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COMPENSATORY POSTURAL ADAPTATIONS DURING CONTINUOUS, VARIABLE AMPLITUDE PERTURBATIONS REVEAL GENERALIZED RATHER THAN SEQUENCE-SPECIFIC LEARNING

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Abstract

We examined changes in the motor organization of postural control in response to continuous, variable amplitude oscillations evoked by a translating platform and explored whether these changes reflected implicit sequence learning. The platform underwent random amplitude (maximum ± 15 cm) and constant frequency (0.5 Hz) oscillations. Each trial was composed of three 15-second segments containing seemingly random oscillations. Unbeknownst to participants, the middle segment was repeated in each of 42 trials on the first day of testing and in an additional seven trials completed approximately 24 hours later. Kinematic data were used to determine spatial and temporal components of total body centre of mass (COM) and joint segment coordination. Results showed that with repeated trials, participants reduced the magnitude of horizontal body COM displacement, shifted from a COM phase lag to a phase lead relative to platform motion and increased correlations between ankle/platform motion and hip/platform motion as they evolved from an ankle strategy to a multi-segment control strategy involving the ankle and hip. Maintenance of these changes across days provided evidence for learning. Similar improvements for the random and repeated segments, however, indicate that participants did not exploit the sequence of perturbations to improve balance control. Rather, the central nervous system (CNS) may have been tuning into more general features of platform motion. These findings provide important insight into the generalizability of improved compensatory balance control with training.

Keywords

platform translation; balance; learning; continuous perturbation; postural coordination; implicit sequence learning

INTRODUCTION

During many of our daily activities, we are exposed to continuous threats to balance such as those experienced while standing on a moving bus, in which the perturbations are variable or unpredictable. Researchers have begun to examine responses to continuous, externally-imposed disturbances by exposing participants to constant amplitude, sinusoidal movements of the support surface (Dietz et. al., 1993; Corna et. al., 1999; Nardone et. al., 2000; Buchanan and Horak, 2001; Ko et. al., 2001; Ko et. al., 2003). Results have demonstrated that these conditions provide an opportunity for the CNS to integrate predictive postural adjustments with automatic responses (Dietz et. al., 1993; Schieppati et. al., 2002) and that this predictive control occurs in as few as three to five oscillations (Bugnariu and Sveistrup, 2006). Findings also suggest that compensatory postural coordination patterns emerge based on instructions given to participants (to adopt a particular strategy), and the dynamics of platform motion (Buchanan and Horak 2001, Ko et. al., 2001; Schieppati et. al., 2002). At slow frequencies of translation, participants choose to 'ride' the platform with very little motion in the lower limb joints while at fast frequencies, participants fix their head and trunk in space by increasing joint motion at the ankle and hip (Buchanan and Horak, 1999).

To date, all of the studies that have explored continuous perturbations using a moving support surface have used highly predictable translations. Environmental challenges faced in cyclical tasks such as walking however, are often unpredictable in the magnitude of an imposing perturbation and tasks such as skiing or standing on a moving bus can be unpredictable in both magnitude and timing. We know from observation of these everyday tasks that it is possible to improve stability with practice but because the disruptions are less predictable, the central nervous system (CNS) cannot adapt in the same way that it does to the constant amplitude/frequency perturbations that have been examined experimentally. In order to begin understanding how balance control is learned under less predictable conditions and to characterize the evolution of the balance response with practice, we exposed participants to variable amplitude/constant frequency surface translations using a methodology designed to explore implicit sequence learning.

