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Does size of error affect the motor adaptation during split-belt treadmill walking?

by

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Abstract

We explored whether size of error affects the motor adaptation during split-belt treadmill walking in healthy adults. The split-belt treadmill has two belts that can be moved at different speeds. Subjects first walked with the two belts at the same speed (tied-belt condition) for the baseline. They then walked with one belt speed remaining at the baseline speed while the other one increased to two times the baseline speed. The increment in belt speed was sudden (creating a large movement error) for one group and incremental (creating a small error) for the other group. Finally, the belt speed returned to the baseline, called post-adaptation period. The asymmetry during post-adaptation, called aftereffect, indicates the magnitude of motor adaptation. We did not find significant difference in the magnitude of the aftereffect between the two conditions. This suggests the size of error has little effect on motor adaptation during split-belt treadmill walking.

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CHAPTER 1. **Introduction**

1.1 Introduction

Humans must constantly alter their patterns of motions for changing situations: for example, walking on various terrains, such as slippery ice, a muddy surface, or sand. In addition, we have to adjust our motions not only for the environment that surrounds us but for our body mechanics that can fluctuate due to fatigue, diseases, injuries or growth etc.

These adjustments occur on different time scales (Lam et al. 2006; Reisman et al. 2007). Some are immediate reactions to a new situation, such as stepping into a hole unexpectedly. Others are adaptive changes that require practice to acquire, such as getting accustomed to new shoes. The former is called feedback adjustment, whereas the latter is called feedforward adjustment (Morton et al. 2006). Within the latter form, the adjustment that occurs when an individual faces a change during an already well-learned task, like walking, is called motor adaptation (Bastian 2010).

1.2 Motor adaptation and motor learning

1.2.1 Motor adaptation

There are several processes for acquiring motor adaptation. When individuals adjust to a change during a particular task, practice is required in order to meet the new motor demand. Once they have adjusted, and the change is removed, individuals are again required practice in order to go back to the previous motion. This phenomenon represents motor adaptation. Motor adaptation is the trial and error process of adjusting movement to new demands (Bastian 2010). Martin et al. (1996a) define motor adaptation as follows:

> "Motor adaptation is the modification of a movement from trial-to-trial based on error feedback in which the following criteria are met. First, the movement retains its identity of being a specific action but changes in terms of one or more parameters. Second, the change occurs with repetition or practice of the behavior and is gradual over minutes to hours. Third, once adapted, individuals cannot retrieve the prior behavior; instead, they show 'after-effects' and must 'de-adapt' the behavior with practice in the same gradual, continuous manner back to the original state." (Martin et al. 1996a)

Motor adaptation is a learning process that occurs in a relatively short timescale of minutes to hours in order to respond to new task demands. When individuals face a new demand of movement, their motions are perturbed. With practice, the perturbations diminish as individuals correct their motions. However, when the new demands are removed after the adjustments are completed, individuals show perturbed motions again. This time, they are approximate mirror images of the previous perturbations. These motions, which are the mirror images to those shown during early adaptation are termed aftereffects (Shadmehr 2004; Reisman et al. 2010).

1.2.2 Motor learning

There are different definitions of the term 'motor learning'. In one case, motor learning is distinguished from motor adaptation, in that motor learning does not require practice to adjust once the new patterns of motions are stored, whereas motor adaptation requires practice to acquire each time. Repeated exposure to adjustments lets individuals learn how to switch between two modifications immediately without practice. This phenomenon is indicative of motor learning (Bastian 2010). Martin et al. (1996) tested whether subjects could store the two motor plans using throwing tasks with, and without prism glasses. In their study, subjects threw balls of clay at a visual target while looking through wedge prism. At first, subjects missed the target in the direction of their prism-bent gaze at the onset of introducing the prisms. Although they gradually adapted with practice and threw at the target exactly, subjects missed the target in the opposite direction when the prisms were removed. However, during the 6-week training, Martin and colleagues found that the subjects eventually learned to make exact throws at the target on the first trial right after switching their situation from using prisms to not using prisms, and vice versa (Martin et al. 1996b). In other words, they could eventually learn new motor plans and how to switch between them. After the new motor plan is learnt, it is stored in the nervous system and is ready to apply immediately when the situation changes. Individuals that went through the motor learning need no adaptation nor de-adaptation to change their movements any more. In this paper, motor learning will refer to this phenomenon.

The term 'motor learning' has also been used to refer to learning a new motion that individuals have not experienced before. That means generating a completely new movement. For example, when individuals learn to drive a motorcycle for the first time, they should acquire totally unfamiliar skills for which the individuals are unlikely to have had experience with: operating accelerator and clutch, balancing at the same time (Bastian 2010). This form means learning from scratch.

1.3 Sensory prediction error

Motor adaptations are driven by error (sensory prediction error).

