synchronously sampled at a rate of 100 Hz. A safety harness was worn to prevent falling incidents. All participants walked on the split belt treadmill adjusted to match their self-selected walking speed (speed = 0.99 ± 0.04 and 0.98 ± 0.06 m/s for adaptation and cuing groups, respectively); these corresponded to gait cycle periods of 1.14 ± 0.07 and 1.11 ± 0.08 s, respectively. Differences were not significant.

To characterize trip recovery kinetic and kinematic responses, seven outcome measures had been defined (Lee et al. 2016): response step time, maximum response step force, recovery time, maximum trunk flexion angle, maximum trunk flexion velocity, trunk flexion angular dispersion, and maximum whole body center of mass velocity. Additional measures of the non-trip/recovery side were processed and analyzed here to further assess and compare motor compensation strategies: hip-upper leg joint angle (between the iliac crest to greater trochanter line and greater trochanter to femur lateral epicondyle line), knee included joint angle, knee and ankle joint path lengths, and peak-to-peak displacement and phase plane of the whole body center of mass from the instant of the trip to the recovery.

Experimental protocol and analysis

Experiment I (E1) evaluated trip recovery learning only from repeated exposure to perturbation over eight trials. In the second experiment (E2), another group of participants received vibrotactile cuing prior to the trips thereby enabling the evaluation of recovery as a function of the stimulus application location (upper arm, trunk, lower leg) and

lead time (250, 500 ms before the trip). In this experiment, one control trial without cuing was followed by six trials with vibrotactile cuing and finally one trial (post-control trial) without cuing.

In each trial of each experiment, participants walked at their self-selected pace while maintaining their gaze on a target placed 4.5 m ahead at eye level. For each trial, the first ten steps (pre-trip) were used to obtain a steady-state cycle, prevent trip anticipation, and compute gait cycle parameters and average speed. Then, a trip was applied to the left foot at random to one of the steps between the 10th and 20th steps and the trial was terminated ten steps after the trip step (post-trip). The location of the cuing stimulus and lead time were randomized in the cuing experiment (E2). No feedback was provided to the participants; the significance of the cue was known but not the delay of the trip. The duration of a trial was less than 1 min, and consecutive trials were separated by a 20-s rest period.

To determine the effect of the trip as a function of the group (cuing vs. learning/adaptation), we performed ANOVA and post hoc multiple comparisons for all additional dependent measures (hip-upper leg joint angle, knee joint angle, knee and ankle joint path lengths, and peak-to-peak displacement of the whole body center of mass) derived from the existing data set (Lee et al. 2016). This analysis also enabled us to explore the effects of learning for the non-cuing group and the effects of lead time and location for the cuing group.

Results

As detailed in previous results (Lee et al. 2016) and synthesized in Fig. 1, simple repetition of trip trials (E1) showed that the values of all outcome measures (response step time

and force, recovery time, maximum trunk flexion angle and velocity, maximum COM velocity) remained similar for trials 1–4 then decreased progressively to become significantly smaller in trial 8 when compared to the 1st trip trial. In the cuing experiment (E2), trip recovery presented immediately (from the 1st trial) a response kinematically similar to the 8th response in E1, which remained quasi-invariant regardless of cue lead time and application location of the vibrotactile cue (Fig. 1). Differences between the control and post-control trials were not significant in either experiment. Note that the 1st trial of each experiment corresponds to an identical trip condition and the 2nd trial in E2 is the first cuing trial.

Furthermore, whole body kinematic responses from the instant of trip up to recovery presented in Fig. 2 illustrate representative results for one subject of each group. Time frames superimposition shows that body segments displacement magnitude/joint angles are reduced by eight practice trials in E1 (a, right panel) or any cuing in E2 (b, center and right panel). In addition, the analyses applied to lower body kinematic data (hip and knee angles and knee and ankle path lengths) show that in the adaptation groups (E1) all measures remained similar for trials 1–4 ($p > 0.1$) then decreased progressively to become significantly ($p < 0.0001$) smaller in trial 8 when compared to the 1st trip trial. In the cuing experiment (E2), trip recovery presented immediately (from the 1st trial) a response kinematically similar (no significant difference, $p > 0.1$) to the 8th response in E1, which remained quasi-invariant (no significant difference, $p > 0.1$) regardless of cue lead time and application location of the vibrotactile cue. Finally, these measures were similar (no significant difference, $p > 0.1$) between the 8th trial in E1 and any cuing trial in E2. All these results can be represented by the same profile presented in Fig. 1. The center of mass (COM) trajectories

