

State-dependent corrective reactions for backward balance losses during human walking

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Abstract

We investigated corrective reactions for backward balance losses during walking. Several biomechanical studies have suggested that backward falling can be predicted by the horizontal position and velocity of the body center of mass (COM) related to the stance foot. We hypothesized that corrective reactions for backward balance losses depend on whether the body moves forward or backward after a perturbation. Using a split-belt treadmill, backward balance losses during walking were induced by rapid decreases of belt speed from 3.5 km/h to 2.5, 2.0, 1.5 and 1.0 km/h. We measured kinematic data and surface electromyography (EMG) during corrective reactions while walking on the treadmill. Phase portrait analysis of COM trajectories revealed that backward balance stability was decreased by the perturbations. When the perturbed belt speed was 1.0 km/h, the COM states at toe-off were significantly lower than the stability limit; a rapid touch-down of the swing foot posterior to the stance foot then occurred, and the gait rhythm was modulated so that the phase advanced. EMG recordings during perturbed steps revealed a bilateral response, including modulation of the swing leg during the recovery. For weaker perturbations, the swing foot placements were anterior to the stance foot and there was a phase delay. In contrast to the bilateral responses for stronger perturbations, unilateral EMG responses were observed for weaker perturbations. The differences in joint kinematics and EMG patterns in the unperturbed swing leg depended on the COM states at toe-off, suggesting the existence of different responses consisting of ongoing swing movements and rapid touch-down. Thus, we conclude that corrective reactions for backward balance losses are not only phase-dependent but also state-dependent. In addition, the control system for backward balance losses predicts the feasibility of forward progression and modulates swing movement and walking rhythm according to backward balance stability.

Keywords—Bipedal locomotion, Backward balance losses, Body center of mass, Phase resetting

1 Introduction

Control of bipedal locomotion maintains dynamic stability under various environments and disturbances. For example, in the case of sudden external forces or slipping, recovery must be induced by multi-joint compensation of balance losses in a small amount of time (a few hundred milliseconds), and the locomotor pattern must then converge to the previous steady pattern. To understand the neuro-mechanical mechanisms of human walking and how these ways relate to the increased incidence of falling in older individuals, numerous studies have attempted to elucidate recovery responses induced by various perturbations. Corrective reactions following various perturbations are functional behaviors for recovering gait stability, and depend on the phase of the gait cycle (Forsberg 1979; Berger et al. 1984; Eng et al. 1994). For instance, a trip perturbation during early swing induces an elevating response of the swing foot to step over an obstacle (elevation strategy), while a trip perturbation during late swing induces a lowering response for rapid touch-down (lowering strategy) (Eng et al. 1994). A “phase resetting” of locomotor rhythm is induced by afferent nerve stimulations in fictive

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locomotion in spinal cats (Baev et al. 1991a, b; Schomberg et al. 1998) and by impulsive perturbations that pull the shank backward during human walking (Kobayashi et al. 2000; Nomura et al. 2009). In human walking, perturbations in early swing induce a phase-delayed response, while perturbations in late swing induce a phase-advanced response. Theoretical investigations suggest that phase resetting improves the dynamic stability of walking (Yamasaki et al. 2003a, b; Nomura et al. 2009; Aoi et al. 2010). Reaction responses for backward balance losses have been investigated using various types of equipment, such as rapidly decelerating treadmills (Berger et al. 1984), low-friction platforms (Tang et al. 1998; Marigold and Patla 2002; Marigold et al. 2003; Bhatt et al. 2005), and treadmills (in which the trunk was pulled backward) (Misiaszek 2003; Misiaszek and Krauss 2005). A common feature of the reported responses was bilateral compensation for the stance and swing legs. This response of the unperturbed swing leg plays a functional role to ensure a sufficient support base for backward balance recovery.

The stability of backward balance can be quantified by the horizontal position and velocity of the body center of mass (COM) (Pai and Patton 1997; Yang et al. 2007, 2008). Since the COM position is posterior to the stance foot at toe-off, a sufficiently large COM velocity is required to avoid backward falling. Yang et al. (2007, 2008) determined a minimum threshold of horizontal COM velocity to achieve movement within the support base during gait and slipping using a detailed biomechanical model activated by biomechanically possible joint torque. Although their model was able to accurately predict the boundary of backward falling of measured slipping movement, the COM states measured during toe-off showed a large margin for the minimum threshold. These findings suggest that higher COM velocity is required to produce the passive walking pattern because the gait pattern of human locomotion shows passive characteristics of musculoskeletal dynamics such as ballistic walking (Mochon and McMahon 1980) and passive dynamic walking (McGeer 1990; Kuo 2002). Assuming that the passive COM dynamics during the single support phase can be simplified using an inverted pendulum model (Kajita and Tani 1995), a necessary condition for forward progression can be represented by a simple relationship between the horizontal COM position and velocity related to the stance ankle (Kagawa and Uno 2010). Figure 1 shows a phase portrait of the COM state. Dashed lines represent the contour plots of mechanical energy per unit mass of the inverted pendulum, which represents the ballistic trajectories of the COM. The COM can move forward beyond the stance ankle position ($x^{com} = 0$) without energy input when the COM state at toe-off is higher than the boundary line of the necessary condition ($E > 0, \dot{x}^{com} > -\omega x^{com}$), where ω is the natural frequency $\sqrt{g/l}$ (g : gravity acceleration, l : constant distance between the COM and the stance ankle). On the other hand, the COM moves backward without the compensatory energy input when the COM state at toe-off is lower than the boundary line ($E < 0, \dot{x}^{com} > -\omega x^{com}$). It is likely that the corrective response for the backward balance losses depends on whether the COM can move forward or not.

In this study, we hypothesized that the corrective reaction for backward balance losses depends on the stability of backward balance. To examine this hypothesis, we investigated corrective reactions for backward balance losses that were induced at heel strike by a rapid decrease in the belt speed of a treadmill. By changing the belt speed, the COM velocity related to the stance foot rapidly decreased at toe-off, which led to a reduction in backward balance stability. The gait kinematics and surface electromyography (EMG) of perturbed walking were also evaluated.

2 Methods

Seven young healthy men (22–24 years) with no history of neurological or musculoskeletal disorder participated in the study. Approval of the experimental procedure was obtained from the Ethics Committee of Nagoya University. All subjects gave their informed consent prior to participation in the experiments.