Sensory prediction error is the discrepancy between the brain's estimations of sensory consequences and the sensory feedback from actual motions when individuals adjust to new environments. Tseng et al. (2007) stated that sensory prediction errors occur when the predicted sensory consequences do not match the motions that are generated from the motor commands. Humans make errors when learning a movement in a novel environment, including using a new tool or responding to change in their bodies due to diseases, development, and also fatigue. With practice, individuals adjust their movement to the unfamiliar environment. As they get accustomed to a new situation, errors which manifested initially decrease gradually. To do this, individuals need to develop new motor commands, which fit into the new environment. The new motor commands should be derived from estimations of planned actions. Systems that compute the predicted consequences of planned actions are called forward models (Shadmehr et al. 2005).

1.4 Feedback and feedforward correction

1.4.1 Feedback correction

The simplest strategy for the nervous system to achieve precise motor control is to modify the motions while they are executed; this is called (on-going) feedback correction. However, this simple strategy has some problems. First, sensory feedback is noisy. Additionally, sensory feedback has delay due to conduction and processing time in the nervous system (Shadmehr 2010). Miall et al. (2007) investigated length of delay in the somatic sensory system when an individual makes a reaching motion, and found that the subjects' reaching motions were determined by sensory information that was approximately 140 ms out of date. The second problem is that the relationship between the motor commands and movements is unstable. Muscle, body mass, segment lengths all change during an individual's development. Diseases and fatigue also affect muscle strength and body mass. Moreover, when an arm grasps a particular object to move, the dynamics profile of the arm changes (Shadmehr et al. 2010). Our central nervous system must adjust their motor plan every time the situation changes, not only due to the conditions of ourselves but also due to the environment around us.

1.4.2 Feedforward correction

In order to solve these problems, the central nervous system has another strategy to adjust movements. That is to predict the consequences of motor commands from the previous experiences and correct the current motions prior to the executions (Shadmehr et al. 2010). The strategy to include the prediction of motor commands into motor control is called (predictive) feedforward control (Morton et al. 2006). The prediction of the consequences of motor commands is called a forward model (Shadmehr et al. 2010). The advantage of incorporating forward models is that we do not have to rely too much on time-delayed feedback from sensory organs (Bastian 2010). However, in order for this strategy to be useful, the estimations of movements have to be accurate. To do this, forward models ought to be recalibrated and updated constantly. Sensory prediction errors are used to recalculate forward models (in other words, internal representations, body schema) according to changeable body dynamics and surrounding situations (Bastian 2010).

In summary, feedback correction occurs immediately after the change of the motor demand, whereas feedforward correction takes more time (e.g. minutes to hours) because feedforward correction requires practice to achieve (Bastian 2010). Feedback adjustments go back to the previous state right after the novel situations are removed because they are not stored by the nervous system. On the other hand, the updated motor commands by feedforward adjustment need to be "unlearned" which requires a certain amount of time because the adjustments are stored (Morton et al. 2006; Choi et al. 2009).

1.5 Size of error affects adaptation

When humans are exposed to a novel situation, they need to adjust their movement by updating their motor command to meet the new demands. Right after individuals are exposed to new dynamics, their motions are perturbed (showing large sensory prediction error), which I will call initial error. The motions gradually return to the previous forms (showing less error, which I will call final error) through updating their motor command, which is generated from modified internal models.

Several researchers have investigated the relationship between the size of error during adaptation and the degree of motor adaptation (Klassen et al. 2005; Kluzik et al. 2008; Criscimagna-Hemminger et al. 2010). For arm movements, two well-studied paradigms are visuomotor adaptation (Ingram et al. 1997; Kagerer et al. 1997; Hatada et al. 2006) and force field adaptation (Huang et al. 2009). Generally, these studies addressing error size introduce the error in two ways: gradually or abruptly. Subjects are divided into two groups, and each experience either gradual or abrupt perturbation. In the abrupt perturbation, the full perturbation is applied from the onset of exposure, generating large errors. In the gradual perturbation, on the other hand, the exposure is introduced incrementally, generating very small errors. Nevertheless, they reach the same full perturbation by the end of the adaptation period just as those experiencing the abrupt perturbation. In each session, subjects participate in three testing periods as follows: 1) baseline period, 2) adaptation period, and 3) post adaptation period. In the baseline period, subjects execute reaching or punching motions aiming to certain targets in the absence of visual distortion or force application to their hand. In the adaptation period, trials are performed under exposure to either gradual or abrupt perturbation. In the post adaptation period, subjects are tested whether they have significant aftereffects by performing under the same situation as the baseline period. For clarity, I will outline the experimental procedures of visuomotor and force field adaptation.

1.5.1 Visuomotor adaptation

In visuomotor adaptation studies, examiners distort subjects' visual perception, and study the consequences on motor commands (Buch et al. 2003). An example of the experiment is as follows: subjects sit in front of a computer screen that displays the movement of subjects' right index finger, on which an infrared marker is attached. A board is placed between subjects' head and shoulder so that their right hand is occluded. Although subjects cannot see their right hand, they can control their index finger's trajectory by watching a computer screen, which displays the position of the infrared marker. Subjects are instructed to make reaching motions by moving their right wrist and forearm as fast and as straight as possible toward one of four targets that is displayed on the computer screen. The order of presentation of the targets is typically pseudo-randomized. After subjects get accustomed to the baseline movements, researchers manipulate error sizes for the adaptation period by presenting a rotated visual feedback, such as a specific rotation of the screen cursor representing the position of the finger (i.e., 90 degrees clockwise). The rotated visual feedback is imposed incrementally (gradual) over trials or suddenly in a single step (abrupt) for each of the two groups of subjects. After subjects have adjusted their reaching motion to the novel situation, visual rotation feedback suddenly returns to the previous state (same as baseline period). Researchers observe the extent of aftereffect (Buch et al. 2003).

