Predictive control of ankle stiffness at heel contact is a key element of locomotor adaptation during split-belt treadmill walking in humans

Ogawa T, Kawashima N, Ogata T, Nakazawa K. Predictive control of ankle stiffness at heel contact is a key element of locomotor adaptation during split-belt treadmill walking, J Neurophysiol 111: 722–732, 2014. First published November 13, 2013; doi:10.1152/jn.00497.2012.—Split-belt treadmill walking has been extensively utilized as a useful model to reveal the adaptability of human bipedal locomotion. While previous studies have clearly identified different types of locomotor adaptation, such as reactive and predictive adjustments, details of how the gait pattern would be adjusted are not fully understood. To gain further knowledge of the strategies underlying split-belt treadmill adaptation, we examined the three-dimensional ground reaction forces (GRF) and lower limb muscle activities during and after split-belt treadmill walking in 22 healthy subjects. The results demonstrated that the anterior component of the GRF (braking force) showed a clear pattern of adaptation and subsequent aftereffects. The muscle activity in the tibialis anterior muscle during the early stance phase was associated with the change of braking force. In contrast, the posterior component of GRF (propulsive force) showed a consistent increase/decrease in the fast/slow leg during the adaptation period and was not followed by subsequent aftereffects. The muscle activity in the gastrocnemius muscle during the stance phase gradually decreased during the adaptation phase and then showed a compensatory reaction during the washout phase. The results indicate that predictive feedforward control is required to set the optimal ankle stiffness in preparation for the impact at the heel contact and passive feedback control is used for the production of reflexively induced propulsive force at the end of the stance phase during split-belt treadmill adaptation. The present study provides information about the detailed mechanisms underlying split-belt adaptation and should be useful for the construction of specific rehabilitation protocols.

HUMAN BIPEDAL LOCOMOTION is flexible enough to accommodate environmental demands. To achieve rhythmic and stable steps in various situations, two types of control strategies, reactive and predictive adjustments, take place. Reactive action is rapidly elicited based on the automatically induced vestibulospinal and spinal reflex system utilizing sensory feedback (Dietz 1992; Sinkjaer et al. 1996). Predictive action can be accomplished over minutes to hours using trial-and-error-based learning, which presumably involves the cerebellar process (Bastian 2006). Split-belt treadmill walking has been utilized as a useful model to reveal the adaptability of human bipedal locomotion and has been studied extensively over the last decade from the perspective of locomotor adaptation (Prokop et al. 1995; Reisman et al. 2005, 2007, 2009, 2010; Morton and Bastian 2006; Choi and Bastian 2007; Choi et al. 2009; Vasudevan and Bastian 2010; Malone and Bastian 2010; Torres-Oviedo and Bastian 2010; Vasudevan et al. 2011; Musselman et al. 2011). As subjects walk in this novel environment, in which two belts are driven independently of one another, adaptive changes of the gait motion are evident, as are the aftereffects upon return to a “tied” speed (Reisman et al. 2005). Previous studies have demonstrated that some variables, such as step length and double support time, showed clear adaptation and subsequent aftereffects, while other variables, such as stride length and stance time, showed merely reactive adjustment at the beginning of the adaptation period (Reisman et al. 2005). These findings indicate that the two distinct types of adjustments, feedback (short term, reactive) and feedforward (longer term, predictive) adjustments, coexist within the same task. Regarding the mechanisms underlying split-belt locomotor adaptation, Morton and Bastian (2006) revealed that cerebellar function is important in predictive but not in reactive adjustments. This is quite reasonable, because the results can be attributed to the well-established notion of an internal model, which is the process for the recalibration of motor command with the new task demand, as originally demonstrated in reaching movements of the upper limbs (Kawato et al. 1987; Shadmehr and Mussa-Ivaldi 1994). Understanding the role of predictive and reactive feedback strategies in locomotor adaptations would give us important information to facilitate gait rehabilitation as well as to elucidate task-specific functional networks underlying human locomotion. While a series of previous studies using split-belt walking have provided plenty of information concerning locomotor adaptation, the details of how the gait pattern would be adjusted are not fully understood. To discuss the strategies underlying locomotor adaptations to split-belt walking, it is particularly important to address the biomechanical characteristics beyond spatiotemporal and kinematic parameters, that is, the behaviors involved in the kinetic variables and muscle activities. The purpose of this study was therefore to elucidate the role of predictive and reactive feedback strategies in locomotor adaptations to split-belt walking, based on the evaluation of ground reaction force (GRF) and electromyography (EMG) in the lower limb muscles.
METHODS

Subjects. Twenty-two volunteers (between 21 and 40 yr of age; 21 men) with no known history of neurological or orthopedic disorders participated in the study. All the subjects gave their informed consent for participation in the experimental procedures, which were approved by the local ethics committee of the National Rehabilitation Center for Persons with Disabilities, Japan. All of the experimental procedures were performed in accordance with the Declaration of Helsinki.

