Effects of repeated walking in a perturbing environment: a 4-day locomotor learning study

Andrèanne Blanchette,1 Helene Moffet,1,2 Jean-Sébastien Roy,1,2 and Laurent J. Bouyer1,2
1Centre for Interdisciplinary Research in Rehabilitation and Social Integration (CIRRIIS), Université Laval, Quebec City, Canada; and 2Department of Rehabilitation, Université Laval, Quebec City, Canada

Submitted 1 December 2011; accepted in final form 5 April 2012

Blanchette A, Moffet H, Roy J, Bouyer LJ. Effects of repeated walking in a perturbing environment: a 4-day locomotor learning study. J Neurophysiol 108: 275–284, 2012. First published April 11, 2012; doi:10.1152/jn.01098.2011.—Previous studies have shown that when subjects repeatedly walk in a perturbing environment, initial movement error becomes smaller, suggesting that retention of the adapted locomotor program occurred (learning). It has been proposed that the newly learned locomotor program may be stored separately from the baseline program. However, how locomotor performance evolves with repeated sessions of walking with the perturbation is not yet known. To address this question, 10 healthy subjects walked on a treadmill on 4 consecutive days. Each day, locomotor performance was measured using kinematics and surface electromyography (EMGs), before, during, and after exposure to a perturbation, produced by an elastic tubing that pulled the foot forward and up during swing, inducing a foot velocity error in the first strides. Initial movement error decreased significantly between days 1 and 2 and then remained stable. Associated changes in medial hamstring EMG activity stabilized only on day 3, however. Aftereffects were present after perturbation removal, suggesting that daily adaptation involved central command recalibration of the baseline program. Aftereffects gradually decreased across days but were still visible on day 4. Separation between the newly learned and baseline programs may take longer than suggested by the daily improvement in initial performance in the perturbing environment or may never be complete. These results therefore suggest that reaching optimal performance in a perturbing environment should not be used as the main indicator of a completed learning process, as central reorganization of the motor commands continues days after initial performance has stabilized.

IN HEALTHY HUMANS, WALKING results from a finely controlled muscle activation pattern that generates accurate and fluid lower-limb movements. The neural control of walking involves interactions between different levels of commands, i.e., central commands, originating from voluntary and automatic drive, and peripheral commands, originating from sensory inputs (Nielsen and Sinkjaer 2002; Patla 1996). Despite these complex interactions, the control of walking demonstrates an important flexibility, as shown by constant adjustments to environmental constraints. Motor adaptation processes have previously been studied using perturbing environments. It has been shown that the muscle activation pattern can be modified while walking with a perturbation applied to the lower limb. Once the perturbation is removed, these modifications persist for several strides, and the locomotor pattern then gradually returns to baseline (Blanchette and Bouyer 2009; Choi and Bastian 2007; Emken and Reinkensmeyer 2005; Fortin et al. 2009; Gordon and Ferris 2007; Kao and Ferris 2009; Lam et al. 2009; Noble and Prentice 2006; Noel et al. 2009; Prokop et al. 1995; Reisman et al. 2005; Savin et al. 2010). The presence of aftereffects suggests that adaptation to a perturbing environment modifies central commands involved during normal walking, a process called recalibration (Lackner and DiZio 2000).