In implicit sequence learning tasks, performers learn to produce serial responses to sequentially presented stimuli (as in playing the piano) unintentionally and without explicit awareness of the regularities in these stimuli. This type of learning is often studied using variants of the serial reaction time (SRT) task introduced by Nissen and Bullemer (1987) or upper limb tracking tasks (Pew, 1974; Wulf and Schmidt, 1997; Magill, 1998). In these studies, a fixed sequence of stimuli evokes responses from participants that are faster, more accurate, or less variable than exposure to random series of stimuli, even though participants are unaware of sequence regularities. In 2001, Shea et. al. reported that implicit sequence learning also

occurred for a complex, whole body task requiring participants to track a waveform on a computer screen with corresponding movements of their centre of pressure. The postural movements in this study were voluntary allowing the CNS to compare predicted outcomes (as signalled by efference copy or predicted sensory consequences) with the actual outcome of the movement as a form of predictive learning that would not occur if participants were responding to a series of externally imposed disturbances. Further, evidence for implicit sequence learning is based primarily on visuomotor tasks (e.g. mirror tracing, serial reaction time tasks) although many skills, particularly those involved in posture control, do not require visuomotor transformation.

It has been shown that postural responses are affected by the predictability of the disturbance and task goals (Horak et. al., 1997). It is presently not known if implicit sequence learning would occur for postural tasks involving externally-imposed perturbations in which the primary goal is to maintain upright stance and not necessarily to predict and follow platform motions. Under these conditions, it is possible that learning may be non-specific. Studies of upper limb SRT tasks have provided evidence for non-specific improvements (Wulf and Schmidt, 1997; Magill, 1998; van der Graaf et. al., 2004; Perez et. al., 2007). The mechanism for these improvements has been attributed to learning how to respond (i.e. how to associate motor responses to stimuli) in order to optimize the procedure for completing the task successfully.

The primary goal of this study was to determine how participants learn to improve balance when exposed to continuous perturbations that are less predictable than those that have been studied to date. Learning would be demonstrated by improvements in postural stability assessed in both spatial and temporal dimensions through increased centre of mass (COM) displacement control and lower limb joint coordination (spatial), and by shifts in the phase relationship between COM and platform motion from phase lag to phase lead (temporal). To ensure that performances are not driven by temporary variables such as motivation or fatigue, these improvements must be maintained after the retention interval (Schmidt and Lee, 1999). Based on the current paradigm, participants could improve by a) learning general characteristics of surface motion, b) tuning in to the specific sequence of platform translations, or c) engaging in both specific and non-specific learning to improve balance control. If improvements were driven by non-specific learning, participants would demonstrate equal improvements in postural stability for both random and repeated sequences. If participants engaged in implicit sequence learning, they would demonstrate a greater rate of improvement in postural stability for the repeated sequence. The second goal of the study was to understand the organizational changes in compensatory postural coordination patterns with repeated exposure to a continuous, variable amplitude perturbation to determine whether experience should be considered an important factor influencing the postural coordination pattern that is used to maintain balance.

MATERIALS AND METHODS

Participants

Twelve healthy adults (six males, six females) aged 19–29 (mean 24.3 ± 2.8 years) volunteered to participate (Protocol A). Following initial analysis of the data, an additional ten healthy adults (five males, five females) aged 22–34 (mean 29.4 ± 3.4 years) completed a modified subset of trials (Protocol B). All participants successfully completed two clinical tests of balance (30-second one legged stance, one legged stance with eyes closed) and provided informed consent prior to data collection. The methods used in the study were approved by the Oregon Health and Science University Institutional Review Board and by the Office of Research Ethics at the University of Waterloo.

Task and Procedures

Participants wore an industrial safety harness and stood on a hydraulically driven, servo-controlled platform that could be moved horizontally forward and backward. A series of platform translations was elicited to generate a continuous perturbation that oscillated at a fixed frequency of 0.5 Hz and variable amplitude ranging from ± 0.5 to 15 cm. The combination of fixed frequency and random amplitude translations also resulted in random velocities of motion.