Experimental protocol. In the present study, we used an experimental protocol established by Reisman et al. (2005) (the protocol shown in Fig. 1A) in their first of a series of studies exploring the split-belt locomotor adaptation.

Subjects walked on a split-belt treadmill (Bertec) with two belts (one under each foot; see the schematic in Fig. 1B), each driven by an independent motor. During the experiment, the treadmill was operated in either a “tied” (two belts moving at the same velocity) or “split” (at different velocities) pattern (Reisman et al. 2005), depending on the testing session. During the baseline period, the treadmill was tied and the velocity was set at 0.5 m/s for the slow and 1.0 m/s for the fast sessions. In the adaptation period, one belt speed was set at 0.5 m/s while the other was set at 1.0 m/s (1:2 ratio). The velocity of the belt underneath each leg was randomly assigned on a subject-by-subject basis. The leg on the fast belt during the adaptation period was defined as the “fast leg” and that on the slow belt was defined as the “slow leg.” Following the adaptation period was the washout period, where the belt condition was again tied at 0.5 m/s. Between testing sessions, the belt condition was changed (continuously without stopping) by the experimenter with acceleration (deceleration) of 0.5 m/s². Subjects were informed about the changes in belt condition but not about whether the belts would be tied or split or whether the speed would be

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Fig. 1. A: time course of the experimental protocol. B: schematic of the experimental setup. The EMG activities in 4 muscles [medial head of the gastrocnemius (MG), tibialis anterior (TA), rectus femoris (RF), and biceps femoris (BF)] and the mediolateral (Fx), anteroposterior (Fy), and vertical (Fz) orthogonal ground reaction force (GRF) components were recorded bilaterally. C: representative waveforms of the EMG and the GRF during the slow baseline period in 1 subject, described bilaterally, and the description of the gait phases. D: description of the GRF data analysis: peak values during each stride cycle (indicated by red arrows) were taken.
increased or decreased. During the experiment, subjects were instructed to walk normally while watching a wall 3 m in front of them. They were told not to look down at the belts to avoid gaining any visual information about the belt conditions. For safety, one experimenter stood by the treadmill during the experiment, and the subjects could hold onto the handrails mounted on either side of the treadmill in case there was a risk of falling. In our test, all subjects completed the testing sessions without using the handrails.

Supplemental experiment (control condition). In addition, we performed a control experiment to determine whether the observed effects (if any) during and after walking in the given environment are derived specifically as a consequence of walking on the asymmetrically driven treadmill or are due simply to task complexity. We referred to an experimental protocol demonstrated by Jayaram et al. (2011). The subjects were 10 healthy men. The subjects walked for a total of 22 min on the same treadmill surface as that used in the main experiment, but the two belts were always operated in the tied condition. During the baseline period, the subjects walked at two different velocities (slow at 0.5 m/s², fast at 1.0 m/s², and again, slow at 0.5 m/s²) for 2 min each. After the baseline period was an adaptation period in which the subjects were required to walk for 10 min at variable velocities [either slow, middle (0.75 m/s²), or fast during the baseline] that changed every 10 s and were centered at the middle. The variable velocities were delivered in random order, and the subjects were thus not provided with information on the upcoming velocities. After the adaptation period, the velocities were returned to the slow speed and the subjects walked at the slow speed for 6 min.