1.5.2 Force field adaptation

For the force field adaptation paradigm, subjects are asked to make point-to-point reaching tasks in the horizontal plane while holding a robotic manipulandum. In the study of Huang et al (2009), subjects are instructed to strike through the target so that they cannot correct their trajectories after onset of the movements. During the adaptation period, the robotic arm applies velocity-dependent curl forces to the subjects’ hand that are perpendicular to the reaching trajectories. For one group, the force field is applied at full strength from the onset of the adaptation period (abrupt). For the other group, the transformation is introduced in a gradually increasing manner (gradual). As in the visuomotor adaptation studies, the force field is removed suddenly after the end of the adaptation period in order to probe how much the subjects compensate for the force field (Shadmehr et al. 1997a; Hwang et al. 2006; Kluzik et al. 2008; Huang et al. 2009).

1.5.3 Size of error affects the extent of adaptation

Kagerer et al. (1997), using visual motor rotation, reported that smaller initial error resulted in more complete adaptation than larger initial errors. In other words, they showed that gradual changes in an environment, which allowed the nervous system to estimate small corrections, leads to a larger aftereffect. Also, Ingram et al. (2000) compared aftereffects for gradual versus abrupt perturbation in visuomotor task. Their study found larger aftereffect for the gradual condition. Further, Kluzik et al. (2008) compared sizes of aftereffect between gradual and abrupt perturbation in force field adaptation task. They found that subjects had larger and longer-lasting aftereffect in the gradual condition than they did in the abrupt condition. Furthermore, Huang et al (2009) probed the time for decay of aftereffect in force field adaptation. They showed that the group experiencing a gradual introduction of errors during adaptation had a slower time course of deadaptation compared to the group experiencing an abrupt introduction of errors (Huang et al. 2009). In other words, aftereffects were retained longer in the group that experienced a gradual perturbation. Moreover, Klassen et al. (2005) made a comparison between gradual versus abrupt perturbation in visuomotor and force field task. They showed that the gradual group in a force field adaptation had a slightly larger retention of the adaptation to the next day of the experiment than that of the abrupt group. Although it is a study with patients with cerebellar degeneration, Criscimagna-Hemminger et al (2010) showed a result that supports the study of Huang et al (Criscimagna-Hemminger et al. 2010). Taking these finding together, the results indicate that introducing errors gradually resulted in a more robust effect on the motor adaptation of upper limb movements than introducing large errors suddenly.

As to the extent of exposure to the distortions, the abrupt group performs more trials under the distortion than those of the gradual group, because the perturbation is full strength from the beginning of the adaptation period in the abrupt condition, whereas it increases with time in the gradual condition (Klassen et al. 2005). In spite of the fact that subjects experience less trials with the full strength of the perturbation, the aftereffect of the group with gradual perturbation is still larger than the abrupt group (Kargerer et al. 1997; Criscimagna-Hemmingger et al. 2010). These results suggest that large and detectable errors are not necessarily required for learning internal models (Klassen et al. 2005).

1.5.4 Relation between error size and generalization

Generalization is the process of transferring the knowledge gained through training in one situation to a different situation. Understanding the ability of generalization has practical importance for rehabilitation (Chriscimagna-Hemminger et. al. 2003). Although generalization does not always work to advantage for rehabilitation, understanding its nature is beneficial for developing training methods and rehabilitation techniques. Malfait and colleagues (2004) tested whether interlimb transfer (generalization from the right to the left arm) occurs after individuals adapt to gradual or abrupt perturbations of the upper limb. At first, subjects adapted their right arm's reaching motion to the horizontal perpendicular force field either gradually or abruptly. After the adaptation, they were measured whether the adaptation transferred to their left arm. There was no interlimb (across the limb) transfer of learning in subjects who experienced gradual adaptation, whereas significant transfer was observed in subjects who experienced abrupt adaptation. Further in the same study, Malfait et al. (2004) tested whether the gradual group makes the transfer within the same limb, but across the different configurations. The subjects showed significant transfer of the adaptation within the same arm, even if the configuration of the movements were different because of the different shoulder angle was used from the adaptation period (Malfait et al. 2004). This finding suggests that the gradual training may produce intralimb transfer of learning. Malfaits' work is supported by the study of Kluzik et al. (2008). They compared the extent of the transfers between gradual and abrupt perturbation, using the force field task. After the force field adaptation period either in the gradual or abrupt perturbation, subjects experienced two kinds of post adaptation periods: robot null condition, in which the force field was turned off; and free space condition, in which the subject kept holding the handle, but the handle was detached from the robot arm. Although there was no difference in the extent of the transfer between the gradual and the abrupt perturbations during the robot null condition, the transfer in the group that experienced the gradual perturbation during the free space condition was larger than those in the abrupt group (Kluzik et al. 2008). Their finding also suggests that the gradual perturbation may encourage intralimb transfer. To explain these results, Criscimagna-Hemminger et al. (2003) suggested that there may be two possible representations of the state of limbs that code the generalization of motion training: 1) an intrinsic, muscle, and joint-like coordinate system: 2) an extrinsic, tool-specific, task structure-like coordinate system (Criscimagna-Hemminger et al. 2003; Kluzik et al. 2008). Malfait et al. (2004) reasoned that better interlimb transfer may indicate subjects attribute the perturbation to extrinsic sources, whereas intralimb transfer corresponds to the intrinsic representations.