2.1 Apparatus and protocol

Backward balance losses were induced by a rapid decrease in the speed of the stance surface at heel strike using a split-belt treadmill (PW-22, Hitachi Information and Communication Ltd.), as shown in Fig. 2A. Use of the split-belt treadmill allows the stance leg to be perturbed without perturbing the speed of the belt of the swing leg, for realistic slip exposure. Gait kinematics and surface EMG data were measured while the subjects walked on the treadmill. Twelve positions of the human body, shown in Fig. 2B, were measured with a 3-dimensional position measurement device (Optotrak Certus, Northern Digital Inc.) at 100 Hz. Thin pressure sensors (Flexiforce Texscan Inc.) were attached to shoe soles, and foot pressure data were simultaneously collected with a 12-bit AD converter (AD12-8USBGY, Contec Co. Ltd.). Surface EMG activity was measured using a bio-signal measurement device (MQ8, Marq Medical). Based on preliminary observations, we assumed bilateral symmetry during walking and equivalent responses for perturbations between the left and right legs, so muscle activity was collected for only the right leg because of the channel limitations of the device. Thus, the EMG responses of the perturbed stance leg were collected when the right belt speed was decreased, and those of the unperturbed swing leg were collected when the left belt speed was decreased. EMG signals from the tibialis anterior (TA), soleus (SOL), medial gastrocnemius (MG), vastus lateralis (VL), rectus femoris (RF), and biceps femoris (BF) were measured at 1000 Hz. The measurements of the positions and EMG were synchronized with a digital trigger.

The unperturbed belt speed V_{un} was 3.5 km/h (0.97 m/s). The gait at the unperturbed speed was comfortable for all subjects. Corrective reactions for eight types of perturbations corresponding to combinations of the perturbed speed ($V_p = 2.5, 2.0, 1.5, \text{ and } 1.0 \text{ km/h}$) and perturbed leg (left or right leg) were measured. The perturbed leg conditions were needed to collect the perturbed and unperturbed EMG responses from the measurement of only the right leg muscles. The upper profile in Fig. 2C shows the belt speed following the onset of perturbation. The belt speed rapidly decreased at heel strike with an acceleration of -10 m/s^2 , and returned to the unperturbed value 0.8 s after the perturbation onset with the same acceleration. A perturbation was applied once every ten cycles. The position of the perturbed cycle in each set of ten cycles was determined randomly. The type of perturbation was also randomized. Preliminarily, we found that a recovery process would require a few steps from the perturbation onset, similar to the stumbling reaction (Cordero et al. 2003). Hence, a perturbation was not applied within three cycles after a perturbed cycle. The subjects were not provided with any cues that might indicate when and which perturbation would appear. Five blocks of data collection were performed with a break between blocks in order to avoid participant fatigued. During one block of the experiment, three perturbed cycles were presented for each type of perturbation, and 240 cycles (3 times \times 8 types of perturbations \times 10 cycles including a perturbed cycle) were measured. Of these 240 cycles, 24 were perturbed and 216 were unperturbed. Subjects were instructed to cross their arms in front of their bodies to prevent marker occlusion.

2.2 Data analysis

The measured position data were filtered by a finite impulse response (FIR) low pass filter with a cutoff frequency of 15 Hz. The angles of the hip, knee, and ankle joints of the right and left legs were calculated in the sagittal plane. The COM position was calculated from the position data and anthropometric data (mass and center of mass) of the body segments, consisting of the foot, shank, thigh, head-trunk, upper arm, and forearm. The anthropometric data were taken from the literature (Winter 2005). Based on a linear inverted pendulum model which simplifies the dynamics of COM movement during single support phase, the backward balance stability was evaluated as the mechanical energy normalized by the body mass at toe-off (Pratt et al. 2006; Kagawa and Uno 2010).

$$E = \frac{1}{2}(\dot{x}^{com})^2 - \frac{1}{2}(\omega x^{com})^2, \quad \omega = \sqrt{\frac{g}{l}}, \quad (1)$$

where x^{com} is the horizontal COM position related to the stance ankle, and ω is the natural frequency of the inverted pendulum model. g indicates gravity acceleration and l indicates the distance between stance ankle and COM position. In this analysis, l was given by the mean value of the distance during the single support phase. When $E > 0$, the COM does not move backward even in case where no compensatory response appeared. When $E < 0$, the COM moves backward without compensation. It should be noted that the unstable area ($E < 0$) includes states in which the stability can be recovered by an appropriate correction response since it is assumed in the model that a COM movement during a single support phase is ballistic (Cavagna and Margaria 1966; Mochon and McMahon 1980).

To quantify the differences in the kinematic patterns among the conditions of perturbed belt speed, we evaluated the step length (L) at touch-down and phase shift ($\Delta\psi$) following the perturbations. The step length L was defined as the swing ankle position related to the stance ankle position at touch-down. However, the differences in step length among the perturbation conditions were directly associated with the perturbed belt speed. Even without any response, the step length would be changed according to the perturbed belt speed because the movement distance of the stance foot on the treadmill is shortened by decreasing belt speed. We also evaluated the horizontal position of the swing ankle in relation to the hip position at touch-down, which indicates modulation of the swing leg.

We evaluated the phase shift based on a peak time of swing knee flexion following a perturbed cycle (see lower profile of Fig. 2C) because the knee joint profiles showed a clear phase shift. The phase shift $\Delta\psi$ was calculated using the following equation (Kobayashi et al. 2000):

$$\Delta\psi = \frac{t_p - t_{un}}{T_{un}}, \quad (2)$$

where $t_p - t_{un}$ indicates the phase difference of perturbed time of maximum knee flexion. t_p is the time of peak knee flexion following a perturbed cycle, and t_{un} is the mean peak time following an unperturbed cycle. T_{un} indicates the mean gait period of unperturbed cycles. Differences in the mechanical energy and step length among the unperturbed and perturbed steps were examined using one-way repeated-measures analyses of variance (ANOVAs). *Post hoc* analysis consisted of Tukey's honestly significant difference (HSD) test. The values of phase shift $\Delta\psi$ in a perturbed condition were examined by single sample *t*-test with null hypothesis that $\Delta\psi = 0$. Differences in the phase shift among the perturbed steps were also examined by ANOVAs and *post hoc* testing. The significance level was set at 0.05.

The EMG signals were full-wave rectified and low-pass filtered at 20 Hz by a FIR low pass filter. The EMG signals were ensemble averaged over fifteen steps for each perturbation to yield the temporal patterns of the recovery response. To quantify the differences in the amplitude of responses according to the perturbation intensity, they were evaluated by the mean amplitude of filtered EMG during the single support phase, where EMG from perturbation onset to 100 ms was eliminated from this analysis because there was no significant response within the time window. To indicate the physiological relevance of EMG, mean amplitude was normalized by the mean EMG of the unperturbed gait during a cycle. Differences in amplitude due to perturbations were examined by one-way repeated-measures ANOVAs and Tukey's HSD tests.

3 Results

Figure 3 shows the COM trajectories of subject C on the phase portrait. These trajectories were plotted from the right heel strike to the touch-down of the left foot. Dashed lines show the trajectories during the double support phase, while solid lines show those during the single support phase. During the double support phase, the COM velocity rapidly decreased in the perturbed steps. There were no corrective responses to regulate the unperturbed COM trajectories during the single support phase. The

trajectories could move beyond the stance ankle position ($x^{com} = 0$) under the unperturbed condition and under perturbation when $V_p = 2.5$ and 2.0 km/h. When $V_p = 1.5$ and 1.0 km/h, the trajectories could not move beyond the stance ankle position. In particular, when $V_p = 1.0$ km/h, the COM velocity rapidly decreased during the single support phase and was negative at touch-down, indicating that the COM moved backward at touch-down.