Data recording. Force sensors mounted underneath each treadmill belt were used to determine three orthogonal GRF components: mediolateral (Fx), anteroposterior (Fy), and vertical (Fz). The force data were low-pass filtered at 4 Hz and were digitized at a sampling frequency of 1 kHz (Power Lab; AD Instruments). EMG activity of the medial head of the gastrocnemius (MG), tibialis anterior (TA), rectus femoris (RF), and biceps femoris (BF) muscles was recorded bilaterally using surface electrodes (Trigno Wireless System; DELSYS). Since the total number of EMG recordings was limited, we selected the pair of extensor and flexor muscles in each shank and thigh muscle. Before placement of the electrodes, the skin was lightly rubbed with very fine sandpaper and was cleaned with alcohol pads. The recorded EMG signals were amplified (with ×300 gain preamplifier), band-pass filtered (20–450 Hz), and digitized simultaneously with the signals from the two force plates.

Data analysis. The obtained GRF and EMG data were analyzed on a stride-by-stride basis for both the fast and slow legs, respectively. From the vertical Fz component of the force data, the moments of foot contact and toe-off were detected using a custom-written program (VEE pro 9.0; Agilent Technologies). On the basis of foot contact and toe-off, the following parameters were calculated as temporal characteristics of gait (see the schematic description in Fig. 1C). 1) Stride time: the time between one foot contact and the subsequent foot contact in the same leg. 2) Step time: the time between the foot contact of one leg and the subsequent foot contact of another leg (i.e., the step time on the fast side is calculated as the time between foot contact on the slow side and the following foot contact on the fast side and vice versa for the slow side). 3) Stance time: the time spent in contact with the walking surface (computed for both fast and slow legs). 4) Swing time: the time spent not in contact with the surface (computed for both fast and slow legs). 5) Double support time: the time spent with both feet in contact with the support surface (i.e., fast double support time between the foot contact of the slow side and the subsequent toe-off in the fast side and vice versa for the slow side).

The force signals were analyzed for the Fx, Fy, and Fz components as the peak values within every stride cycle (refer to Fig. 1D). For the anteroposterior (Fy) component, both the positive and the negative peaks were calculated to assess both the anterior braking component appearing immediately after the foot contact and the posterior propulsive component immediately before toe-off (Fig. 1D).

The EMG signal for each muscle was full-wave rectified after subtraction of the DC component. The integrated EMG (iEMG) for both stance phase and the swing phase was computed for every stride. We analyzed the muscle activities during the stance phase in more detail, where time series changes of the EMG activities in each muscle were separated into the early stance phase (0 to 50% of the stance phase) and the late stance phase (50 to 100% of the stance phase).

From the temporal parameters, the GRF, and the iEMG data, we excluded the values for the first stride of each testing session from the later analysis due to the acceleration (deceleration)-induced disturbance of gait stability upon the change of belt conditions. To allow intersubject comparison, all the data were normalized to averages of those during the baseline period, which we defined as the last 50 strides of the second slow baseline period. Even though the total time of gait session is identical among subjects, the total number of steps would be different due to the relative contribution between stride length and cadence. The normalized values were then divided into bins of 10 s each in duration. This process was important to consider the time-dependent nature of adaptive and de-adaptive processes, because the number of stride cycles taken was variable across subjects.

Statistics. Statistical analysis was performed for the changes in each variable (temporal parameters, GRFs, and iEMGs) among the different testing periods: the slow 1 period, the fast period, the slow 2 period during the baseline, the first 10 s of the adaptation, the last 10 s of the adaptation, the first 10 s of the washout, and the last 10 s of the washout. ANOVA for repeated measures was used. When repeated-ANOVA gave significant results, Bonferroni’s post hoc comparisons were performed to test for differences between testing periods. Correlation coefficients were calculated to test the relationships among variables. Data are presented as the means ± SE. Significance was accepted at P < 0.05.

RESULTS

Temporal characteristics. Figure 2A portrays the time series variation of the temporal parameters throughout the experimental protocol. With exposure to the split belt condition, these parameters showed a general decrease (except for stance time and swing time in the fast leg) from those during the slow baseline (significant differences from the baseline are shown as filled circles), regardless of the leg (either fast or slow). During the 10-min adaptation phase, all the parameters gradually and only slightly increased toward the baseline. To characterize the “capability of adaptation,” Fig. 2B compares the parameters at different time points (see METHODS). In some parameters, such as stance time (P < 0.01) and double support time (P < 0.01) in the fast leg, and step time (P < 0.01) and swing time (P < 0.001) in the slow leg, there were significant differences between the first and the last 10 s of the 10-min adaptation period (significant differences are shown as solid lines), indicating the capability of adaptation. In contrast, other parameters, such as stride time in the fast leg and stance time, double support time, and stride time did not show such changes. When the belt condition was returned to tied, all the subjects exhibited a pronounced limp despite the belt condition being identical to the baseline condition, as reported in a previous study (Reisman et al. 2005). There were significant differences from the baseline period in step time (P < 0.05) and swing time (P < 0.05) in the fast leg, while other parameters did not show such differences in either the fast or the slow leg. Early in the 6-min washout period (in the first 1–2 min), those initially modulated parameters converged almost to the baseline values.