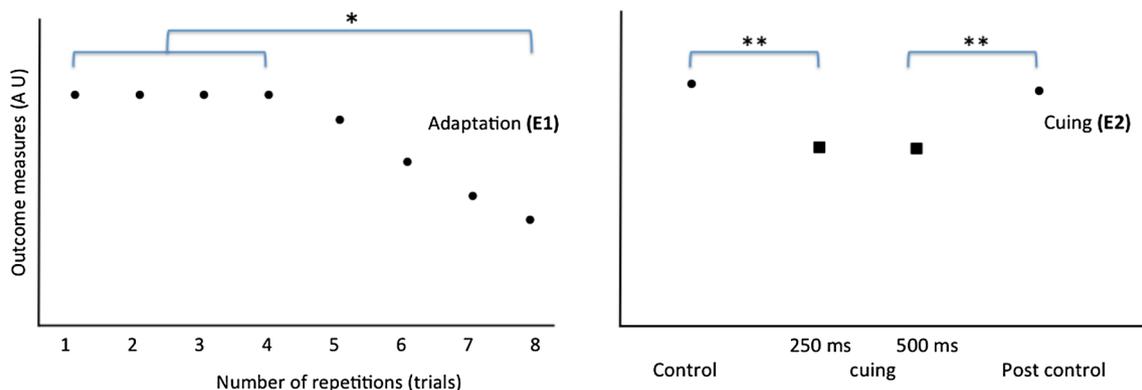


Fig. 1 Synthesized representation of outcome measures (response step time and force, recovery time, maximum trunk flexion angle and velocity, maximum COM velocity) in arbitrary unit (AU) for each experiment [Adaptation (E1); Cuing (E2)]. All measures exhibit a

similar profile that differs only between experiments. Statistical significance indicated by $**p < 0.0001$ and $*p < 0.05$ is similar for all measures. *Filled circle* mean of an outcome measure for a trial; *filled square* mean of an outcome measure for any stimulus location