Protocol A: Random Amplitudes and Velocities—Trials were composed of three, 15-second segments containing seemingly random oscillations; however, the middle segment included a sequence of platform movements that occurred in every trial. Participants were not informed about the repeated nature of the middle segment. Combined, the three segments produced a 45-second trial (Fig. 1). Oscillation magnitudes were pseudo-randomly generated from a pool of amplitudes with the constraint that an oscillation at the start of a new segment could not differ by more than 8 cm from the preceding oscillation. This criterion was incorporated to ensure smooth transitions between segments. Participants were instructed to maintain balance while standing with eyes open, arms crossed at the chest and to avoid stepping if possible. Testing consisted of six blocks of seven trials with a 2-minute rest period between blocks. Participants returned for a seven-trial retention test approximately 24 hours following practice to examine a) whether learning had occurred and b) whether the repeated segment was learned more effectively than the random segment.

Protocol B: Matched Amplitudes and Mean Velocities—The random segments in Protocol B were generated from a pool of the 15 amplitudes that defined the repeated segment to ensure that the mean amplitude and velocity of platform translation were the same across segments. There were no restrictions on the direction of translation in the random segments; a forward translation in the repeated segment could appear as an oscillation in the forward or backward direction in a random segment. Again, no information was given to participants about the regularities in this segment. Participants were instructed to maintain balance and avoid stepping if possible while standing with eyes open and arms crossed at the chest. Testing consisted of seven trials.

Data Recording

A Motion Analysis System (Santa Rosa, Calif., USA) with six cameras captured three-dimensional spatial coordinate information about body segment displacements and the movement of the platform. Reflective markers were placed bilaterally on the following landmarks: head of the fifth metatarsophalangeal, lateral malleolus, lateral femoral condyle, greater trochanter, acromion process, and lateral mandibular joint. Markers were also placed on the platform. Data were sampled at 60 Hz and low pass filtered using a 2nd order, dual pass Butterworth filter with a cut-off frequency of 5 Hz. The position of the centre of mass (COM) of each body segment in the antero-posterior (AP) direction was calculated using the kinematic data and anthropometric data provided by Winter (1990). Whole body COM position (in space) in the AP direction was derived from the weighted sum of the individual segment COM locations. Ankle, knee and hip joint angles were calculated from adjacent segments.

Outcome Measures

Mean gain of the COM (COM peak displacement/platform peak displacement) and relative phase of the COM (COM time peak/platform time peak) were derived as the primary outcome measures. The ratio of maximum COM displacement to maximum platform displacement was calculated for each peak and valley event during platform motion and these values were averaged for each segment within a trial to determine mean gain and mean gain variability. Theoretically, a COM gain of 1.0 would correspond to equal displacements of the platform and COM in space (similar to the 'ride' strategy described in Buchanan and Horak, 1999) and would occur if participants were following platform motion. Small COM gain was considered improved balance control as participants stabilized their COM in space (Buchanan and Horak, 1999). Relative phase was calculated using the time values of the peaks to compute a point estimate of maximum COM relative to maximum platform position on a cycle-by-cycle basis (Zanone and Kelso, 1992). These values were averaged for each segment within a trial to determine mean relative phase and relative phase variability. We considered increased phase leads of COM relative to platform motion as an indication of improved predictive control and changes in correlation between joint kinematics and platform motion as evidence for changes in postural control strategy. Additional outcome measures included mean gain variability and mean relative phase variability of the COM, and correlations between platform motion and lower limb hip, knee, and ankle joint angles. We also correlated the change in COM phase with the change in COM gain from early to late training to examine whether changes in gain were driven by changes in phase. When inspected, all COM phase changes ranged from 6.66° to 14.59° (mean = $10^\circ \pm 2.74$) with the exception of two participants whose phase change was greater than 1.5 standard deviations from the mean and therefore, were removed from this analysis. Finally, we calculated the RMS amplitude of platform motion for random and repeated segments to investigate whether platform characteristics accounted for behavioural performance.

Data Analysis

All variables were compared between segment two (repeated) and segment three (random) to for trials in which participants did not take a step. The

first segment was omitted from the analyses to ensure that events induced by the onset of platform translation did not interfere with the investigation of sequence learning. In total, 40/588 trials were omitted from protocol A resulting from 16 steps taken in the repeated segment and 24 steps taken in the random segments. 3/70 trials were omitted from protocol B (2 steps repeated segment, 1 step random segments).