Ground reaction force. The time series changes of the GRF were to a great extent different among the components (mediolateral, anterior, posterior, and vertical), and based on these
differences the changes could be categorized into three different patterns. The results are described in Fig. 3 for the whole experimental protocol (left) and for the comparison among different time points (right) to address the capability of adaptation. Figure 3, middle, highlights the first part of each learning and washout periods. At the beginning of the adaptation period, the mediolateral and the posterior components (A and D) of GRF showed significant deviations from the baseline at the beginning of split-belt period in both the slow ($P < 0.05$ for mediolateral, and $P < 0.01$ for posterior) and the fast leg ($P < 0.001$ for mediolateral, and $P < 0.001$ for posterior). Here, the slow leg values were adjusted to be near those in the slow baseline and the fast leg values were adjusted to be near those in the fast baseline. In the adaptation period, the mediolateral component in the fast leg gradually decreased toward the fast baseline values after initial overshoot. The comparison between the first and last 10 s of the adaptation period showed a significant difference ($P < 0.05$). The other comparisons did not show such a change. Upon return to the tied belt condition, there were significant aftereffects in the fast ($P < 0.01$) and slow ($P < 0.01$) legs in the mediolateral component and only in the slow leg in the posterior component ($P < 0.05$). The vertical component, on the other hand (Fig. 3B), showed somewhat different behavior from the mediolateral or the posterior components described above. At the beginning of the adaptation period, the relationship between the values for the fast leg and those for the slow leg were flipped from the baseline values (the fast leg values approached the slow baseline values and the slow leg values approached the fast baseline values). Only the slow leg showed significant deviation from the baseline initially ($P < 0.01$), and it did not exhibit any capability of adaptation during the 10-min test period. There were no evident aftereffects in either the fast or slow legs in this component.

Among the four different components of the GRF, the anterior component showed the clearest signs of adaptation and washout in both legs (Fig. 3C). At the initial stage of the adaptation period, the mean value in the fast leg was adjusted to be close to the slow baseline value, whereas in the slow leg ($P < 0.001$) it was near the value of the fast baseline period. There were steep changes in the first min followed by moderate changes lasting for the remaining 9 min during the adaptation period, where the relationship between the legs flipped early in the period. At the completion of the adaptation period, the value in the fast leg was adjusted to be close to that of the fast baseline and the value in the slow leg was adjusted to be close to that of the slow baseline. There were significant differences between the first and last 10 s in both the fast ($P < 0.001$) and slow ($P < 0.001$) legs. The washout phase started with pronounced deviation from the baseline in both legs, and there were gradual changes toward the baseline values, with the overall pattern of change into the opposite direction to that during the adaptation period. The statistical comparisons demonstrated significant deviation from the baseline at the beginning of the washout phase [$P < 0.001$ (fast) and $P < 0.01$ (slow)] and differences between the initial and the last 10 s in the washout in both the fast ($P < 0.001$) and slow ($P < 0.01$) legs.

**EMG responses.** Figure 4 shows the time series changes in the EMG activity for the whole experimental protocol (left) and for the comparison among different time points at selected time periods during the stance and the swing phases (right). Generally, the EMG responses were more variable than were the temporal parameters and ground reaction force data.

During the initial stage of the adaptation period, activities in the BF muscle in the fast leg and the RF and TA muscles in the slow leg increased during the stance phase. The activity of these muscles exhibited a clear adaptive curve, with the values gradually decreasing toward the baseline values. At 10 min, the values were almost identical to the baseline values, despite the fact that the subject was walking on a split treadmill surface. The statistical comparison revealed in those muscles that there were initially significant differences from the baseline values [$P < 0.001$ (fast BF), $P < 0.001$ (slow RF), and $P < 0.01$...
There were also statistically significant differences in these muscles between the initial and final 10 s in the 10-min adaptation phase, demonstrating the capability of adaptation. With the return to the tied belt condition, the TA, RF, and BF muscles in the fast leg and the MG and RF muscles in the slow leg showed augmented activity. Although the belt condition was identical to that in the baseline period, the EMG activities were significantly different from those in the baseline period. These activities gradually decreased toward the baseline level within the first 2 min or so. Around 5 min in the washout phase, the levels of these activities were similar to the baseline values.