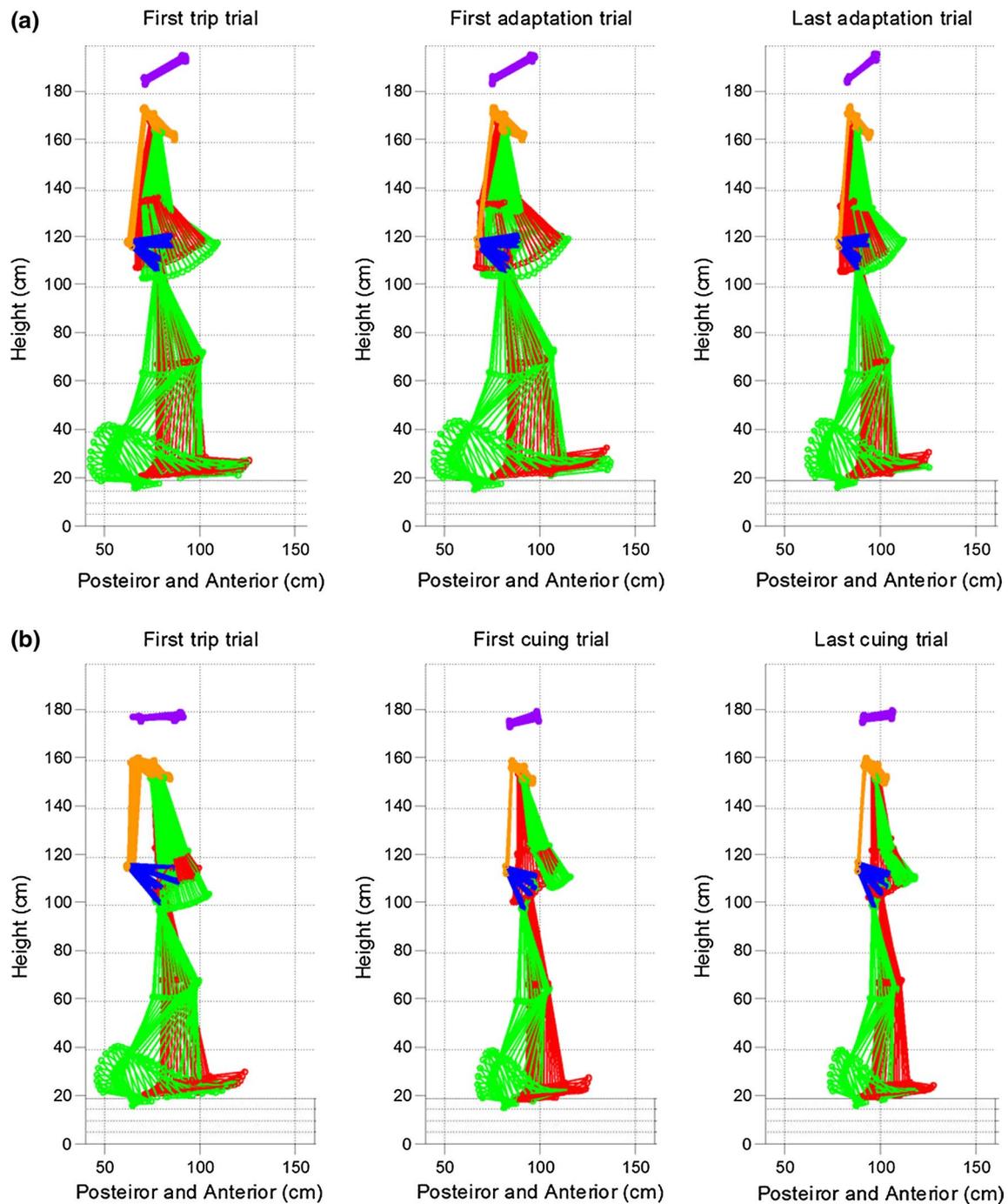


Fig. 2 Representative kinematic profiles obtained from the instant of trip up to recovery in the adaptation group (a) and cuing group (b) for one participant of each group. Green and red colors represent, respec-

tively, the *right* and *left* upper and lower extremities, other colors indicate the pelvis, trunk, and head (color figure online)

(left) and phase plane contours (right) from the step preceding the trip up to recovery for one subject of each group are presented in Fig. 3. Colors indicate the 1st, 2nd, and 8th trial. The phase plane contours show that in each experiment the center of mass trajectories are significantly larger for the first trip trial than for the last adaptation or all cuing

trials, respectively. In addition, marks on the trajectories (left panel) show that the delay of the response to trip is ≈ 300 ms shorter for the 8th adaptation trial and the first cuing trial when compared to first trip trials.

Figure 4 shows the peak-to-peak magnitude of the COM displacement between the instants of trip and recovery