The difference in adaptation between gradual and abrupt perturbation comes from how the nervous system accredits the errors. In other words, on which representation the nervous system puts emphasis as the cause of the errors. When a perturbation is introduced gradually, the nervous system attributes the errors to the representation of their own arms (intrinsic representation) (Kluzik et al. 2008). The nervous system infers that the internal model of their arms should be modified. For that reason, the intralimb transfer of learning is good. In contrast, when a perturbation is applied abruptly, the nervous system assigns the error to the representation of the tools or outside environments (extrinsic representation). The nervous system infers tools or the surrounding environments are the reason for the altered dynamics (Kluzik et al. 2008). Hence, the transfer between limbs is good, because it is the tool that contains the altered dynamics.

1.6 **Split-belt treadmill**

1.6.1 What is the split-belt treadmill?

As well as upper limb (reaching motions), researchers study motor adaptation during walking in order to optimize rehabilitation for gait (Vasudevan et al. 2010). Although treadmill training in general improve walking velocity in subjects with chronic stroke (Hesse 2008; Patterson et al. 2008; Mulroy et al. 2010), training using split-belt treadmills are more suitable for attenuating walking asymmetry post-stroke (Reisman et al. 2007).

A split-belt treadmill is a treadmill, which has two belts on which the subject walks (Malone et al. 2010). The speed of the belts is controlled individually (for some treadmills, the two belts can run in opposite directions), driving each of the subject's legs at a different speed. Although it depends on what the researchers are investigating, subjects are instructed not to watch their steps while they are walking so that subjects do not think about their walking. This is because subjects' attention to their walking may change the rate of adaptation and deadaptation (Malone et al. 2010). By using a split-belt treadmill we can manipulate the factors that can affect the subjects' adaptation in locomotion and study interlimb coordination as well as intralimb coordination (Reisman et al. 2005).

1.6.2 Adaptation during walking on the split-belt treadmill

When individuals modify their locomotor pattern in response to a change in the environment, such as on the split-belt treadmill, some parameters alter right after the situation is changed, while others take longer (Lam et al. 2006; Reisman et al. 2007). The former is called (reactive) feedback adjustment, whereas the latter is called (predictive) feedforward adjustment. Feedback adjustments are the phenomena that occur immediately after the change of the motor pattern in response to unexpected sensory information, and need little time to go back to the previous pattern when the novel demand is removed (see section on Feedback Correction, above). On the other hand, feedforward adjustments occur more slowly (e.g. minutes to hours) because they need practice to acquire and get back to the previous state (Morton et al. 2006; Choi et al. 2009). The most commonly used measures for feedback and feedforward adaptation to split-belt walking are as follows.

1.6.3 Feedback measures

Frequently used feedback measures for treadmill walking are stride length and stance time (Reisman et al. 2005, 2007). The reason why they are classified as feedback is because individuals can change these parameters immediately in reaction to the change of the belt speeds (Choi et al. 2009).

In over ground walking, stride length is calculated as the distance traveled by the ankle marker from foot contact to the subsequent foot contact of the same leg; however, there is no real forward progression on a treadmill. Therefore, stride length is calculated as the horizontal distance traveled by the ankle marker between initial contact and subsequent lift-off of the same leg (Morton et al. 2006). Stance time is the duration of stance phase. Stance time is often expressed as a percentage of the stride time (the time interval from contact of one leg to next contact of the same leg) (Reisman et al. 2007; Musselman et al. 2011). Further, stride length is a spatial parameter, while stance time is a temporal parameter (Reisman et al. 2007).

1.6.4 Feedforward measures

Feedforward measures need practice to adapt (Choi et al. 2009). Generally used measurements of feedforward parameters for treadmill walking are center of oscillation, step length, double limb support, and phase shift (Reisman et al. 2007; Malone et al. 2010).

Center of oscillation is the midpoint of the limb angle between heel strike and toe off for each leg. Limb angle is the angle between a vertical line and the line connecting the hip and the foot in the sagittal plane (Malone et al. 2010). Step length is the anterior-posterior distance between the ankle markers of each leg at heel strike of the leading leg (Reisman et al. 2005). Double limb support is the time that both feet are in contact with the ground expressed as a percentage of the stride time for each leg (Reisman et al. 2007). Phase shift is obtained by calculating the cross-correlation function between limb angle trajectories of the two legs (Choi et al. 2007). Phase shift is the lag time from zero at peak cross-correlation. Possible phasing values range from 0 to 1 stride cycle. In normal walking, phase is 0.5, which means the left and the right leg are exactly alternating (Malone et al. 2010).