During the swing phase, the TA (P < 0.01) and BF (P < 0.01) muscles in the fast leg and RF muscle in the slow leg (P < 0.05) showed augmented activities in the early adaptation period compared with those at baseline, where only the BF in the fast leg (P < 0.05) and the RF in the slow leg (P < 0.05) exhibited a clear pattern of adaptation. In the following washout period, only the BF muscle showed an initial enhancement of the activity (P < 0.01) and a pattern of washout toward the baseline level. In the RF muscles of the fast limb, the activities were lessened even below baseline levels.
in the washout period ($P < 0.01$), and the reductions resulted in statistically significant differences between the initial and final 10 s of the period in both legs [$P < 0.01$ (fast) and $P < 0.01$ (slow)].

In contrast to the TA muscles during the stance phase (initially increased activity and subsequent decrement in the slow leg during the adaptation period and the emergence of the aftereffect in the fast leg), the activities in the MG exhibited contrastive behavior. Figure 5A presents representative EMG waveforms in the TA and MG muscles under stride cycles at different time points of the experiment. Figure 5B highlights a distinct adaptive process between the slow (blue) and fast (red) legs of the TA EMG in the early stance phase and the MG EMG in the late stance phase. At the initial stage of the adaptation period, the TA EMG in the slow leg showed higher values, and then at the completion of the adaptation period, the values in the fast leg were adjusted to be close to those of the fast baseline and the values in the slow leg were adjusted to be close to those of the slow baseline.

The washout phase started with a pronounced deviation from the baseline in the fast leg, and there were gradual changes toward the baseline values. In contrast to the TA muscle, only the slow leg showed significant deviation from the baseline initially ($P < 0.01$), and it did not exhibit any capability of adaptation during the 10-min test period in the MG muscle. In the washout period, both legs showed higher values and then gradually recovered to the baseline values. Figure 5C focuses on the EMG activity under particular phases and in particular muscles where activity is essential for functional gait, that is, the mean EMG activity of the TA muscle during the early stance phase and that of the MG muscle during the late stance phase. A pattern of adaptation and subsequent aftereffects with relatively longer time course is found in the TA muscle ($P < 0.01$ to the baseline in the early washout period and $P < 0.01$ between early and late washout periods in the fast leg), while such activities are less evident in the MG muscle.

Figure 5D shows the relationship between the extent of adaptation of the slow/fast leg and the washout of contralateral leg in each TA/MG muscle, respectively (top/bottom). The regression line and the correlation coefficient value and its significance are indicated in the figure. A significant positive correlation was found in both muscles ($P < 0.05$), suggesting that the EMG patterns obtained on one side in the adaptation
Regarding the GRF data, a significant negative correlation was found only in the braking force of the slow leg (fast leg: \( r = -0.180 \), n.s., slow leg: \( r = -0.459 \), \( P < 0.05 \)). No significant correlation was found in propulsive force in both legs (fast leg: \( r = -0.064 \), n.s., slow leg: \( r = -0.159 \), n.s.).

**Relationship between the different variables.** Figure 6 illustrates the relationship between the extent of adaptation and aftereffects for each variable (EMG_MG, EMG_TA, GRF_Braking, GRF_Propulsive). In the TA muscle, a positive correlation between adaptation and aftereffects was found in the fast leg (fast leg: \( r = 0.429 \), \( P < 0.05 \), slow leg: \( r = 0.29 \), n.s.). In the MG muscle, both the fast and slow legs showed a positive correlation between adaptation and aftereffects (fast leg: \( r = 0.755 \), \( P < 0.05 \), slow leg: \( r = 0.446 \), \( P < 0.05 \)).

**Tied-random (control) condition.** Figure 7 shows the time series changes of the step time, braking GRF, and EMG activity in TA and MG muscles during the tied-random condition and the split-belt treadmill condition. The tied-random condition did not show any aftereffect in the postperturbation period, whereas the split-belt treadmill condition showed clear aftereffects in the washout period.