Figure 4 shows stick diagrams of the perturbed walking patterns for a typical subject C when $V_p = 2.5, 2.0, 1.5,$ and 1.0 km/h. Both the step length at touch-down and the duration of the swing phase decreased with V_p . When $V_p = 1.0$ km/h, the placement of the swing foot at touch-down was posterior to the stance foot. Figure 5 shows the swing ankle joint trajectories related to the hip joint position, eliciting modulation of swing movement. Figure 5A shows the paths in the sagittal plane from heel strike of the contralateral leg to touch-down. Despite the shortened step length when $V_p = 2.0$ km/h, the paths were similar to those during unperturbed walking. On the other hand, paths were obviously shortened when $V_p = 1.0$ km/h. Figures 5B and C show the horizontal and vertical velocity of ankle position in relation to hip position. The velocity profiles when $V_p = 2.0$ km/h were equivalent to the profiles of unperturbed walking. When $V_p = 1.0$ km/h, the horizontal velocity was rapidly decreased from 0.2 s. Furthermore, the minimum peaks of the vertical velocity were also decreased, and they became earlier.

Figure 6 shows the profiles of the joint angles of the perturbed stance leg (left column) and the unperturbed swing leg (right column), where the perturbation onset was 0 s. The earliest perturbation effects were found at the stance ankle joint in which dorsiflexion movements were prevented by perturbations. Following the perturbed ankle angle, hip extension movements were prevented. The perturbations induced modulations of the trajectories of the unperturbed swing joint around the middle part of the swing phase. When $V_p = 1.0$ km/h, rapid hip extension was found before touch-down. On the other hand, hip extension was delayed when $V_p = 2.0$ km/h. In addition, the phase resetting of joint trajectories was observed in perturbed walking. The phase delay and advance related to the unperturbed profile were observed in perturbed walking when $V_p = 2.0$ and 1.0 km/h, respectively.

Figure 7A shows the mean and standard deviation (SD) of the mechanical energy per unit mass E at toe-off among all subjects. The mechanical energy was decreased by the perturbation. When $V_p = 2.5$ and 2.0 km/h, the mechanical energy was positive, whereas when $V_p = 1.5$ and 1.0 km/h, the mechanical energy was negative. Our analysis indicated significant differences among all the conditions ($P < 0.05$). Figure 7B shows the mean and SD of the step length L at touch-down after the perturbation onset. The step length decreased with V_p . When $V_p = 1.0$ km/h, the step length was negative, indicating that the foot placements of the swing leg were posterior to the stance foot. The differences in step length were significant between the unperturbed steps and perturbed steps ($P < 0.05$), except for $V_p = 2.5$ km/h. Figure 7C shows the mean and SD of the horizontal position of the unperturbed swing foot ankle in relation to hip position at touch-down. Although the position was decreased according to the perturbation intensity similarly to the step length, there were no significant differences between unperturbed steps, $V_p = 2.5$ and 2.0 km/h. The positions in $V_p = 1.5$ and 1.0 km/h were significantly decreased. The mean and SD of the phase shift $\Delta\psi$ are shown in Figure 7D. The phase was delayed under the perturbed condition of $V_p = 2.5, 2.0,$ and 1.5 km/h ($P < 0.05$), whereas it was advanced when $V_p = 1.0$ km/h ($P < 0.05$). The phase shift of $V_p = 1.0$ km/h is significantly different from those of the other weaker perturbations ($P < 0.05$).

Figure 8 shows the ensemble averaged EMG of TA, SOL, VL, and BF of the perturbed stance leg (left column) and the unperturbed swing leg (right column). EMG patterns of MG were similar to those of SOL, and the patterns of RF were similar to those of VL. Excitatory responses of the perturbed and unperturbed legs were evoked except in SOL of the perturbed leg. TA and VL of the perturbed leg, which accelerate the body forward, were explicitly activated for both of $V_p = 2.0$ and 1.0 km/h. When $V_p = 1.0$ km/h, the activities of VL and BF of the unperturbed leg, which contribute to rapid touch down, were significant, and their latency was approximately 0.1 s. When $V_p = 2.0$ km/h,

the activity of the unperturbed leg muscles was relatively small, and much less than when $V_p = 1.0$ km/h. Although an explicit response of BF was found in $V_p = 2.0$ km/h, the amplitude was much smaller and the latency was longer.

Figure 9 shows the mean EMG amplitude and its SD during the single support phase among all subjects. The differences in EMG amplitude were significant for all muscles ($P < 0.05$). In all perturbed conditions, excitatory responses of TA and VL and inhibitory responses of SOL were found in the perturbed leg. For the weaker perturbation ($V_p = 2.5$ and 2.0 km/h), although clear reaction-related activity was found in the muscles of the perturbed leg, the activity of the unperturbed leg muscles was quite weak. Differences in the amplitude of the unperturbed leg muscles were not significant between $V_p = 2.5$ and 2.0 km/h except TA in $V_p = 2.5$ km/h. For the stronger perturbation ($V_p = 1.5$ and 1.0 km/h), greater reactive EMG amplitude was observed for the perturbed and unperturbed legs.

4 Discussion

A major finding in this study was that even though the perturbation onsets were applied at the same phase of heel strike, different corrective reactions were induced according to the backward balance stability. When the COM state at toe-off following a perturbation onset was significantly lower than the boundary line for forward progression, a rapid touch-down of the swing foot posterior to the stance foot occurred. The trajectories of ankle position relative to the hip position indicate that the posterior placements were a consequence of modulations of swing trajectories. For rapid touch-down, strong muscle activities of the unperturbed swing leg were evoked with a latency of 0.1 s. After the perturbation exposure, the phase of locomotor rhythm was advanced. When the state at toe-off was over or around the boundary, subjects maintained the swing movement without rapid touch-down. In addition, the phase was delayed in contrast to the phase advance in the rapid touch-down response. The muscle activity of the unperturbed leg was similar to the steady patterns, indicating that weaker perturbation induced a unilateral recovery response in contrast to the bilateral response involved in the rapid touch-down. These results indicate two types of recovery, consisting of the rapid touch-down and ongoing swing movement, depending on whether the COM was able to move forward or not. Previous studies indicated that the corrective responses depend on the phase of perturbation onset (Forssberg 1979; Berger et al. 1984; Eng et al. 1994). Our results provide evidence of another aspect of corrective responses for backward balance loss, indicating that they are state-dependent behaviors.

4.1 Functional recovery for backward balance loss

Assuming that the COM dynamics during the single support phase can be simplified using an inverted pendulum model, the acceleration and deceleration of the COM by gravity were proportional to the COM position related to the stance ankle position (Kajita and Tani 1995). As shown in the phase portrait of the measured COM (Fig. 3), the COM velocity rapidly decreased when COM position and velocity were lower than the boundary of the necessary conditions for ballistic forward progression. When $V_p = 1.0$ km/h, the COM velocity rapidly decreased during single support phase and could not move forward beyond the stance ankle position. When the COM states were over or around the boundary, the COM was able to move forward. These results indicate that the COM movements during the single support phase strongly depended on the COM state at toe-off. These state-dependent behaviors result from the unstable dynamics of the COM, which are similar to those of an inverted pendulum. For the perturbed COM velocity, the regulation of the COM trajectory in the steady pattern did not appear even though the COM states were over the boundary. The COM regulation during the single support phase is inefficient because the movement has to cope with gravity.