For Protocol A, the COM data were compared across blocks of trials on day one to explore acquisition performance. Joint angle data were compared during early (block 1) and late (block 6) training to examine the shift in control strategy with practice. The retention block on day two was compared to early (block 1) and late (block 6) training on day one for all variables to examine learning. Two-way (segment $\times$ block) repeated measures ANOVAs, conducted separately for acquisition and retention phases, were used for all statistical comparisons. For acquisition, primary outcome measures were analyzed in a 2 (segment) $\times$ 6 (block) ANOVA while a 2 (segment) $\times$ 2 (block) ANOVA was used to analyze the joint angle data. Retention performance was analyzed using a 2 (segment) $\times$ 3 (block) ANOVA. *Post hoc* analyses were conducted using Tukey's studentized range (HSD) tests unless otherwise noted. For correlational analyses, R values were transformed into z scores prior to statistical examination. For Protocol B, the COM data were analyzed in a 2 (segment) $\times$ 7 (trial) ANOVA. *Post hoc* analyses were conducted using paired t-tests with Bonferroni corrections. For all tests, an acceptable significance level was 0.05.

RESULTS

Protocol A: Random Amplitudes and Velocities

Acquisition Performance—Comparisons between random and repeated segments revealed that participants did not exploit the repeating sequence of perturbations to improve balance control. The analysis of mean gain indicated a significant interaction between segment and block ($F(5,55) = 5.35$; $p = 0.0004$; Fig. 2). Main effects analyses of training blocks for each segment type revealed that mean gain decreased for both repeated ($F(5,55) = 12.32$; $p < 0.0001$) and random ($F(5,55) = 7.34$; $p = 0.0001$) segments by an average of 15% (0.61 ± 0.14 to 0.51 ± 0.084) and 13% (0.66 ± 0.16 to 0.56 ± 0.10) respectively. *Post hoc* analyses revealed a significantly lower COM gain for the repeated versus random segment as early as block one ($p = 0.032$) but the difference in mean gain between segment types during late training was no greater than that during early training ($t(11) = -0.144$; $p = 0.89$). For both segments, gain values were less than 1.0, indicating that participants did not follow platform motion to maintain balance. Together these results suggest that the difference between repeated and random segment types occurred during very early exposures to the task but did not differentiate further with training.

Analysis of mean gain variability (not shown) indicated a significant interaction between segment and training block ($F(5,55) = 6.39$; $p < 0.0001$). Main effect analyses of training block for each segment type revealed that the interaction was caused by fluctuation of the gain variability in the random segment only ($F(5,55) = 6.16$; $p = 0.0001$). Mean gain variability did not decrease for repeated ($p=0.40$) or random ($p = 0.052$) segments from early to late training.

In addition to changes in the magnitude of COM displacement, relative phase of the COM shifted from a phase lag ($-10.26^\circ \pm 3.14$) to phase lock ($2.66^\circ \pm 7.69$) for both repeated and random segments ($F(5,55) = 20.25$; $p < 0.0001$; Fig. 3), indicating that participants were able to improve predictive control of COM motion. Analysis of relative phase variability (not shown) indicated a significant interaction between segment and block ($F(5,55) = 3.89$; $p = 0.0043$). Main effect analyses of training block for each segment type revealed that phase variability decreased significantly for both repeated ($F(5,55) = 3.00$; $p = 0.018$) and random ($F(5,55) = 10.28$; $p < 0.0001$) segments with training. Post hoc analyses revealed that the repeated segment had significantly lower phase variability in block one only ($p = 0.017$). The correlation between change in COM phase and change in COM gain from early to late training was low for both repeated and random segments ($R^2 = 0.14$ and $R^2 = 0.41$ respectively) suggesting that the improvements in predictive control of COM motion did not determine improvements in COM gain.