Several authors suggested that an approach consisting of walking in a perturbing environment could be helpful in the rehabilitation of persons with walking limitations (e.g., Bastian 2008; Blanchette and Bouyer 2009; Choi and Bastian 2007; Emken and Reinkensmeyer 2005; Lam et al. 2009, 2011; Noel et al. 2009; Reisman et al. 2007, 2010a, b). A few studies have investigated the longer-term effects of a training program, consisting of walking in a perturbing environment (>12 sessions), on the locomotor pattern of persons with walking disabilities, resulting from a central nervous system (CNS) lesion (Lam et al. 2009, 2011; Reisman et al. 2010b). Results obtained in these studies support the idea that repeated walking in a perturbing environment might have the potential to improve overground locomotor performance after CNS lesion. However, before considering this approach as a potential tool for locomotor rehabilitation, it is necessary to address how short-term modifications, caused by walking in a perturbing environment (adaptation), are transformed into longer-term gains (learning). The general hypothesis proposed in the above studies is that repeated adaptations to, and recoveries from, a given perturbation applied during walking might lead to the learning of a new locomotor program for this specific perturbing environment [as hypothesized in Reisman et al. (2010a)]. This newly learned locomotor program would be stored independently of the baseline locomotor program. When subjects are re-exposed to the perturbing environment, this “context-specific” program is recalled, and initial performance is improved compared with the first exposure. Similarly, when the perturbation is removed, subjects return to their baseline locomotor program.

Locomotor learning has been reported after a single session of walking in a perturbing environment when subjects are placed a second time in the same perturbing environment (Fortin et al. 2009; Gordon and Ferris 2007; Malone et al. 2011). Results from these studies suggest that locomotor performance in the perturbing environment can be improved as soon as on this second exposure. However, how locomo-
tor performance evolves across repeated walking sessions with the perturbation was not addressed. Furthermore, these studies have focused mainly on the performance in the presence of the perturbation. A comparison of locomotor performance after perturbation removal (aftereffects) could indicate the extent to which repeated walking sessions with the perturbation reduce the reliance on central command recalibrations.

To begin addressing these questions, in the present study, the locomotor pattern of healthy subjects was quantified during and after walking in a perturbing environment on 4 consecutive daily sessions. In a previous study, we identified peak foot velocity and hamstring electromyographic (EMG) activity as the main variables affected by a single exposure to a perturbation, consisting of an elastic tubing attached between the foot and the front of the treadmill during walking (Blanchette and Bouyer 2009). The effects of walking with this perturbation on locomotor performance were compared here across days. Aftereffects were also compared across days to address how repeated exposures to the perturbation reduce the reliance on central command recalibrations. We hypothesized that peak foot velocity error would gradually be reduced with repeated sessions of walking in this perturbing environment and that such reduction would be accompanied with an increase in hamstring activation. A concomitant, gradual reduction in aftereffects was also expected across days. Contrary to what was expected, however, whereas our results suggest that there are clear evidences of locomotor learning after a single exposure to a perturbing environment, reliance on recalibration of the baseline locomotor program was still necessary on day 4. Separation between the newly learned and baseline programs may therefore either take longer than suggested by daily improvement in initial performance in the perturbing environment or may never be complete. Preliminary results have been presented in abstract form (Blanchette and Bouyer 2006).

MATERIALS AND METHODS

Subjects

Ten healthy volunteers (25.1 ± 2.9 years old; 70.4 ± 8.5 kg; 173.2 ± 5.2 cm; five females), drawn from the Université Laval student population, participated in this study. Subjects had no history of musculoskeletal or neurological disorders that could affect their performance. None of them had already participated in a locomotor learning experiment. All subjects read and signed a formal consent form describing the experimental procedure and their involvement in the study. This protocol was approved by an authorized institutional human research review board.

General protocol

The experimental protocol was reproduced on four consecutive sessions, separated by ~24 h. On each daily session, subjects walked on a motorized treadmill for three periods: before (5 min), during (10 min), and after (10 min) exposure to a perturbation applied to the right lower limb. The first walking period (“CONTROL”) served to characterize baseline walking. During the second walking period (“PERTURBATION”), subjects walked with an elastic tubing attached between their right foot and the frame of the treadmill. Instruction to the subjects was to “resist the force and try to walk normally”.

Modifications caused by walking with the perturbation on the locomotor pattern (adaptation) were studied. The third walking period (“POST”) was used to document recovery following perturbation removal. This experimental protocol was used in a previous study focusing on the effects of a single exposure to a perturbing environment during walking (Blanchette and Bouyer 2009).