For the state-dependent behavior of the COM, different responses were observed in the kinematics and EMG patterns of the unperturbed swing leg. When the COM was able to move beyond the stance ankle, subjects maintained the swing movements without rapid touch-down. When the COM

could not move beyond the stance ankle, the rapid extension movements of the swing hip and decrease of horizontal and vertical ankle velocity in relation to hip position appeared at the middle swing phase, and the foot placement at touch-down was posterior to the stance foot. Although the EMG amplitude of the perturbed leg was significantly increased for all perturbed conditions and the amplitude was increased gradually according to the perturbation intensity, the EMG of the unperturbed leg showed two types of response corresponding to the different kinematics patterns. For weaker perturbations, the EMG amplitude of the unperturbed leg was not significant, except TA in $V_p = 2.0$ km/h. The activity of TA is thought to contribute to producing toe-clearance and avoid unexpected landing (Marigold et al. 2002). The significant responses of VL and BF for greater perturbation indicate that they are responsible for rapid touch-down. The response of SOL before touch-down may play a roll in pre-activity for impact-absorption and body support at touch-down. Similar pre-activity was observed in previous studies during other actions, such as stepping, hopping (Melvill Jones and Watt, 1971a), unexpected falls (Melvill Jones and Watt, 1971b), and self-initiated falls (Santello and McDonagh 1998). Although the differences in the COM trajectories among the perturbations are a consequence of passive dynamics, the differences of kinematics and EMG of the unperturbed swing leg resulted from the control of balance recovery by the central nervous system (CNS). These results suggest that the control system for backward balance losses predicts the feasibility of forward progression and modulates the swing movement and walking rhythm according to the stability of backward balance.

It is likely that the CNS controls the placement of the swing foot and the phase resetting, rather than regulating a steady pattern of COM movement. Even though the responses of the perturbed leg were significant for weaker perturbations, they were insufficient to regulate the steady pattern. Foot placement is critically important for initiating the subsequent swing movement (Winter 1995; Pratt et al. 2006). Decreasing the step length plays a role in recovery responses, because the distance between the COM position and the stance ankle of the subsequent swing movement is shortened, improving backward balance stability. Phase resetting also plays a functional role in recovering balance and converging to the steady-state pattern (Yamasaki et al. 2003a, b; Nomura et al. 2009; Aoi et al. 2010). From the viewpoint of nonlinear dynamical system theory, Yamasaki et al. (2003a) suggested the functional roles of the phase resetting as follows; first, relocating the perturbed state point from outside the basin of attraction of the limit cycle to inside. Second, reducing convergence time to the limit cycle. In the case of stumbling, an elevating strategy and phase delay appear in the early swing phase, while a lowering strategy and phase advance appeared in the late swing phase (Eng et al. 1994; Kobayashi et al. 2000). Cordero et al. (2005) suggested that the lowering strategy is more energetically expensive but less risky for falling, and when making a choice of strategies, a tradeoff between stability and efficiency should be considered. The rapid touch-down response for backward balance losses is similar to the response of the lowering strategy for stumbling with respect to phase modulation and energy cost. One possible interpretation of this similarity is that both the responses, which each lower the swing foot, are evoked to abort the swing movement and to restore stability by a common neural mechanism that predicts future falling.

A number of researches have demonstrated phase-dependent reflex reversal between excitation and inhibition during walking in animals (Forssberg et al. 1975, 1977; Forssberg 1979; Duysens and Stein 1976, Duysens and Pearson 1978) and humans (Yang et al. 1990; Eng et al. 1994; De Serres et al. 1995). In the elevation strategy for stumbling in human, swing TA showed excitatory response, while it showed inhibitory response in the lowering strategy (Eng et al. 1994). De Serres et al. (1995) suggested that the parallel excitatory and inhibitory pathways from sensory feedback generated the phase-dependent reflex reversal. In our experiments, the evoked EMG amplitude monotonically increased or decreased with increasing the perturbation intensity and did not show reflex reversal which depends on the state. It can not be revealed from our experimental results whether the two types of response were generated by a parallel or common neural mechanism. One possible explanation is that a common neural mechanism modulates the swing movements depending on sensory feedback

related to a threshold detecting future falling.

4.2 Methodology for inducing backward balance losses

In this study, backward balance losses were induced by a rapid decrease in a unilateral stance surface using a split-belt treadmill. Berger et al. (1984) investigated compensatory responses using the impulsive velocity change of the stance surface on a treadmill. For impulsive perturbations, we investigated the compensations for perturbations such as step functions to elucidate the dependence on backward balance stability. Our methodology is not equivalent to an environment that induces slips because the perturbed stance surface was maintained at a constant velocity. However, the rapid touch-down response when $V_p = 1.0$ km/h was similar to responses to slips on movable platforms (Tang et al. 1998; Marigold and Patla 2002; Bhatt et al. 2006) with respect to the kinematic patterns and the latency of muscle activity. The inhibitory responses of SOL and MG of the stance leg were in accord with those reported in a previous study by Nashner (1980). Consistent with the current findings, Bhatt et al. (2005) used a movable platform and showed that step length was reduced following a slip, and the duration from toe-off to touch-down was shorter when gait velocity was slow. This result suggests that a primal neural mechanism for recovering backward balance evoked the compensatory responses that occurred when $V_p = 1.0$ km/h in the present study.

We evaluated EMG responses of the right leg only, under the assumption that the reactive responses of right and left legs were equivalent. Although the basic gait patterns in healthy adults show bilateral symmetry, a number of studies indicate that the movements of the right and left legs do not show perfect agreement (Sadeghi et al. 2000; Goble et al. 2003; Seeley et al. 2008). In our experiments, basic patterns of the responses according to the perturbed conditions (ongoing swing movement or rapid touch-down) of the right and left legs were equivalent in terms of kinematics. However we confirmed that some subjects showed asymmetric swing trajectories in the rapid touch-down recovery. Further investigations using bilateral EMG and kinetic data are required to clarify bilateral differences in the recovery response.

When slip perturbations are repeated using a moving platform, adaptive behavior occurs within a few steps (Marigold and Patla 2002; Bhatt et al. 2006). In our paradigm, however, we could not observe the remarkable adaptations reported in previous studies. Simultaneous learning for different environments requires prior contextual cues to identify each environment (Wada et al. 2003). Lack of prior cues about the timing and intensity of perturbation was likely to have prevented the adaptation of compensation to our study. To avoid occlusion of our position measurements, the subjects crossed their arms in front of their bodies. Arm raising is a typical behavior in the response for backward balance losses (Marigold et al. 2003; Misiaszek and Krauss 2005). Restriction of arm movement enhances the reactive responses of leg muscles, but the pattern and latency of muscle activation are not affected (Misiaszek and Krauss 2005). As mentioned by Tang et al. (1998), arm restrictions do not dramatically affect locomotor or compensation patterns.