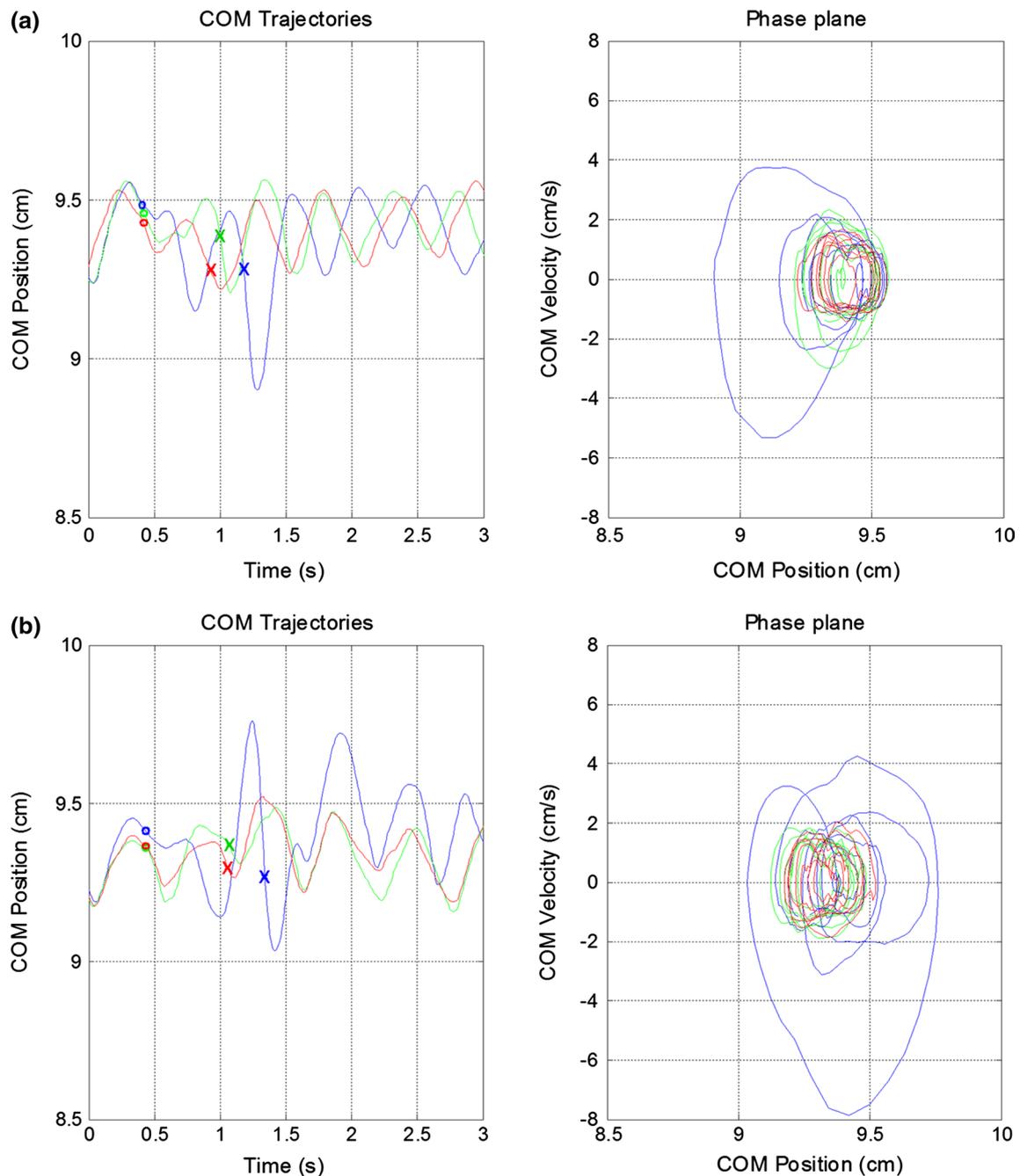


Fig. 3 Representative center of mass trajectories and phase plane contours obtained from the step preceding the trip up to recovery for one subject of each group. **a** Blue, green, and red indicate the 1st, 2nd, and 8th trial in the adaptation experiment. **b** Blue, green, and red

indicate the 1st trip trial, first and last cuing trial in the cuing experiment. Circle and cross marks indicate the instant of trip and first step response, respectively (color figure online)

across all participants in each group. The repetition effect was significant [$F(7,72) = 8.61, p < 0.0001$] for the adaptation group (E1), as shown in Fig. 4a. Post hoc multiple comparisons showed that the peak-to-peak COM displacement was significantly smaller (49.38 %) for trial 8 than trials 1–4. For the cuing group (E2), the ANOVA also indicated a significantly [$F(2,77) = 57.78, p < 0.0001$] lower (47.12 %)

peak-to-peak COM displacement for cued than control trials. In addition, this analysis also showed that this measure was not influenced by stimulus location ($p > 0.87$), lead time ($p > 0.42$), or by their interaction ($p > 0.75$), which equates to no difference between cuing trials in E2, as shown in Fig. 4b. Furthermore, the post hoc analysis showed no significant difference ($p > 0.99$) between control and post-control trials.