Prior to testing, subjects walked on the treadmill to familiarize themselves with the environment and to select a comfortable walking speed (3.9–4.0 km/h). This walking speed was then used throughout all daily sessions. During walking, subjects had to look at a target placed 3.5 m ahead of them and to lightly touch the frame of the treadmill with the tip of their fingers to minimize anteroposterior body displacement that would affect the force applied by the elastic. Subjects were asked to stand still with their feet on either side of the treadmill belt between walking periods. At the beginning of each walking period, subjects stepped on with the left lower limb first, once the belt had reached the predetermined speed. Similarly, they stepped aside before the belt stopped at the end of each walking period. This procedure was used to avoid experiencing acceleration/deceleration phases of the moving belt.

The perturbation was produced using Thera-Band silver elastic tubing (Hygenic, Akron, OH). The elastic was attached to a strap located at the level of the metatarsophalangeal joint of the right foot and to an anchor point placed on the anterior superior part of the treadmill frame. This configuration produced a perturbation that pulled the foot forward and up when the right lower limb was unloaded (swing phase) but had little effects during the rest of the gait cycle (stance phase). In an effort to normalize the force applied with the elastic across subjects, peak force intensity was calibrated for each subject to ~40% of the maximal voluntary contraction produced while standing on the left lower limb and pulling back as hard as possible with the right lower limb. The same elastic tubing was used on each day. Equation 1 represents a force-stretching relationship for a 40-cm Thera-Band silver elastic tubing (Blanchette and Bouyer 2009), i.e., the average length used in the present experiment

\[ y = 0.00002x^2 - 0.0062x^2 + 1.0203x + 2.7349 \]  

(1)

where \( y \) corresponds to the force (N) and \( x \) to the elastic stretching (percent of resting length). More details about general protocol and perturbation generation can be found in Blanchette and Bouyer (2009).

![Fig. 1. Modifications within daily sessions in absolute peak foot velocity error caused by walking in a perturbing environment. Mean (n = 10 subjects) normalized (% of baseline) absolute peak foot velocity error during swing for the 5 epochs analyzed on each day. Error bars represent a 95% confidence interval on day 1 data. *Statistically significant difference from baseline on each day (P < 0.05); †+ statistically significant difference from baseline on days 1–3; NS, no statistically significant difference from baseline.](http://jn.physiology.org/ by 10.1152/jn.01098.2011 • www.jn.org)
Recordings

Spatiotemporal gait parameters, kinematics, and EMG activity of seven muscles of the right lower limb were recorded during each walking period. Contacts with and off the ground were detected using custom-made footswitches placed under the big toes and heels of both lower limbs.

Three-dimensional (3D) movement kinematics of the right lower limb were measured using the Optotrak 3020 (Northern Digital, Waterloo, Canada). Four triads of infrared-emitting diodes were placed on the foot, shank, thigh, and pelvis, respectively. Infrared-emitting diodes were sampled at a frequency of 100 Hz. Twelve anatomical landmarks were digitized to reconstruct 3D movements, i.e., big toe, heel, fifth metatarsal tuberosity, medial and lateral malleoli, medial and lateral femoral condyles, greater trochanter, anterior superior spinous processes (right and left), and iliac crests (right and left).

EMG activity of seven muscles of the right lower limb was recorded using disposable surface electrodes (Kendall Medi-Trace 200, Covidien, Mansfield, MA) and a custom-made EMG amplifier. Electrodes were placed according to the Surface Electromyography for the Non-Invasive Assessment of Muscles project recommendations (Freriks et al. 1999) in a bipolar configuration over tibialis anterior (ankle dorsiflexor), medial gastrocnemius (ankle plantarflexor and knee flexor), soleus (ankle plantarflexor), rectus femoris (knee extensor and hip flexor), vastus lateralis (knee extensor), medial hamstring (MH; knee flexor and hip extensor), and lateral hamstring (LH; knee flexor and hip extensor). Interelectrode distance was ~2 cm. EMG signals were then band-pass filtered (10–500 Hz) and digitized at a sampling frequency of 1,000 Hz for offline analysis. To reproduce electrode placement between sessions, each electrode position was marked on the subjects’ skin with pencil ink after each session.