Within the feedforward parameters, center of oscillation is classified as a spatial parameter, while double support and phase shift are classified as temporal parameters (Choi et al. 2009; Malone et al. 2010). Recently, step length has been thought of as having both spatial and temporal characteristics because it is adjusted under the influence of both components (Malone et al. 2010). For each of the above terms except for phase shift, the difference between the fast and the slow leg's measurement is calculated in order to probe the symmetry of locomotion.

1.6.5 Factors that affect split-belt treadmill adaptation

1.6.5.1 Treadmill speeds

Vasudevan et al. (2009) probed how locomotor adaptation is affected by the speed at which individuals are trained. They trained healthy subjects at a certain split-belt speed combination and tested aftereffects at various speeds. They observed the largest aftereffects at the slow belt speed during split-belt training (Vasudevan et al. 2010).

The difference in speed between the fast and the slow belt during adaptation also affects the outcomes. Reisman et al. (2005) tested healthy subjects at different speed ratios, 2:1, 3:1, and 4:1 (the slow belt moved at 0.5 m/s). They showed that larger asymmetry occurred in the beginning of the adaptation period for the greater speed ratios, and it took longer (more steps) to get back to symmetry within the adaptation period for the greater speed ratios than those for smaller ratios (Reisman et al. 2005). The former finding indicates that adaptation is speed specific, and the latter indicates that the greater the difference in speed between the two belts, the larger the aftereffect will be.

1.6.5.2 Age of subjects

In addition, age has an important effect on adaptation. Vasudevan et al. (2011) compared the difference of adaptation in walking between 6 different age groups. In their study, children could modify the reactive parameters of their walking, and could adapt temporal coordination of feedforward parameters; however, children under 6 years old could not adapt the spatial coordination of feedforward parameters. Even 11-year old children had slower rates of adaptation and deadaptation of spatial coordination compared to adult subjects (Vasudevan et al. 2011). Further, they also pointed out that there are similarities in adaptation between young children and adult patients who had damage in their cerebellum. These findings suggest that all factors of locomotor adaptation do not mature simultaneously.

1.6.5.3 Effect of damage to specific parts of the nervous system

Studies uncovered that distinct regions of the nervous system have influence on locomotor adaptation. Forssberg et al. (1980) showed that spinal cats, who had completely transected spinal cords, could adjust their walking in reaction to a split-belt treadmill, but they did not study adaptation over time. Their results suggest that higher nervous centers, such as the cerebral cortex and brain stem, might not be necessary for the reactive feedback control. As for the feedforward control, Morton et al. (2006) investigated the walking of individuals with cerebellar damage on a split-belt treadmill. In that study, subjects were able to adjust to the split-belt condition by changing stride length and stance time immediately (feedback adjustments), whereas they were disrupted in adjustment of step length, double support, and phasing (feedforward adjustments) (Morton et al. 2006). Within the feedforward adjustments, cerebellar subjects had smaller aftereffects in step length, which has both spatial and temporal characteristics, than double support and phasing, which represent pure temporal aspects of walking. Vasudevan et al. (2011) proposed that there is a similar tendency in the adaptation of young children who are not able to adapt the spatial parameters (Vasudevan et al. 2011).

In contrast to the cerebellar deficits, Reisman et al. (2007) show that patients with cerebral stroke can make both feedback and feedforward adjustments (Reisman et al. 2007). In addition, although it cannot be compared with stroke patients directly, individuals who have had hemispherectomy could adapt in spatial parameters, but could not adapt in temporal parameters (Choi et al. 2009). Taking these findings together, it suggests that the cerebellum is more important for adaptation, especially spatial adjustments, than cerebral structures which are less critical for adaptation. Additionally, within the cerebellum, midline cerebellar structures might be more related to adaptation of walking because subjects who have clinical signs of more damage to the midline of the cerebellum are more impaired in split-belt adaptation (Morton et al. 2006). For animal subjects, Yanagihara and his associates (1996) tested whether decerebrate cats can adapt to walking on a split-belt treadmill. They found that the decerebrate cats whose vermis was disrupted could not adapt, whereas those with damage to other parts of their cerebellum retained the ability to adapt (Yanagihara et al. 1996).