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**Fig. 5.** A: representative waveforms of the EMG activities in the TA and MG muscles for both the fast and slow legs (those on the fast and slow belts during the adaptation period, respectively) at different time points. Each waveform represents an ensemble average of five consecutive stride cycles under the respective time points and is time normalized to stride cycles. B: mean of the time series changes of the EMG activities in the TA muscle during the first half of the stance phase and in the MG muscle during the last half of the stance phase. Filled circles represent the EMG activities during the first half of each gait cycle, and the open circles are those of the last half of the gait cycle. Averaged value of each 10 s bin are shown at top, and each step data at the beginning of adaptation and washout periods (first 50 steps) are shown at right. C: comparisons of each parameter at different time points (top: early stance of TA; bottom: late stance of MG). All the data were normalized to those of the baseline values (for details, see METHODS). Filled circles indicate statistically significant differences from those during the baseline period, and the solid lines show the significant differences between the variables. Error bars indicate means ± SE. Differences were considered significant at \( P < 0.05 \). D: relationship between the extent of adaptation of the slow/fast leg and the washout of the contralateral leg in the TA/MG muscle, respectively (top/bottom). Regression lines and the correlation coefficients and their significance are indicated in A-D.
pattern adjustments made by subjects on an asymmetrically driven split-belt treadmill were not fully understood.

The novel contribution of the present study is to provide the specific patterns of the predictive feedforward and reactive feedback control strategies based on the GRF and EMG results. As clearly shown in the Fig. 3, the anterior component of the GRF in slow leg showed a clear pattern of adaptation and subsequent aftereffects, which is comparable to those originally identified in the reaching movement of the upper arm, which is the process for the recalibration of motor command with the new task demand (Kawato et al. 1987; Shadmehr and Mussa-Ivaldi 1994). Although the type of movement differs between upper limb motion and bipedal walking, adaptation to the split-belt treadmill can also be regarded as a process of trial-and-error-based adjustment of gait behavior in response to differently driven belts. At the initial part of split-belt walking, the central nervous system does not correctly predict the extent of perturbation and causal postural disturbance (movement error) due to the split belts. With continuous exposure to the split-belt condition, the subjects could finally establish the predictive feedforward motor command that enabled them to minimize the extent of postural disturbance presented by the split-belt condition.

Concerning this point, the authors of previous studies suggested the significance of feedforward mechanisms in human locomotion by comparing specific muscle activity during an “adapted state” in an imposed force field and upon the unexpected removal of the force field with the use of gait robotics (Lam et al. 2006) and an elastic band (Blanchette and Bouyer 2009). Taking the present results into account together with these previous findings, it is likely that the process comprising the braking force can be regarded as a predictive feedforward component of the motor control for bipedal walking. Given the importance of cerebellar function for acquiring the predictive feedforward model (Imamizu et al. 2000; Bastian 2006), similar neural processes might be involved in the split-belt treadmill adaptation.

In contrast, the posterior GRF showed a consistent increase/decrease in the fast/slow leg during the adaptation period and was not followed by subsequent aftereffects, suggesting that propulsive force can be regarded as the result of reactive adjustment which is presumably generated by an automatic feedback action. The manner of changes between anterior and posterior forces might reflect the existence of distinct control strategies underlying split-belt locomotor adaptation. The results obtained from lower limb EMG muscle also demonstrated a unique pattern due to the split-belt treadmill adaptation. In the following section, the detailed mechanisms underlying the split-belt treadmill adaptation and implications for the future use of the split-belt treadmill adaptation will be discussed.

Two distinct strategies underlying split-belt treadmill adaptation.