Fig. 2. Stride-by-stride modifications in absolute peak foot velocity error caused by walking in a perturbing environment for each daily session. Mean (n = 10 subjects) normalized (% of baseline) absolute peak foot velocity error during swing for each stride of the 3 walking periods on each daily session. Gray areas represent a 95% confidence interval on each data point.
Data analysis

Data analysis was performed using custom software written in Matlab (MathWorks, Natick, MA). Footswitch signals placed under the big toes and heels were used to identify the exact moment of toe-off and heel-strike during each stride of the three walking periods. The relative hip, knee, and ankle angular positions were reconstructed offline. Data were synchronized on heel-strike and time normalized to 60% for stance and 40% for swing. Each stride was then divided into 50 bins of equal width (2% of the gait cycle), and the mean amplitude within these bins was reported. As displacements during walking are mainly observed in the sagittal plane, the rate of foot displacement was calculated from the resultant of the vertical and horizontal rate of right big-toe displacement. The amplitude of peak foot velocity was then normalized to the mean of the last 100 strides of the CONTROL walking period (baseline). The “velocity error” was obtained by taking the absolute value of the difference between the velocity of each stride and mean velocity measured in baseline.

Before rectification, EMG signals were digitally filtered with a zero-lag 4th order Butterworth band-pass filter (20–450 Hz). Data were separated into individual strides based on heel-strike and time normalized to 60% for stance and 40% for swing. Each stride was then divided into 50 bins of equal width (2% of the gait cycle), and the mean EMG amplitude within these bins was reported. Amplitude normalization was also applied to the EMG signals by dividing each value by the highest bin measured in the daily baseline (percent peak baseline).

To estimate the time course of recovery in velocity error, an exponential decay curve was fitted to the first 100 strides of the postperturbation walking period using the least squares method (SigmaPlot 8.0, Systat Software, San Jose, CA)

\[ y = y_0 + a \cdot e^{(-bx)} \]  

where \( y \) is the peak foot velocity error, and \( x \) is the stride number. The time constant was extracted from this equation (1/b) and represented the number of strides required to reduce aftereffect amplitude to 37% of its initial value (a). It must be noted that this measure is independent of the actual initial magnitude of aftereffects, thereby simplifying comparison across participants.

Statistics

The following five epochs were defined for each day (Fig. 1):

- “Baseline pattern”: mean of the last 100 strides of the CONTROL walking period;
- “Initial pattern with the perturbation”: mean of the first five strides of PERTURBATION walking period;
- “Final pattern with the perturbation”: mean of the last 100 strides of PERTURBATION walking period;
- “Initial pattern postperturbation”: mean of the first five strides of POST walking period;
- “Final pattern postperturbation”: mean of the last 100 strides of POST walking period.

Two-way repeated measure ANOVAs were first used to determine whether walking with the perturbation was having an overall effect on velocity error and MH mean amplitude within and across days. Paired \( t \)-tests with Bonferroni corrections were then used for multiple pairwise comparisons.

RESULTS

Kinematics

An interaction effect between epochs (within-day comparisons) and days (across-day comparisons) was observed in velocity error (\( F = 14.377; P < 0.001 \)). This result suggests that within-day effects of walking with the perturbation depend on the daily session.