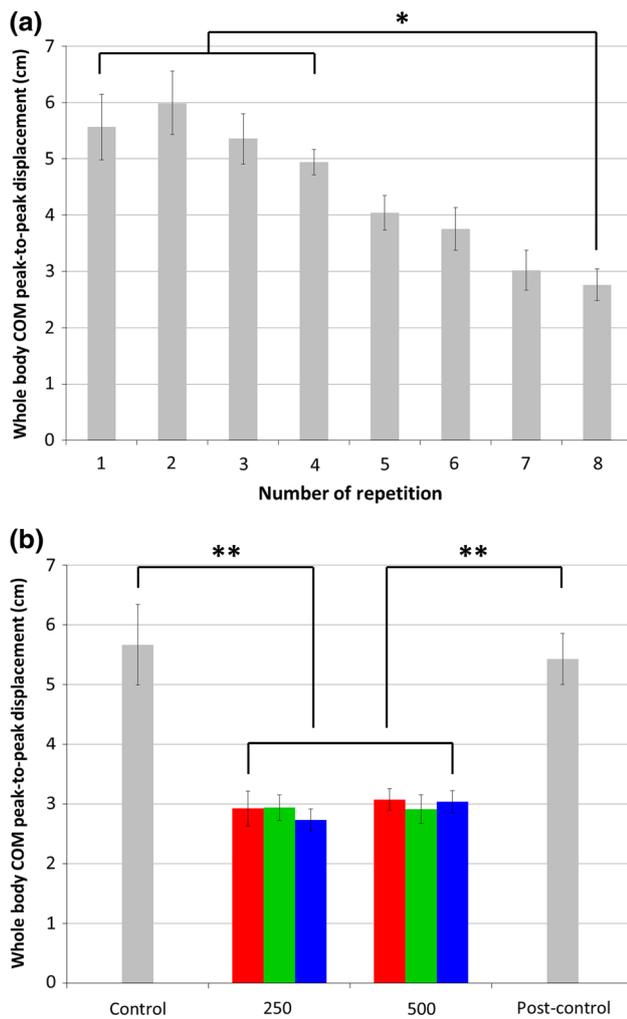


Fig. 4 Peak-to-peak COM displacement from the instant of trip up to recovery across all participants in the adaptation group (a) and cuing group (b). In b, Red, green, and blue bars correspond to vibrotactile cuing applied to upper arm, trunk, and lower leg, respectively, for each lead time (i.e., 250 and 500 ms). Gray bars correspond to control and post-control trials without cuing. Error bars indicate standard error of the corresponding average (** $p < 0.0001$ and * $p < 0.05$) (color figure online)

Discussion

The data included in the current analysis clearly show that vibrotactile cuing immediately triggers a trip corrective response kinematically similar to the progressively adaptive response that results from eight trials when learning by repetition. Furthermore, the immediate compensatory response neither varies with the cuing lead time nor with the location of application of the vibrotactile cuing stimulus. These three major features suggest a difference between learning and cuing in the processes leading to a “unique” recovery action (motor program) and emphasize that resolving time uncertainty may be the critical issue in movement programming.

Learning compensation strategies through practice has been demonstrated for a large variety of tasks, including adaptive responses to unpredictable (Shadmehr and Mussa-Ivaldi 1994; Kawato 1999) and delayed (Levy et al. 2010) perturbation of force or repeated-trip or slip perturbations (Mansfield et al. 2010; Pai et al. 2010; Bieryla and Madigan 2011; Wang et al. 2012). In these contexts, improvement of responses to force perturbation is proposed to be primarily associated with the adaptation of motor command(s) (Shadmehr and Mussa-Ivaldi 1994; Karniel and Mussa-Ivaldi 2003; Bestmann et al. 2008) through the update of an internal model (Wolpert et al. 1995; Wolpert and Ghahramani 2000). The evolution of the internal model is presumed to allow a progression from primarily feedback to primarily feedforward correction of perturbation-induced error as feedback control is too slow to engender effective corrective movements. This adaptation evolving with practice is necessary to build a control strategy/motor program that reduces the movement outcome error when the motor response to changing environmental conditions is not pre-determined (no pre-existing motor program/internal model for such conditions). However, in the present case, it is reasonable to postulate that a feedforward internal model for trip compensation derived from life experiences (learning) is already available. And this model is more generic than specific since treadmill trip is a most likely unknown experience for the participants in the present study.

Several results support the pre-existence/availability of an internal model and associated motor program to compensate the trip perturbation. First, the acquisition of posture compensation in response to changes in body’s extrinsic frame of reference (solid contacts) appears to occur early in life and supports posture reorganization induced by perturbation of proprioceptive information (Martin et al. 2015). Second, the motor response in the cue experiment is immediate (1st trial) with very short lead times (250 or 500 ms) and exhibits narrow variability in kinematic characteristics with repetition and random selection of cue parameters. Hence, it is proposed that in the present context of a not-so unfamiliar perturbation, all successive responses resulting in an adapted response on the 8th trial and cued responses (any trial) illustrate the execution of the same motor program primarily based on a feedforward motor command. When compared to cued trials, differences in kinematics observed in the early trials of the non-cuing experiments are only due to a longer delay, as predicted by control theory. Nevertheless, the availability of a motor program/internal model may present a paradox/dilemma since its utilization is not revealed earlier in the non-cuing experiment. Hence, it is logical to assume that if the two experiments lead to the same solution for trip recovery then the respective processes leading to this motor outcome may be different.