Joint angle correlations with platform motion demonstrated a change in postural coordination with training. Ankle angle correlations were negative and became stronger with training ($F(1,11) = 10.97$; $p = 0.0069$; Fig. 4). A main effect of segment type indicated that correlations were significantly stronger for the repeated segment ($F(1,11) = 103.26$; $p < 0.0001$). Knee angle was modestly correlated with platform motion but this relationship did not become stronger with training ($F(1,11) = 0.26$; $p = 0.62$). Inspection of the data revealed that the correlation was driven by six participants who adopted a flexed knee posture to maintain balance. Hip angle was not correlated with platform motion in early training but demonstrated an increase with practice ($F(1,11) = 8.03$; $p = 0.016$). Again, the repeated segment was more strongly correlated with platform motion than the random segment and this effect existed in both early and late training as evidenced by the main effect of segment type ($F(1,11) = 22.43$; $p = 0.0006$).

Retention Performance—On day two, participants did not demonstrate significant losses in the performance gains achieved during training on day one. The maintenance of these improvements provides evidence for learning. Group COM gain scores remained near 0.53 and joint angle correlations with platform motion remained highly negative for the ankle and positive for the hip, suggesting that participants maintained a strategy which aimed to stabilize their COM in space rather than follow platform motion. Most participants also maintained their ability to predict the frequency of platform motion as demonstrated by COM relative phase scores that remained near zero.

Statistical analysis of COM gain indicated a main effect of block ($F(2,22) = 8.73$; $p = 0.0016$) and segment ($F(1,11) = 59.36$; $p < 0.0001$) but post hoc analysis revealed that COM gain during retention testing was not significantly different from late training for random or repeated segments ($p = 0.21$) indicating that there was no differential loss of improvement between segment types during the retention interval (Fig. 2). There was also a main effect of block ($F(2,22) = 10.72$; $p = 0.0006$) and segment ($F(1,11) = 49.43$; $p < 0.0001$) for COM gain variability. Post hoc analysis revealed that COM gain was even less variable during retention testing on day two compared to late training on day one ($p = 0.0001$). Analysis of COM phase indicated a main effect of block ($F(2,22) = 31.83$; $p < 0.0001$) but again, post hoc analyses

revealed that performance during the retention block on day two was not significantly different from late training ($p = 0.059$) and remained significantly different from behaviours adopted in early training ($p < 0.0001$) (Fig. 3). There was an interaction between block and segment for COM phase variability ($F(2,22) = 5.69$; $p = 0.010$) but post hoc analyses revealed that variability did not increase during the retention interval for either the random ($p = 0.64$) or repeated segment ($p = 0.75$) and there was no significant difference between segment types during retention testing ($p = 0.38$). In addition to maintenance of changes for COM measures, post hoc analyses of joint angle correlation with platform motions revealed no significant loss in the relationship between ankle joint and platform motion ($p = 0.94$) or hip joint and platform motion ($p = 0.75$) during the retention interval ($F(2,22) = 10.85$; $p = 0.005$) and ($F(2,22) = 6.36$; $p = 0.0066$); Fig. 4) respectively. For both measures however, there was a main effect of segment type indicating that the repeated segment ($F(1,11) = 76.59$; $p < 0.0001$) was more highly correlated with platform motion than the random segment ($F(1,11) = 30.28$; $p = 0.0002$) in both late training and retention testing. Together, these results demonstrate that similar to COM outcomes, the differences between segment types did not increase during the retention interval and as such, the repeated segment was not learned more effectively than the random segments.

Protocol B: Matched Amplitudes and Mean Velocities

To ensure that the differences between segment types which emerged early in training were not driven by differences in the characteristics of platform motion (e.g. level of challenge) for repeated versus random segments (Vaquero et. al., 2006; Chambaron et. al., 2006), we examined RMS amplitude of the platform signal for individual trials in early training (block one) for Protocol A. Results revealed consistently lower RMS amplitude for the random versus repeated segments but comparable RMS amplitudes for the random segments across trials. Based on these findings, we could not rule out the possibility that differences in outcome measures between segment types were driven by a platform artefact.