Effects of walking with the perturbation on lower-limb kinematics within daily sessions. In the initial pattern with the perturbation, velocity error was statistically increased com-

Fig. 3. Modifications caused by walking with the perturbation on the lower-limb joint angular displacements. Mean (\( n = 10 \)) relative angular displacements of the 3 lower-limb joints (hip, knee, and ankle) in the final pattern with the perturbation (black lines) compared with baseline (gray areas) on each daily session. Each stride was divided into 50 bins of equal width (2% of stride duration). Data were time normalized to 60% for stance and 40% for swing. Error bars represent a 95% confidence interval.
compared with the baseline pattern for each daily session (days 1–3: $P < 0.001$; day 4: $P = 0.002$). A stride-by-stride analysis (Fig. 2) demonstrated that velocity error gradually decreased to reach a steady state within the first 5 min of the walking period with the perturbation. In the final pattern with the perturbation, this error was still statistically higher than baseline (day 1: $P = 0.002$; day 2: $P = 0.013$; day 3: $P = 0.016$; day 4: $P = 0.021$). Velocity error remained increased in the first strides following perturbation removal. This increase was statistically significant on the first 3 daily sessions (days 1 and 2: $P < 0.001$; day 3: $P = 0.005$) but not on day 4 ($P = 0.168$). The error decreased gradually and returned to baseline in the final pattern postperturbation (Fig. 2).

From a global lower-limb kinematic perspective, even if initial effects varied across subjects (data not shown), all participants reached a similar pattern at the end of the walking period with the perturbation (Fig. 3). Whereas no modification was observed in adapted hip angular position compared with baseline, a slight reduction was present in peak knee flexion during swing. Furthermore, the ankle joint was kept more dorsiflexed in the final pattern with the perturbation than in baseline, as reported previously (Blanchette and Bouyer 2009). This effect at the ankle had minimal impact on foot kinematics due to the short length of the foot segment compared with the thigh and shank, however.

Effects of repeated walking sessions with the perturbation on lower-limb kinematics. Multiple comparison analysis shows that repeated walking sessions in the perturbing environment had an effect on velocity error, measured only in the initial patterns, with the perturbation and postperturbation across days. After identifying epochs affected by repeated walking sessions with the perturbation (initial patterns with and postperturbation), a characterization of how performance evolved in these two epochs across consecutive days was performed. In the initial pattern with the perturbation on day 1, a velocity error of 28.2 ± 6.2% (Fig. 1) was measured, and this error decreased to 11.2 ± 4.0% on day 2 ($P < 0.001$). Thereafter, no statistically significant differences were found between days 2 and 3 ($P = 0.999$; day 3: 12.0 ± 3.7%) or between days 3 and 4 ($P = 0.999$; day 4: 10.4 ± 3.6%). Therefore, the most important reduction in velocity error measured in the initial pattern with the perturbation occurred between the 1st and the 2nd day. Moreover, the time constant before reaching a steady state while walking with the perturbation was higher on day 1 than on the other daily sessions, and no major difference was observed across days 2–4 (Fig. 4).

Now focusing on the initial pattern postperturbation, a velocity error of 23.5 ± 5.9% was observed on day 1. A statistically significant reduction in the amplitude of these aftereffects occurred on the second exposure to the same perturbation ($P < 0.001$; day 2: 15.8 ± 5.5%). This error continued to decrease between days 2 and 3 ($P < 0.001$; day 3: 9.8 ± 5.7%), but this reduction was not statistically significant between days 3 and 4 ($P = 0.482$; day 4: 7.1 ± 4.7%), despite a continuing reduction in actual value. Gradual modifications in aftereffects across days were not only observed in amplitude but also in the number of strides before returning to the baseline level (Fig. 4). On day 1, velocity error returned toward baseline with a time constant of 11 strides ($R^2 = 0.97$), and this value decreased on the subsequent daily sessions to reach five strides ($R^2 = 0.97$) on day 2, four strides on day 3 ($R^2 = 0.89$), and three strides on day 4 ($R^2 = 0.73$).

Regarding lower-limb joint kinematics, a visual comparison of the final pattern with the perturbation across days (Fig. 3) suggests that no major modifications (amplitude and/or timing) in hip, knee, and ankle angular displacements were induced by repeated sessions of walking with the perturbation.