Cuing: Preparation for action triggered by “precues” (Rosenbaum 1980, 1983) is a well-known process benefiting from prior information about parameters of the movement to be executed and/or reduction in time uncertainty, as in the current experiment (Requin et al. 1991; Riehle 2005). This a priori knowledge contributes to a significant reduction in reaction time. In our second experiment, the cue removes time uncertainty as it indicates the imminence of a trip, with the exception of the first and last trial. Hence, the relatively short 250 ms lead time of the cue enables a substantial (about 200 ms) reduction in response time and shows that 650 ms (lead time + response time) is sufficient to select and initiate an adequate motor program. This response may be considered optimal or at least sufficiently efficient by the sensorimotor system since it is not improved by repetition, while learning is possible, as discussed below. Furthermore, the side to be tripped (left or right) is not indicated to the participant and thus completely unknown on the first trial. If this knowledge were to be inferred after a few trials then it would contribute to a further reduction in the response time (Rosenbaum 1980), which is not the case. Hence, it can be assumed that limb selection (a parameter not included in the cue) is most likely triggered by the trip and thus after the pre-selection of the action goal (trip recovery) triggered by the cue. This perspective is consistent with the well-supported independence of program dimensions/features (see for review Rosenbaum 1983; Leuthold and Jentzsch 2011).

Non-cuing: Recent studies based on Bayesian theory have shown that the occurrence of external events can be estimated from prior knowledge of their stochastic behavior in time (Miyazaki et al. 2005; Wolpert and Landy 2012). Similarly, the stochastic properties of a moving target can also be learned to predict hand (Neilson et al. 1988) and eye–hand tracking movements (Martin et al. 1991). Therefore, in the absence of cues, the probabilistic structure of trip occurrence is likely learned to allow a progressive reduction in response time. Furthermore, temporal uncertainty may also be compensated (Hudson et al. 2008). It is of note that in the current task, five trials are necessary to observe “anticipation”, as indicated by the first reduction in response time, and eight trials are sufficient to predict the delay necessary to obtain a “sufficiently efficient” response. Indeed, “functionally good enough” is the alternative to an optimization process, especially when the cost function is most likely unknown (de Rugy et al. 2012) and requires computation. In the present case, learning does not consist of updating the internal model/feedforward motor command per se but rather update the response delay compatible with the internal model. This perspective is in agreement with the reduction in cost (loss function) associated with the motor programming effort (Kibbe and Kowler 2011; Wolpert and Landy 2012) and behavior optimization based on the expected value of motor outcome

(Trommershauser et al. 2003). Furthermore, our hypothesis is congruent with a recent work proposing that the update of feedforward motor commands with repetition to successively correct previous errors is performed by adding time-shifted responses to the previous motor command (Albert and Shadmehr 2015). This time shift is the correlate of the reduction in response time in our experiment.

In both cases, reduction in time uncertainty is the key. Furthermore, assistance to the feedforward motor command by spinal reflexes is expected since anticipation and attention (as driven by the vibrotactile cue) contribute to an increase in the gain of the stretch reflex via an increase in fusimotor sensitivity (Al-Falahe and Vallbo 1988; Hospod et al. 2007; Ribot-Ciscar et al. 2009). In addition, preparation to action and attention also increases corticospinal excitability (Mars et al. 2007; Bestmann et al. 2008), which in turn increases motoneuron accessibility, or in other words, also increases the gain of peripheral loops. Finally, postural threat also enhances the gain of vestibular reflexes (Horslen et al. 2014), which are implicated in balance control. Therefore, the integration at spinal level of all these facilitatory influences is likely to enhance peripheral reflex-based corrections of perturbation, whose latencies are compatible with walking at a natural pace.