1.7 Using motor adaptation for rehabilitation

1.7.1 Positive impact of split-belt treadmill walking for stroke patients

Post-stroke patients can improve their symmetry of walking through training using a split-belt treadmill (Reisman et al. 2007). Although the effect is transient, the findings are important because it suggests that stroke patients still have the capability to alter their nervous system in response to changing environmental demands. By testing adaptation, we can determine whether the nervous system still retains the ability to learn new movements (Bastian et al. 2008), and using a split-belt treadmill, we can manipulate the asymmetry of the walking. In a case study with split-belt treadmill training, Reisman et al. (2010) reported that after repeated training over days, a post-stroke patient could improve his symmetry of step length and increase his walking speed. Further, they reported that the effect was still present 1 month after the training (Reisman et al. 2010). In another study, Reisman and others (2009) probed whether adaptation is transferred from training on the split-belt treadmill to walking over ground by comparing aftereffects between treadmill and over ground walking in patients. Indeed, there was larger transfer with post-stroke subjects than control subjects. That means training on a split-belt treadmill could be beneficial for recovering symmetrical walking. Several groups tried to improve walking abilities of post-stroke patients using (tied-belt) treadmill exercise and standing balance exercise (Winstein et al. 1989; Silver KHC et al. 2000) but they did not find significant improvement in interlimb symmetry. On the other hand, Kahn et al (2009) tested whether they can reduce asymmetry in walking of post-stroke patients by training subjects walking unilaterally on a treadmill. They asked the subjects to step with only their unimpaired leg on the treadmill, while they stood with their impaired leg to the side of the treadmill. They found that asymmetry of step length over ground attenuated after the training (Kahn JH et al. 2009). Taking these findings together, it seems that training walking in s left-right asymmetric manner can enhance interlimb symmetry during walking, and the split-belt treadmill is a suitable apparatus for this purpose.

1.7.2 Prism adaptation for stroke patients with hemineglect

Rossetti et al. (1998) applied the prism adaptation to stroke survivors who have neglect symptoms, and found positive effects on their body-midline estimates from neurophysiological tests (Rossetti et al. 1998). For healthy subjects, Hatada et al. (2006) report that they observed aftereffects for more than 7 days when the prism distortion was introduced gradually in a single session of exposure. The aftereffects decreased within 6 hours; however, they increased again after Day 1 without training. The increase lasted until Day 3, and was still significant on their last measurement at Day 7 (Hatada et al. 2006). These results have yet to be replicated, and it still remains unknown whether gradual introduction of a prism distortion could make the aftereffect endure longer for the stroke patients.

1.7.3 Gradual introduction of error better for patients with cerebellar deficits

Criscimagna-Hemminger et al. (2010) tested whether size of error in motor adaptations affects the adaptation in patients with cerebellar degeneration. The findings show that patients with more severe disease experience more benefit from gradual perturbations than control subjects and mildly impaired patients. This fact suggests that gradual introduction of a perturbation (smaller error size) might improve the motor adaptation in people with severe cerebellum damage (Criscimagna-Hemminger et al. 2010).

As mentioned above, size of error affects motor adaptation.

However, most studies of this topic are with upper limbs (reaching, punching, or throwing). Little is known about adaptation of lower limbs (walking). If gradual perturbation enhances motor adaptation in walking, it might be a beneficial way for the rehabilitation of patients who have damage in their nervous system, such as stroke or cerebellar degeneration. The purpose of this study is to investigate the relationship between error size and motor adaptation in walking on a split-belt treadmill in healthy adults. This study will provide a basis for comparison with healthy children and adults with cerebellar injury.

1.8 **Predictions**

We anticipate that with a gradual introduction of the speed differential during split-belt adaptation, the aftereffect will be larger than when the speed differential is introduced abruptly. Moreover, the time course of the deadaptation will also be slower with gradual perturbations compared to abrupt perturbations.

CHAPTER 2. **Methods**

2.1 **Participants**

Sample size estimate was obtained by using step length changes reported by other studies (Reisman et al. 2005; Morton et al. 2006). Step length is a global measure of both timing and spatial aspects of walking, and hence the best measure for calculating sample size. We estimated that the aftereffect size for abrupt perturbation would be similar to the control subjects from the above studies, which was a step length difference between the right and left leg of ~0.1 m. We estimated that the difference in aftereffect between gradual and abrupt perturbations might be approximately half the normal aftereffect size, i.e., 0.05 m. The standard deviation is estimated to be ~0.05m, which is similar for both the published data and our pilot data. When we calculated the minimum sample size using on-line calculator (DSS research .com) so that the statistical power is above approximately 80% with alpha value 0.05 (5%), then the sample size was 16 per group. According to this, 32 healthy adults (15 males and 17 females; mean±SD, 26.3±5.76 yr) were recruited from undergraduate and graduate students at the University of Alberta. They confirmed that they did not have any disease or pain that affects walking prior to the experiment, had not had previous experience walking on a split-belt treadmill. The project was approved by the Human Ethics Committee at the University of Alberta, and all subject provided written informed consent.