5 Conclusions

In the present study, we examined the following hypothesis: that corrective reactions for backward balance losses depend on whether the body moves forward or backward following perturbations during walking. The results revealed that compensatory responses to perturbations exhibited state-dependent functional behaviors. More unstable cases such as rapid touch-down reactions appeared with stronger perturbations. Differences in kinematics and EMG patterns of the swing leg were found in the early and middle swing phases. We conclude that the corrective reactions to perturbations in bipedal walking are not only phase-dependent but also state-dependent. Taken together with previous findings, the current results suggest that corrective responses are determined by balancing the tradeoff between the risk of future falling and the efficiency of compensation.

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Figure captions

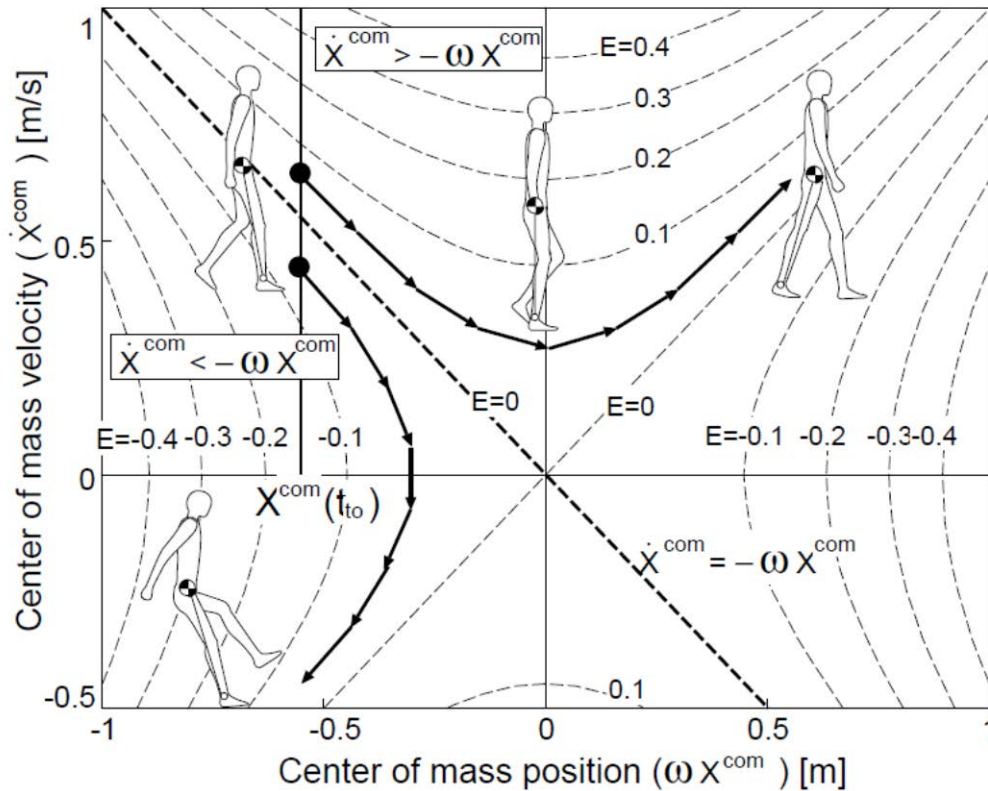


Fig. 1 Phase portrait of the horizontal position and velocity of the body center of mass (COM). The horizontal position represents the product of the COM position and natural frequency (ωx^{com}). The contour plots of the mechanical energy correspond to ballistic COM trajectories. The interval between the trajectories is 0.1 J/kg. The thick dashed line with negative slope shows the critical velocity of the position required for the necessary conditions to be satisfied. When the COM state at toe-off is over the critical line, the COM moves beyond the stance ankle without compensation. On the other hand, the COM moves backward without any recovery effort when the COM states are under the critical line. It should be noted that the unstable area ($E < 0$) includes states in which the stability can be recovered by appropriate compensation since the model is based on a ballistic walking concept.

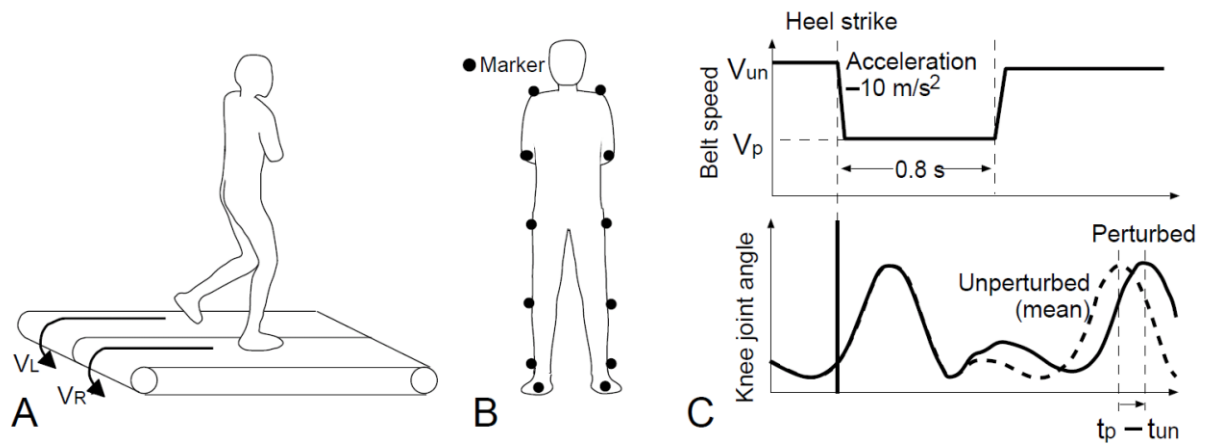


Fig. 2 Experimental setup. A: Illustration of walking on a split-belt treadmill. The speed of the left and right belts can be independently controlled. B: Twelve markers were attached to the body of a subject, and the positions of the markers were measured. C: Profiles of belt speed and contralateral knee joint angle following perturbation onset. In the belt speed profile (upper), V_{un} and V_p are the unperturbed and perturbed belt speeds, respectively. The belt speed rapidly decreased at heel strike with an acceleration of -10 m/s^2 . The belt speed was maintained constant for 0.8 s before returning to the unperturbed speed. In the contralateral knee joint pattern (lower profile), the phase shift represents the difference in time at maximum knee flexion between the mean profiles of unperturbed walking and perturbed walking normalized by the mean period of unperturbed walking.