To conclude, we propose that compensatory responses for the cuing and non-cuing groups are based on the retrieval of a motor program/stabilization strategy via two different processes. The results strongly suggest that motor response timing (when) and motor program structure and parameters (how) stem from distinct processes. Hence, “when” is a significant component of adaptation. Finally, cuing presents a definite advantage over learning in terms of time (immediacy), robustness, and flexibility (delay and application location). Wearable technology is likely to be available in the near future to allow trip prediction compatible with vibrotactile cuing as 250 ms lead time is sufficient.

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Compliance with ethical standards

Conflict of interest None.

References

- Albert ST, Shadmehr R (2015) The feedback response to error is a teaching signal during motor adaptation. Program No 710.20. In: Neuroscience meeting planner; Washington, DC; Online. Society for Neuroscience, Chicago
- Alexander BH, Rivara FP, Wolf ME (1992) The cost and frequency of hospitalization for fall-related injuries in older adults. *Am J Public Health* 82:1020–1023

- Al-Falahe NA, Vallbo AB (1988) Role of the human fusimotor system in a motor adaptation task. *J Physiol* 401:77–95
- Berniker M, Körding K (2011) Bayesian approaches to sensory integration for motor control. *WIREs Cogn Sci* 2:419–428. doi:10.1002/wcs.125
- Bestmann S, Harrison LM, Blankenburg F, Mars RB, Haggard P, Friston KJ, Rothwell JC (2008) Influence of uncertainty and surprise on human corticospinal excitability during preparation for action. *Curr Biol* 18:775–780. doi:10.1016/j.cub.2008.04.051
- Bieryla KA, Madigan ML (2011) Proof of concept for perturbation-based balance training in older adults at a high risk for falls. *Arch Phys Med Rehabil* 92:841–843. doi:10.1016/j.apmr.2010.12.004
- Blake AJ, Morgan K, Bendall MJ et al (1988) Falls by elderly people at home: prevalence and associated factors. *Age Ageing* 17:365–372
- de Rugy A, Loeb GE, Carroll TJ (2012) Muscle coordination is habitual rather than optimal. *J Neurosci* 32:7384–7391. doi:10.1523/JNEUROSCI.5792-11.2012
- Horslen BC, Dakin CJ, Inglis JT, Blouin JS, Carpenter MG (2014) Modulation of human vestibular reflexes with increased postural threat. *J Physiol* 592:3671–3685. doi:10.1113/jphysiol.2014.270744
- Hospod V, Aimonetti JM, Roll JP, Ribot-Ciscar E (2007) Changes in human muscle spindle sensitivity during a proprioceptive attention task. *J Neurosci* 27:5172–5178
- Hudson TE, Maloney LT, Landy MS (2008) Optimal compensation for temporal uncertainty in movement planning. *PLoS Comput Biol* 4:e1000130. doi:10.1371/journal.pcbi.1000130
- Karniel A, Mussa-Ivaldi FA (2003) Sequence, time, or state representation: how does the motor control system adapt to variable environments? *Biol Cybern* 89:10–21. doi:10.1007/s00422-003-0397-7
- Kawato M (1999) Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 9:718–727
- Keele SW (1981) Behavioral analysis of movement. American Physiological Society, Baltimore, MD
- Kibbe MM, Kowler E (2011) Visual search for category sets: tradeoffs between exploration and memory. *J Vis*. doi:10.1167/11.3.14
- Kim KH, Gillespie RB, Martin BJ (2014) Negotiated control between the manual and visual systems for visually guided hand reaching movements. *J Neuroeng Rehabil* 11:102. doi:10.1186/1743-0003-11-102
- Lee BC, Martin BJ, Thrasher TA, Layne CS (2016) The effect of vibrotactile cuing on recovery strategies from a treadmill-induced trip. *IEEE Trans Neural Syst Rehabil Eng*. doi:10.1109/TNSRE.2016.2556690
- Leuthold H, Jentzsch I (2009) Planning of rapid aiming movements and the contingent negative variation: are movement duration and extent specified independently? *Psychophysiology* 46:539–550