Statistical analysis of the primary outcome measure (COM mean gain) for participants exposed to the modified protocol indicated a segment $\times$ trial interaction ($F(6,50) = 3.05$; $p = 0.013$) but post hoc analysis (Bonferroni correction) revealed no consistent difference between random and repeated segments (Fig. 5) suggesting that the differences observed between segment types in protocol A resulted from differences in platform characteristics.

DISCUSSION

In the current study, participants demonstrated the ability to learn adaptive postural responses to continuous, variable amplitude platform motion as evidenced by the maintenance of postural control changes across days of testing. Unlike the results of Shea et. al. (2001) and those who have reported implicit motor sequence learning in upper limb tracking tasks (Pew, 1974; Wulf & Schmidt, 1997; Magill, 1998), performance improvements in the current study could not be attributed to implicit learning of the temporal relationship between perturbation sequence elements. Early differences in behaviour did emerge between random and repeated segments in Protocol A but these differences did not increase with practice as would be expected if

participants exploited their prior exposure to the repeated segment. Furthermore, the differences between the segment types no longer existed once the average amplitude and velocity of the perturbation sequences were matched in Protocol B. Thus, changes in balance performance with practice were driven by non-specific learning.

The goal of the current task was to avoid falling without taking a step. Theoretically, this goal could have been achieved in one of three ways: 1) by tracking the motion of the platform using a 'ride' strategy which would have produced COM mean gain values close to 1.0, 2) by "anti-tracking" the motion of the platform such that when the platform moved forward, the COM moved backward and vice versa, or 3) by minimizing COM motion in space which could serve to stabilize gaze or minimize energy expenditure. In the current study, participants aimed to minimize their COM motion with practice. Although participants might have improved their COM control further by knowing the sequence of perturbations in the repeated segment, this information was not necessary to avoid falling (Cleeremans and McClelland, 1991; Chambaron et. al., 2006).

Based on the platform dynamics in the current study, participants could have exploited prior knowledge of up to three features of platform motion to improve postural stability: 1) the sequence of platform amplitudes and/or resulting changes in velocity, 2) the forward and backward turnaround times (frequency) since this feature was held constant, or 3) the boundaries of platform motion. Based on our results, participants did not learn the sequence of amplitudes. A COM shift from phase lag to phase lock however, provides evidence for a control strategy that utilized the frequency of platform motion. It appears however, that learning was not limited to the tuning of the turnaround time. Since the magnitude of COM displacement improved (became smaller) with training and COM phase/gain correlations were weak, we suggest that participants also gathered information about the boundaries of platform motion, allowing the CNS to establish an appropriate gain to withstand the largest perturbations. If the improvements in gain had been driven by predictions about the frequency of platform motion, we would have expected the correlation to be stronger. Instead, the results suggest that COM gain changes were independent of phase changes. Changes in gain control with practice are also observed when young, healthy participants receive a random mixture of discrete perturbations (Horak et. al., 1989; Beckley et. al., 1991).

We propose that the current study lends further support to Chambaron et. al. (2006) who argue that evidence for sequence learning in continuous tracking tasks might be driven in part by peculiarities in the repeated segment and not implicit sequence learning per se. We propose therefore, that implicit sequence learning does not occur for compensatory posture control. From a functional view, it is reasonable to suggest that postural motor learning is non-specific. In an environment that contains an infinite number of challenges to stability, the posture control system must be flexible. Acquiring general knowledge about features in the environment serves better to achieve this flexibility than developing a series of motor responses that are limited to serving a specific sequence of stimuli.