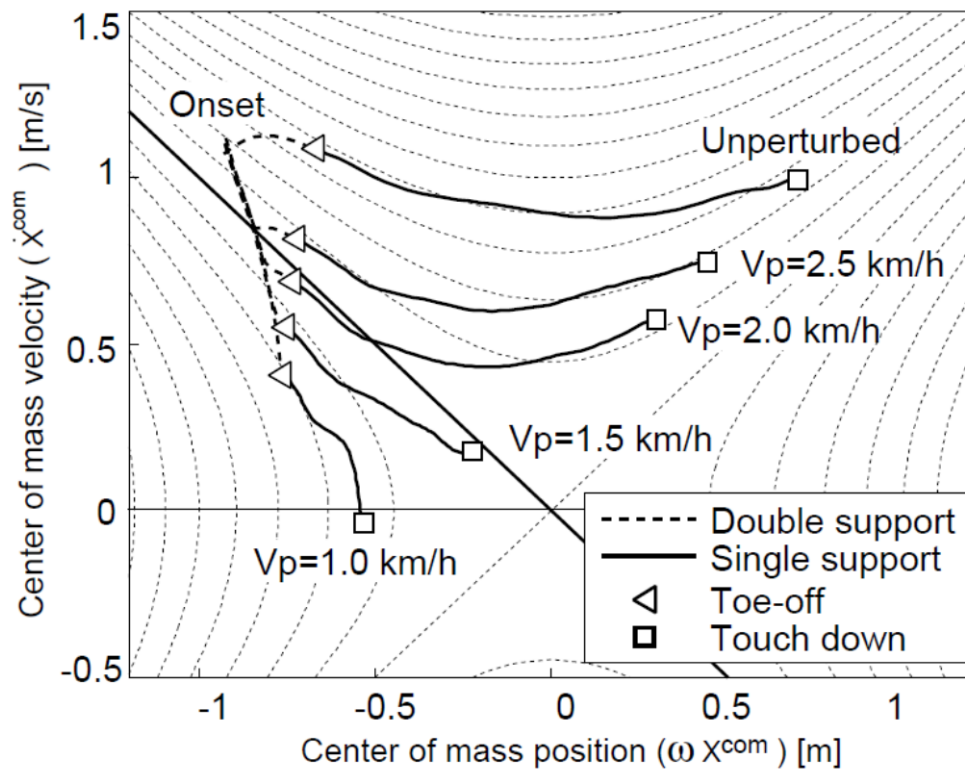


Fig. 3 Trajectories of the measured COM position and velocity on the phase portrait from right heel strike to left touch-down. Dashed and solid lines indicate the trajectories during the double support and single support phases, respectively. Triangles and squares denote the states at toe-off and touch-down, respectively.

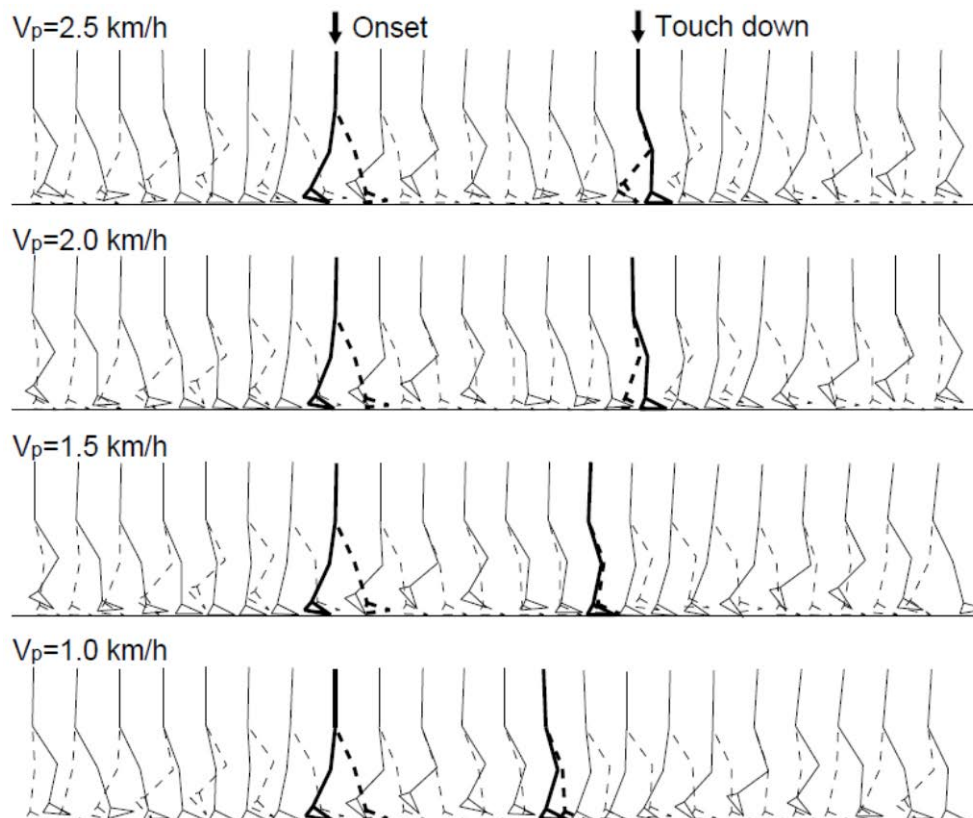


Fig. 4 Stick diagrams of compensatory movements for perturbations when $V_p = 2.5, 2.0, 1.5,$ and 1.0 km/h. These figures show the results of a typical subject C. Solid lines denote the unperturbed leg and trunk while dashed lines denote the perturbed leg. The first thick lines illustrate the postures at perturbation onset, while the second lines illustrate the postures at touch-down. The time interval of each picture is 0.1 s.

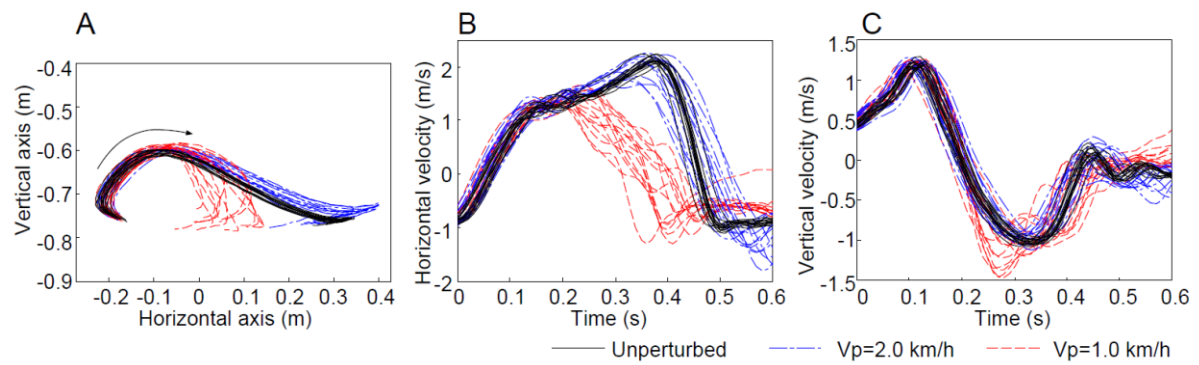


Fig. 5 Trajectories of swing ankle position in relation to hip position. Solid lines, dotted dashed lines, and dashed lines show unperturbed, perturbed ($V_p = 2.0$), and perturbed ($V_p = 1.0$ km/h) trajectories. A: Paths of ankle joint from contralateral heel strike to touch-down. The origin of the paths is the hip position. B: Horizontal velocity of ankle position. C: Vertical velocity of ankle position.