**EMG activity**

After a description of the effects of repeated walking sessions with the perturbation on kinematics, the emphasis will now be put on muscle activations. Despite minor modifications in other muscle activity, the main change observed in the final muscle activation pattern with the perturbation on day 1 consisted of an increase in LH and MH EMG activity (Fig. 5), between 42% and 80% of the gait cycle (from 20% before toe-off to 20% after). A similar strategy of modifications in the final muscle activation pattern with the perturbation was adopted on each day (Fig. 5). As changes in LH and MH EMG...
profiles were similar, only MH activity is reported here for the sake of simplicity and for avoiding redundancy in the text. A significant interaction effect between epochs and days was present in MH mean amplitude measured between 42% and 80% of the gait cycle \( (F_{11005}^{H11005} = 6.386; P_{11021}^{H11021} = 0.001) \), demonstrating that modifications that occurred between epochs depend on the daily session.

**Effects of walking with the perturbation on MH EMG activity within daily sessions.** MH mean amplitude was statistically significantly increased in the initial pattern with the perturbation of each daily session compared with baseline \( (P_{11021}^{H11021} = 0.001) \) for each day; Fig. 6). This muscle activation still remained higher than the baseline in the final pattern \( (P_{11021}^{H11021} < 0.001) \) for each day). After removing the perturbation, aftereffects were present on each daily session, as demonstrated by the stride-by-stride graph in Fig. 6. A statistically significant difference between MH mean amplitude was identified between baseline and the initial pattern postperturbation on days 1 \( (P < 0.001) \) and 2 \( (P = 0.002) \), but significance was not obtained on days 3 \( (P = 0.999) \) and 4 \( (P = 0.999) \). At the end of this walking session, MH mean amplitude had returned to the baseline level on each daily session.

**Effects of repeated walking sessions with the perturbation on MH EMG activity.** As observed in velocity error, repeated walking sessions in a perturbing environment had an overall effect on MH mean amplitude measured in the initial pattern with the perturbation and postperturbation across days, whereas no statistically significant differences were observed in the baseline (Fig. 7) and in the final patterns with the perturbation and postperturbation.

In the initial pattern with the perturbation, MH mean amplitude increased significantly from 63.4 \( \pm 13.9\% \) on day 1 to 80.4 \( \pm 24.9\% \) on day 2 \( (P = 0.014) \). A visual analysis of MH activation profiles (Fig. 7) showed that EMG burst around...
toe-off started earlier on the second exposure to the perturbation than on the first. A significant decrease was then observed between days 3 and 4 ($P = 0.999$; day 4: 58.5 ± 12.1%).

After perturbation removal, repeated walking sessions with the perturbation caused a gradual decrease in MH activity burst around toe-off (Fig. 7), similarly to what was observed in peak foot velocity error. MH mean amplitude was 45.9 ± 20.3% on day 1 and reached 32.6 ± 17.0% on day 2 ($P = 0.100$). This decrease in aftereffects amplitude continued on day 3 to reach 12.8 ± 3.2% ($P = 0.003$) and then 9.6 ± 2.5% on day 4 ($P = 0.999$).

**DISCUSSION**

In a previous study, we identified peak foot velocity and hamstring EMG activity as the main variables affected during and after a single session of walking with an elastic tubing attached between the participants’ right foot and the frame of the treadmill (Blanchette and Bouyer 2009). In the present study, the same experimental procedure was reproduced on 4 consecutive days to characterize perturbation-induced locomotor learning mechanisms. Lower-limb kinematics and muscle activation were measured at key moments of the adaptation and recovery processes and were compared within and across days.

**Short-term effects of walking in a perturbing environment**

On day 1, when subjects were exposed to the perturbing environment, an initial error in peak foot velocity was present during walking. This movement error gradually decreased as subjects walked with the perturbation to reach a plateau within 10 min. These modifications were accompanied with changes in MH mean amplitude. When the perturbation was removed, aftereffects were present in foot kinematics (as quantified using velocity error) and MH mean amplitude and then gradually returned to baseline. These results are consistent with what has been documented previously in several studies (e.g., Blanchette and Bouyer 2009; Choi and Bastian 2007; Emken and Reinkensmeyer 2005; Fortin et al. 2009; Lam et al. 2006; Noble and Prenticce 2006; Noel et al. 2009; Reisman et al. 2005; Savin et al. 2010).