2.2 Experimental paradigm

The paradigm consisted of walking on a split-belt treadmill (Woodway USA, MED-PRO). The treadmill has two separate belts driven by independent motors. The speed of each belt (for each leg) was controlled independently (Reisman et al. 2006). During the testing periods, participants walked on the treadmill with the two belts either moving at the same speed (tied configuration) or different speeds (split configuration). Generally, participants were involved in three testing periods as follows: 1) baseline, 2) split-belt (adaptation), 3) tied-post (post adaptation) (see Figure 1A). During the baseline period, participants walked on the treadmill with belts at the same speed (0.5 m/s) for 1~2 trials. Although the preferred walking speed for healthy adults is reported around 1.2 m/s (Dingwell et al. 2006), we used slower speeds because the results of the present study will be used for comparison in future studies. These future studies will focus on motor adaptation in patients with brain damage, who walk slower than healthy adults. Indeed, Riesman et al. (2010) trained a post-stroke patient on a split-belt treadmill at 1.0 m/s for the fast belt, and at 0.5 m/s for the slow belt. Also, the patient in Reisman's study could not complete the training that consisted of six 5-minute bouts for the first session because of fatigue (Reisman et al. 2010). Thus, we limited each trial to be 3 minutes in the present study. Participants took rests between the trials by standing on the side of the treadmill. The break times lasted approximately 40~60 seconds.

The split-belt (adaptation) period followed the baseline period for 5 trials (15 minutes in total), following the protocol used by Reisman and associates in a study with post-stroke patients (Reisman et al. 2009). During the split-belt period, one of the two belts was driven faster than the other (2:1 ratio of fast to slow speed), making participants walk asymmetrically. The speed of the fast belt was set to 1.0 m/s either at the onset of the split-belt period (abrupt perturbation), or increased in an incremental manner during the first 4 trials of the split-belt period (gradual perturbation—details below). All subjects walked at the full 2:1 ratio for the final 3 minutes of the adaptation period. Finally during the tied-post period, the belt speed was the same as those of the baseline (0.5 m/s). In order to make the number of steps during the tied-post period approximately the same as those of the split-belt period, the tied-post period lasted for 7 trials (21 minutes in total). This is because the cadence is slightly faster during the split-belt period because one belt is fast. The total experiment was approximately 2 hours including setting up time.

Participants were distributed into 2 groups (shown in Figure 1B): Group 1 experienced the gradual perturbation, and Group 2 experienced the abrupt perturbation. The fast-going leg and the assignment to groups were determined by block-randomization (block size = 4), so that the subject numbers in each of the groups, and which leg was on the fast belt first was balanced between groups.

2.3 Familiarization trial

A very short trial at which the speed ratio is 2:1 was inserted after the first baseline trial. Then the second baseline trial followed, before the split-belt period (Figure 1). The purpose of this familiarization trial is to acquaint the participants with the split-belt configuration in order to avoid the surprise factor affecting the initial error size during early adaptation. The number of steps of this familiarization trial was restricted to approximately 5 steps.

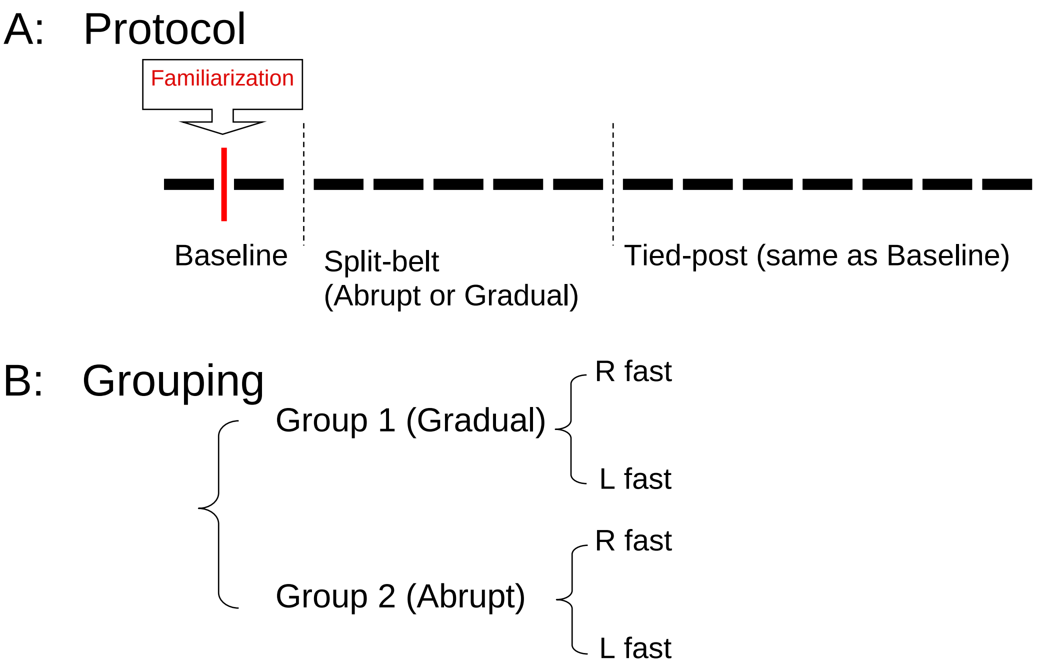

Figure 1. Protocol of the experiment and grouping of subjects
A: Two belts moved at the same speed during the baseline period. A very short split-belt trial was interspersed between two baseline trials (familiarization trial). During the split-belt (adaptation) period, each group experienced either gradual or abrupt perturbation. During the tied-post (post adaptation) period, the speeds of the two belts were the same as the baseline period again. B: Participants were assigned into two groups. Fast-going leg (left or right) was assigned within the each group. Assignment to the groups and fast-going leg were determined by block-randomization, so that the numbers in each group, and which leg was on the fast belt first was balanced.