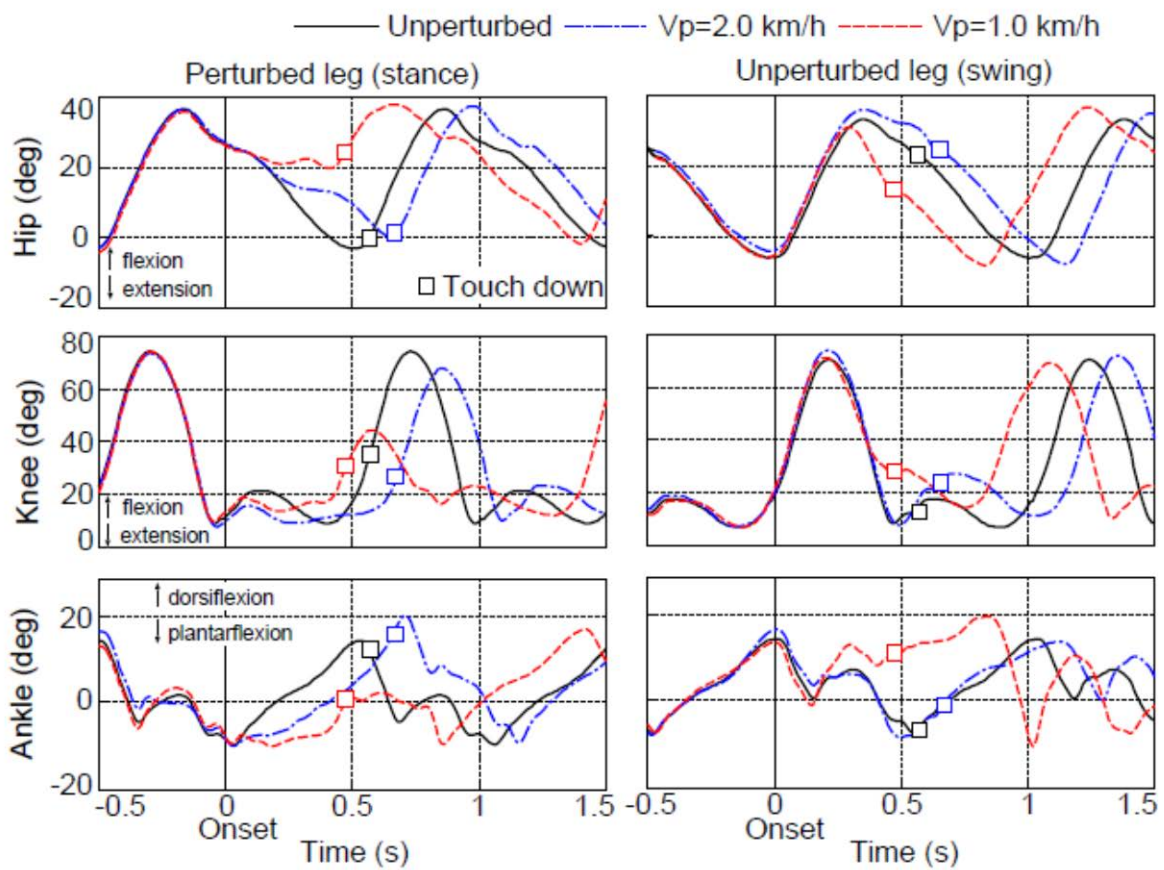


Fig. 6 Profiles of hip, knee, and ankle angles of a typical subject C. The figures show the profiles from 0.5 s before perturbation onset to 1.5 s after onset. Solid lines, dotted dashed lines, and dashed lines show unperturbed, perturbed ($V_p = 2.0$), and perturbed ($V_p = 1.0$ km/h) stepping, respectively. Squares indicate the states at touch-down.

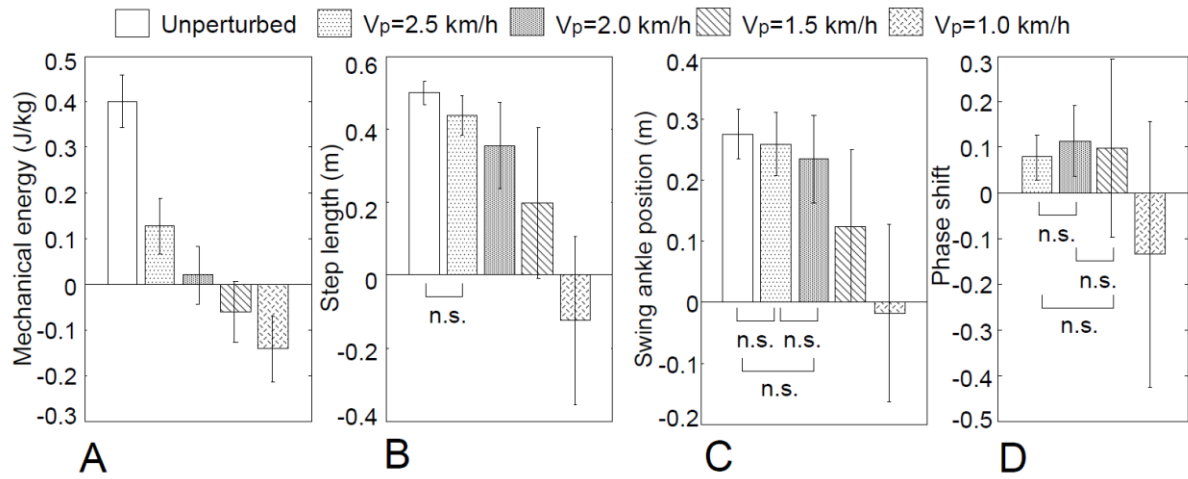


Fig. 7 Mean and SD of mechanical energy (A), step length (B), swing ankle position related to hip position at touch-down (C), and phase shift (D). In the pairs marked as “n.s.,” no significant differences were found. For the other pairs, the differences were significant ($P < 0.05$).