In the context of locomotor adaptation to a perturbing environment, subjects need to detect the movement error induced by the perturbation and adapt their muscle activation pattern to this environment until they reach a steady state, using a trial-by-error process (Schmidt and Lee 2005). After perturbation removal, these modifications persist and then gradually disappear. Considering that such aftereffects cannot be due to augmented feedback, resulting from the action of the perturbation on the lower limb (feedback mechanisms), they are usually considered as an indicator of recalibration in central commands (feedforward mechanisms) (Lackner and DiZio 2000).

**Learning effects induced by repeated walking sessions with the perturbation**

It has been previously documented that short-term modifications, produced by a single exposure to a perturbing environment, are stored by the CNS and can be recalled on the first strides of a subsequent exposure (Fortin et al. 2009; Gordon and Ferris 2007). These studies have only focused on the first strides of the second exposure to the perturbation, however.

---

Fig. 6. Stride-by-stride modifications in MH mean amplitude caused by walking in a perturbing environment for each daily session. Mean ($n = 10$ subjects) normalized (% of baseline) MH mean amplitude, measured between 42% and 80% of the gait cycle for each stride of the 3 walking periods on each daily session. Gray areas represent a 95% confidence interval on each data point.
These initial evidences of learning have led to the suggestion that repeated walking sessions in a perturbing environment could potentially lead to longer-term modifications in the locomotor pattern [as discussed in Reisman et al. (2010a)]. With the use of a slightly different paradigm, consisting of repeated adaptations and recoveries all occurring on the same day, Malone et al. (2011) recently showed that modifications in the structure of a training session can affect adaptation on the 2nd day. In the present study, the focus was to determine whether additional learning is possible when exposures to the perturbation are presented on several consecutive days.

An overall learning effect on velocity error and MH mean amplitude was clearly demonstrated in the initial patterns with the perturbation and postperturbation across the 4 daily sessions. Whereas we expected a gradual decrease in the initial errors across consecutive days, the most important reduction in velocity error occurred between the 1st and the 2nd day, and this trend was not observed in the remaining days. In MH activation, statistically significant changes were identified in mean amplitude between days 1 and 2, as well as between days 2 and 3, whereas no significant difference was observed between days 3 and 4. MH activation profiles seemed therefore to stabilize on the 3rd daily session of walking with the perturbation. Regarding aftereffects, a different pattern of changes was observed, as velocity error and MH mean amplitude decreased gradually across days. Furthermore, the number of strides before returning to baseline also decreased gradually across daily sessions. To our knowledge, this study was the first to examine howaftereffects are affected by repeated walking sessions with the perturbation.

No changes in the final pattern with the perturbation across days

Surprisingly, repeated walking sessions with the same perturbation did not have a statistically significant effect on the final pattern with the perturbation across days. Regardless of the difference observed in the initial pattern between days, velocity error and MH mean amplitude reached a plateau in the final pattern with the perturbation, which was similar across days. No major modifications across daily sessions were observed in adapted lower-limb joint angular positions either. Taken together, these findings suggest that optimal performance was therefore already reached on day 1 at the end of the PERTURBATION walking period.

This optimal performance was, however, different from baseline, as shown by a residual velocity error in Fig. 1. Such findings could imply that movement was optimized for the perturbing...
environment. In upper-limb reaching, it is possible to predict adapted movement trajectories by using a “minimum cost algorithm”. This algorithm suggests that subjects try to minimize movement cost rather than completely cancel out deviations from baseline (Isawa et al. 2008). A residual movement error can therefore remain to minimize movement cost. In a study focusing on constraints applied during treadmill walking, Bertram (2005) showed that minimization of metabolic cost appears to dominate walking control when speed-step combinations are imposed to subjects. Metabolic cost is therefore a likely explanation for the fact that our subjects converged toward the same adapted pattern, no matter how many times they were exposed to the same perturbing environment, and that this pattern was different from baseline.