- Leuthold H, Sommer W, Ulrich R (2004) Preparing for action: inferences from CNV and LRP. *J Psychophysiol* 18:77–88. doi:10.1027/0269-8803.18.23.77
- Leuthold H, Jentzsch I (2011) Are temporal response features prepared in fixed order? Inferences from movement-related potentials. *Psychophysiol* 48:633–644. doi:10.1111/j.1469-8986.2010.01126.x
- Levy N, Pressman A, Mussa-Ivaldi FA, Karniel A (2010) Adaptation to delayed force perturbations in reaching movements. *PLoS one* 5:e12128. doi:10.1371/journal.pone.0012128
- Mansfield A, Peters AL, Liu BA, Maki BE (2007) A perturbation-based balance training program for older adults: study protocol for a randomised controlled trial. *BMC Geriatr* 7:12. doi:10.1186/1471-2318-7-12
- Mansfield A, Peters AL, Liu BA, Maki BE (2010) Effect of a perturbation-based balance training program on compensatory stepping and grasping reactions in older adults: a randomized controlled trial. *Phys Ther* 90:476–491. doi:10.2522/ptj.20090070
- Mars RB, Bestmann S, Rothwell JC, Haggard P (2007) Effects of motor preparation and spatial attention on corticospinal excitability in a delayed-response paradigm. *Exp Brain Res* 182:125–129. doi:10.1007/s00221-007-1055-4
- Martin BJ, Roll JP, Di Renzo N (1991) The interaction of hand vibration with oculomanual coordination in pursuit tracking. *Aviat Space Environ Med* 62:145–152
- Martin BJ, Lee BC, Sienko KH (2015) A cutaneous positioning system. *Exp Brain Res* 233:1237–1245. doi:10.1007/s00221-014-4194-4
- Mathers LJ, Weiss HB (1998) Incidence and characteristics of fall-related emergency department visits. *Acad Emerg Med* 5:1064–1070
- Miyazaki M, Nozaki D, Nakajima Y (2005) Testing Bayesian models of human coincidence timing. *J Neurophysiol* 94:395–399. doi:10.1152/jn.01168.2004
- Neilson PD, O'Dwyer NJ, Neilson MD (1988) Stochastic prediction in pursuit tracking: an experimental test of adaptive model theory. *Biol Cybern* 58:113–122
- Pai YC, Bhatt T, Wang E, Espy D, Pavol MJ (2010) Inoculation against falls: rapid adaptation by young and older adults to slips during daily activities. *Arch Phys Med Rehabil* 91:452–459. doi:10.1016/j.apmr.2009.10.032
- Perry J (1992) Gait analysis: normal and pathological function. SLACK Incorporated, New Jersey
- Requin J, Brener J, Ring C (1991) Preparation for action. Wiley, New York
- Ribot-Ciscar E, Hospod V, Roll JP, Aimonetti JM (2009) Fusimotor drive may adjust muscle spindle feedback to task requirements in humans. *J Neurophysiol* 101:633–640
- Riehle A (2005) Preparation for action: one of the key functions of the motor cortex. CRC Press, Boca Raton, FL
- Rosenbaum DA (1980) Human movement initiation: specification of arm, direction, and extent. *J Exp Psychol Gen* 109:444–474
- Rosenbaum DA (1983) The movement pre-cueing technique: assumptions, applications, and extensions. North-Holland, Amsterdam
- Schiller JS, Kramarow EA, Dey AN (2007) Fall injury episodes among noninstitutionalized older adults: United States, 2001–2003. *Adv Data* 392:1–16
- Schmidt RA, Marteniuk RG, Newell KM (1975) A schema theory of discrete motor skill. *Psychol Rev* 82:225–260. doi:10.1037/h0076770
- Shadmehr R, Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14:3208–3224
- Trommershauser J, Maloney LT, Landy MS (2003) Statistical decision theory and trade-offs in the control of motor response. *Spat Vis* 16:255–275
- Wang TY, Bhatt T, Yang F, Pai YC (2012) Adaptive control reduces trip-induced forward gait instability among young adults. *J Biomech* 45:1169–1175. doi:10.1016/j.jbiomech.2012.02.001
- Wolpert DM, Ghahramani Z (2000) Computational principles of movement neuroscience. *Nat Neurosci* 3(Suppl):1212–1217. doi:10.1038/81497
- Wolpert DM, Landy MS (2012) Motor control is decision-making. *Curr Opin Neurobiol* 22:996–1003. doi:10.1016/j.conb.2012.05.003
- Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. *Science* 269:1880–1882