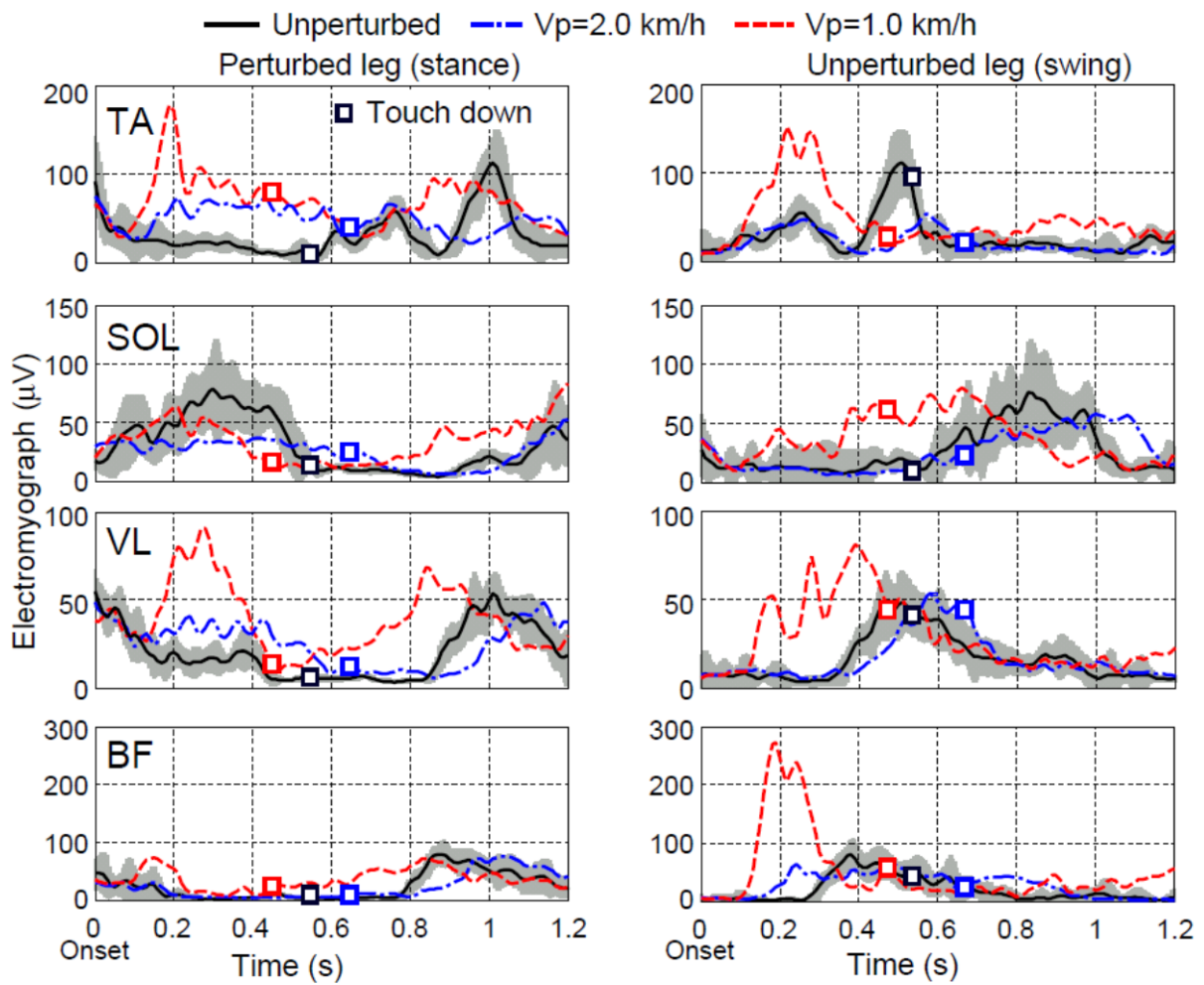


Fig. 8 The ensemble averaged EMG activities of a typical subject C. Profiles are TA, SOL, VL, and BF of the perturbed stance leg (left column) and unperturbed swing leg (right column) from perturbation onset (0 s) to 1.2 s. The solid lines show the profiles of unperturbed steps, and the dashed and dash-dotted lines show the profiles of perturbed steps when $V_p = 2.0$ and 1.0 km/h, respectively. Gray areas indicate one SD around the EMG profile in the unperturbed walking.

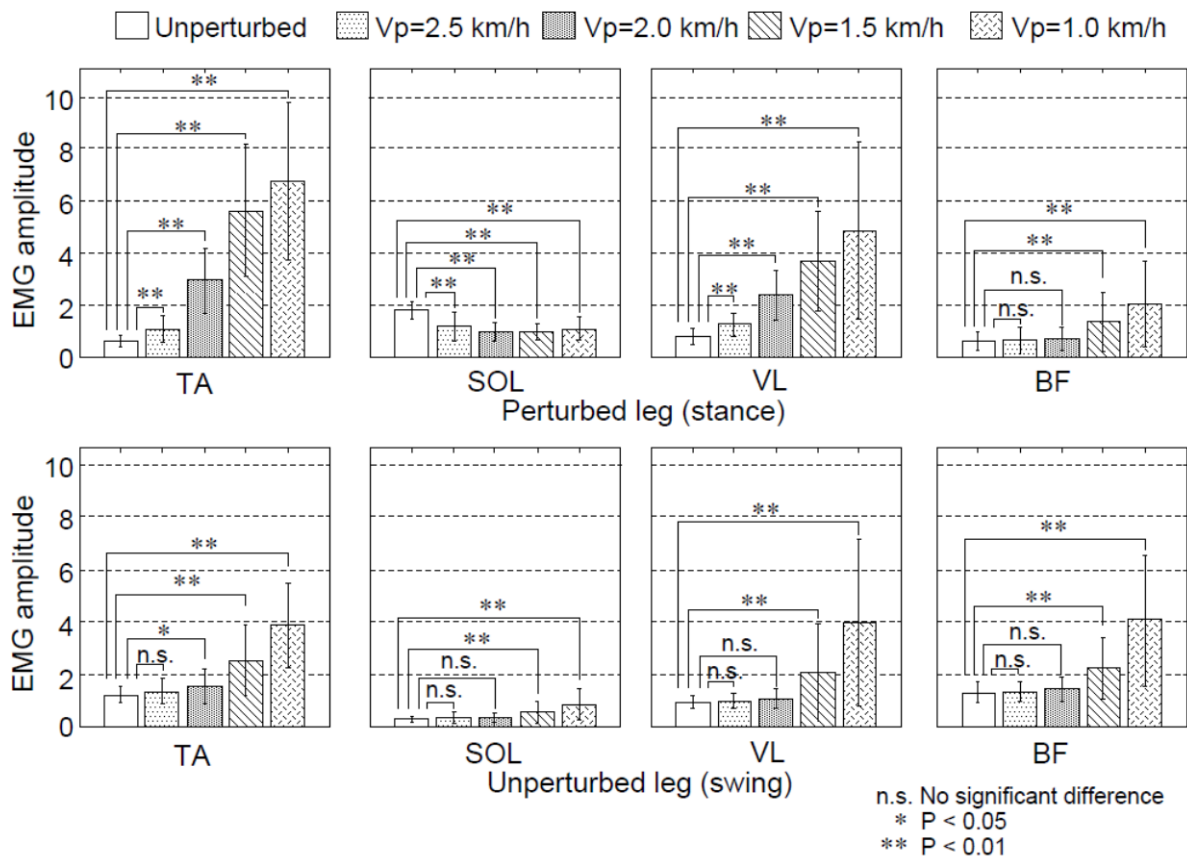


Fig. 9 The mean EMG amplitude from 0.1 s after perturbation onset to touch-down. The amplitude was normalized by the mean EMG of unperturbed walking in a cycle. The upper figures show the values from the perturbed leg and the lower figures show those from the unperturbed leg.