Evidence for the extraction of general features in an unpredictable environment has been reported for both upper limb and discrete compensatory postural tasks. In these studies, postural motor responses tended toward a default value corresponding to either a medium sized perturbation in Horak et. al. (1989) or to the largest perturbation in Beckley et. al. (1991), depending on the degree of unpredictability and the risk. Ioffe et. al. (2004) also reported a general strategy of voluntary posture control in a random target task requiring corresponding movements of the centre of pressure. It should be noted that in the current study, sequence learning might have been masked by a transition period between relatively short segment intervals. While this possibility is conceivable, Perruchet et. al. (2003) have also reported that lengthy intervals can result in an overload of information that makes it difficult to learn the task; creating an equally disadvantaged training condition.

Changes in postural coordination patterns with practice

The second goal of the present study was to describe the postural patterns that emerged with practice and to determine whether experience should be considered an important factor influencing the postural coordination pattern used to maintain balance (Horak and Macpherson, 1996; Horak et. al., 1989). Since we were interested in observing the evolution of balance control with practice, we chose 0.5 Hz as the frequency of platform motion. This frequency is not associated with the emergence of a characteristic postural control pattern (Buchanan and Horak, 2001) and therefore we reasoned that it would offer the greatest opportunity for change. Early in training, participants adopted an ankle strategy to maintain equilibrium as evidenced by large negative correlations between ankle and platform motion. This finding is similar to that reported by Ko et. al. in 2001 for constant amplitude oscillations near 0.5 Hz. As participants became more familiar with the task however, hip-platform correlations increased suggesting the addition of compensatory motions at the hip to allow better stabilization of the COM in space. There was no change in knee-platform correlations indicating that the involvement of this joint in the evolution of a learned balance response was minimal. The joint motion of the lower limbs that accompanies this trunk-locked-in-space strategy serves to limit the transfer of reactive forces and decreases the energy requirements necessary to maintain whole-body stability (Sparrow and Newell, 1994). In this way, participants learn to maintain balance with greater energy efficiency.

Environmental challenges are often unpredictable in magnitude and/or timing and our expertise in responding to these challenges is a reflection of learning, not short term adaptation. Most studies of posture control have focussed on the latter and are limited in their ability to provide insight into strategies resulting from long term improvements. Under the current conditions, any attempt to learn specific characteristics of the perturbation may overload the processing capacity of the CNS and its ability to respond quickly enough to maintain balance. The present results are important in describing the capability of the nervous system to engage in relatively permanent changes in compensatory posture control by extracting regularities from a variable environment and adopting a generalized control strategy to maintain balance.

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Figure 1.

An example of variable amplitude platform motion (range ± 15 cm). The plot represents an overlay of two trials illustrating repeated and random segments. The repeated segment is denoted by the area shaded in grey.

Figure 2.

A) Group changes in COM gain with training. Repeated segment performance is denoted by *white* squares. Random segment performance is denoted by *black* squares. Error bars represent standard error of the mean. Asterisks indicate significant differences between blocks while block outlines indicate significant differences between segment types ($p < 0.05$). B) Individual changes in COM gain with training.

Figure 3.

A) Group changes in COM relative phase with training. Repeated segment performance is denoted by *white* squares. Random segment performance is denoted by *black* squares. Error bars represent standard error of the mean. Asterisks indicate significant differences between blocks ($p < 0.05$). B) Individual changes in COM relative phase with training.

Figure 4. Group correlations between joint angle and platform motion. Repeated segment performance is denoted by *white* markers. Random segment performance is denoted by *black* markers. Ankle joint correlations are represented by *squares*, knee joint correlations are represented by *diamonds*, and hip joint correlations are represented by *triangles*. Error bars represent the standard error of the mean. Asterisks indicate significant differences between blocks while block outlines indicate significant differences between segment types ($p < 0.05$).

Figure 5.

Group averages of COM gain for each trial in block one (Protocol B). Repeated segment performance is denoted by *white* squares. Random segment performance is denoted by *black* squares. Error bars represent the standard error of the mean. Block outlines indicate significant differences between segment types ($p < 0.05$ with Bonferroni correction).