The emergence of the adaptive and the subsequent de-adaptive phenomena with and after walking on a split-belt treadmill has been studied extensively by Bastian and colleagues over the last decade (Reisman et al. 2005, 2007, 2009; Morton and Bastian 2006; Choi et al. 2007, 2009; Vasudevan and Bastian 2010; Malone and Bastian 2010; Torres-Oviedo and Bastian 2010; Vasudevan et al. 2011; Musselman et al. 2011). Based on a series of split-belt treadmill experiments, Bastian and colleagues clearly dissociated different forms of locomotor adaptation, reactive and predictive adjustments, in the central nervous system. However, the details of the specific gait
sequent aftereffects in the EMG activity of the MG muscle, other parameters showed a clear difference between the slow (blue) and fast leg (red). These results also suggested different roles of each leg in split-belt adaptation. These interpretations are in agreement with the previous study stated that the slow moving leg was used as the primary support to stabilize the body equilibrium during the prolonged swing of the contralateral leg (Dietz et al. 1994; Duysens et al. 2004). Moreover, our results are in line with the previous report that the emergence of aftereffects after walking on an asymmetrically driven treadmill surface was always merged with a speed identical to that of the slower side during the adaptation periods (Vasudevan et al. 2010).

In addition to the contrasting braking force results between the fast and slow legs, other GRF parameters also showed remarkable differences between the legs, e.g., the larger shift of the lateral GRF and the enhancement of propulsive force in the fast leg. These results might reflect the larger amount of perturbation and optimal ankle stiffness by an error-based learning process during the adaptation period, and they may
finally acquire predictive control of the ankle stiffness at the heel contact.

Regarding the control of ankle stiffness in the early stance phase during walking, it was demonstrated that a significantly large motor-evoked potential (Capaday et al. 1999) and long-latency stretch reflex (Christensen et al. 2000) are induced in the TA muscle at the early stance during walking. These findings strongly suggested that the enhancement of the excitability of TA corticospinal and stretch reflex pathways is necessary as an action to prepare for the upcoming perturbation at the heel contact. In light of these findings, it is likely that the total involvement of the cortical process is relatively larger at the beginning of adaptation to the split-belt-induced perturbation and, then, error-based learning enables the subject to update the internal model for walking, which presumably takes place in the cerebellum (Morton and Bastian 2006, Jayaram et al. 2012).

It might be speculated that the adaptation and subsequent aftereffects observed in split-belt treadmill walking are due merely to the difficulty of treadmill walking because some parameters showed gradual changes even during the baseline period. It is thus necessary to discuss the process of the induction of a learning effect due to split-belt treadmill walking. To investigate this matter, we conducted a supplemental experiment in 10 subjects with a protocol similar to that employed by Jayaram et al. (2011) using a protocol where the belts are tied the entire time but the speeds are frequently varied (every 10 s). Although the total duration and walking distance in this experimental condition were similar between the tied-random and split-belt treadmill walking, the tied-random condition did not show any aftereffect in the postperturbation period (Fig. 7).

This result suggests that the adjustment of gait behavior in response to bilateral belt speed changes does not require any updating process of the internal model for walking. During the tied-random condition, the subjects needed only a few steps to adjust their walking stability after the belt speed change. This is because humans can adjust their walking by using an automatically induced reflex system utilizing sensory feedback and previous experience. However, the split-belt treadmill-induced perturbation is unusual, and no prior experience can be used as a template for gait adjustment. As a result, the subjects achieved stable walking by their trial-and-error-based learning.

Conclusion and implication. The present results regarding GRF and muscle EMG activities provide useful information for discussions of the motor control and learning process during split-belt adaptation and subsequent aftereffects. Our findings indicate that predictive feedforward control is required to set optimal ankle stiffness in preparation for the impact at the heel contact, and passive feedback control is utilized for the production of reflexively induced propulsive force at the end of the stance phase during split-belt treadmill adaptation. This conclusion might have direct implications for the construction of specific rehabilitation protocols for the improvement of gait asymmetry in poststroke patients. It is plausible that interventions using a split-belt treadmill have the potential to make systematic adjustments of imbalances between breaking and propulsive forces and asymmetry between paretic and intact legs.

GRANTS
This work was supported by Grant-in-Aid for Young Scientists (A) (#22680045) to N. Kawashima and Grant-in-Aid for Young Scientists (B) to T. Ogawa (Research Project Number: 23700638) from Japan Society for the Promotion of Science.

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

AUTHOR CONTRIBUTIONS
Author contributions: T. Ogawa and N.K. performed experiments; T. Ogawa and N.K. analyzed data; T. Ogawa and N.K. interpreted results of experiments; T. Ogawa and N.K. prepared figures; T. Ogawa and N.K. drafted manuscript; N.K. conception and design of research; N.K. edited and revised manuscript; N.K., T. Ogata, and K.N. approved final version of manuscript.

REFERENCES