**Neurophysiological mechanisms underlying locomotor learning**

As mentioned earlier, the neural control of walking involves different levels of commands. Whereas peripheral sensory inputs are involved in correction during movement execution (feedback control) (Nielsen and Sinkjaer 2002), central commands, from voluntary and automatic drive, predict the muscle activation pattern needed to perform the movement before the execution (feedforward control). This prediction can be updated based on sensory information provided by peripheral commands. In the motor learning process, the control of movement changes gradually from feedback to feedforward as a function of practice (as discussed in Schmidt (1975) and Seidler et al. (2004)]. Movement execution becomes less reliant on feedback, as the CNS becomes more efficient in predicting the optimal pattern. When these principles are applied to locomotor adaptation and learning paradigms, they suggest that repeated adaptations and recoveries to a given perturbation during walking might lead to a newly learned locomotor program for this specific perturbing environment [as hypothesized in Reisman et al. (2010a)]. In such a situation, adaptation by trial and error would no longer be needed to adopt the new program; an immediate switch, without practice, between the baseline and the newly learned locomotor programs would be possible. Indeed, this hypothesis would predict that as the newly learned locomotor program becomes stored separately from the baseline program, aftereffects should disappear. In the present study, the gradual decrease in aftereffects across days suggested that reliance on central command recalibrations decreased with repeated walking sessions with the perturbation. An improvement in the ability of the CNS to predict the optimal locomotor pattern, which should be adopted in the presence of the perturbation, could explain this phenomenon. However, these results cannot quantify the relative contribution of changes in voluntary vs. automatic drive to this locomotor learning.

Aftereffects can be observed in velocity error and MH mean amplitude of each daily session when presented on a stride-by-stride basis (Figs. 2 and 6), suggesting that recalibration in central commands was still involved after 4 daily sessions of walking with the perturbation. Whether complete switch between the baseline and newly learned program is possible therefore remains an open question. Considering that aftereffects gradually decreased across days, more walking sessions with the perturbation may potentially help in addressing this question. No statistical significance between the initial pattern postperturbation and baseline pattern was obtained within the 4th daily session, however. The absence of significant differences can be due to the statistical test used in the present study, as paired r-test with Bonferroni corrections is known to be one of the most conservative statistics used for multiple pairwise comparisons. Although decreasing the probability of type 1 error (concluding that there is a difference when there is not), it necessarily increased the probability of type 2 error (concluding that there is no difference when there is).

**Clinical implications**

A training based on walking in a perturbing environment could be helpful in the rehabilitation of persons with walking limitations. The present experiment can contribute to the development of such training programs by providing a better understanding of the motor learning processes induced by repeated sessions of walking in a perturbing environment. One of the main findings of this study is that reaching optimal performance in the perturbing environment should not be used as an indicator of a completed learning process, as central reorganization of the motor commands continues days after performance has stabilized.

**ACKNOWLEDGMENTS**

The authors thank subjects for their participation in this project and M. Guy St-Vincent for his valuable technical assistance during data collection. The authors also thank the Canadian Space Agency for supplying the motorized treadmill used in this study.

**GRANTS**

Financial support was provided by a grant from Canadian Institutes of Health Research (CIHR) to L. Bouyer. A. Blanchette was supported by studentships from the Multidisciplinary Team in Locomotor Rehabilitation (CIHR) and the Centre for Interdisciplinary Research in Rehabilitation and Social Integration. L. Bouyer was supported, in part, by a scholarship from the Fonds de la recherche en santé du Québec (FRSQ).

**DISCLOSURES**

No conflicts of interest (financial or otherwise) are declared by the author(s).

**AUTHOR CONTRIBUTIONS**


**REFERENCES**