2.4 Protocol of gradual perturbation

During the gradual perturbation period, the speed of the fast belt increased by 0.04 m/s every 71 seconds so that it would reach 1.0 m/s within 12 minutes (4 trials). The manner in which the fast belt speed was incremented is shown in Figure 2. The belt speed ratio between fast and slow belt during the last (5th) trial of the adaptation period was fixed at 2 : 1 (Figure 2).

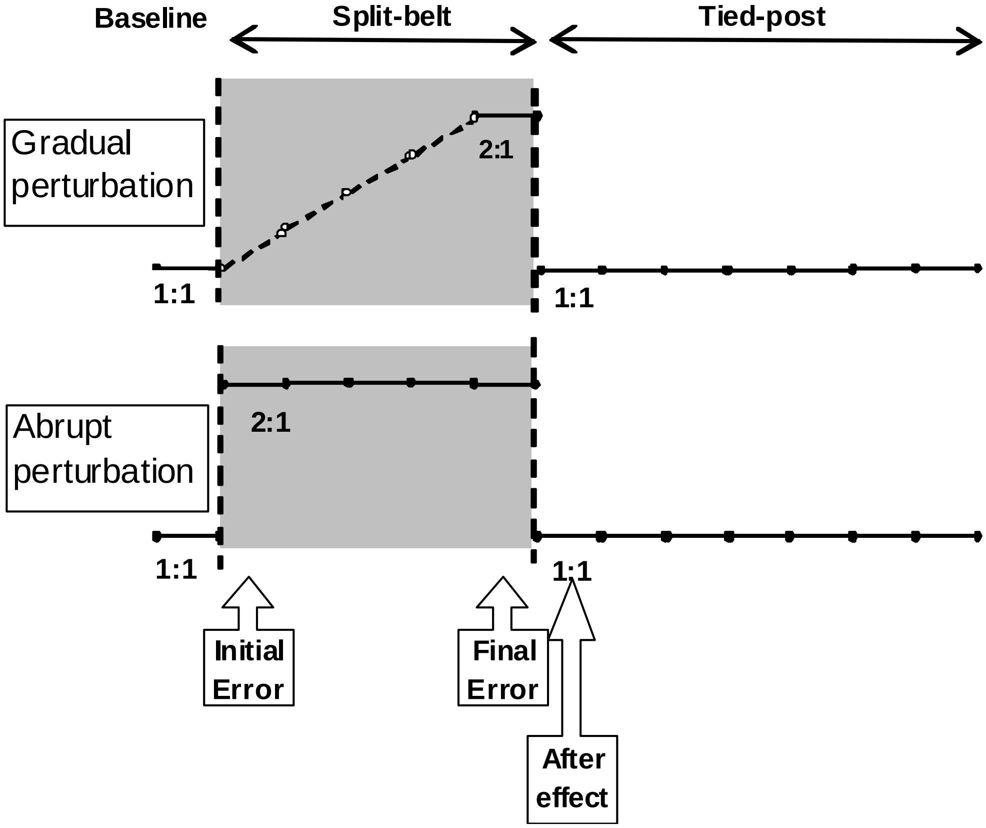

Figure 2. The fast belt speed for gradual and abrupt perturbations. During the baseline, there was no speed difference between two belts (ratio was 1:1). After the second baseline (tied-belt) period, adaptation (split-belt) period followed. During the gradual perturbation, the speed of the fast belt increased for 4 trials of the adaptation period. The speed ratio between fast and slow belt during the 5th trial was fixed at 2:1. As for the abrupt perturbation, the speed ratio was 2:1 from the onset of the adaptation period. For both perturbations, speed difference was back to the same as those of the baseline period after the adaptation period. Block arrows represent the measurements for studying the change in symmetry. Initial error is the difference between the average of the last 10 steps of the baseline period and the first 10 steps of the adaptation period. Final error is the difference between the average of the last 10 steps of the baseline period and the last 10 steps of the split-belt period. Aftereffect is the difference between the average of the last 10 steps of the baseline period and the first 10 steps of the tied-post period.

2.5 **Instructions to subjects**

Before starting the session, the experimenter told participants that the two belts would move at different speeds in some trials during the experiment. They were not told which leg would be the fast-going or the condition of the perturbation (gradual or abrupt). The experimenter controlled the belt speeds while the participants were walking. The participants got on or got off from the moving treadmill belts according to the verbal instructions from the experimenter. For safety, participants held onto the handrail in front of them while they were walking. Participants watched a movie of their choice, situated directly ahead of them. They were asked not to look down or around, and not to think about their walking.

2.6 **Data collection**

An experimenter controlled the treadmill belt speeds from behind the participant. In order to record the motion of the legs, 5 infrared-emitting markers were attached to each leg of a participant, as follows: iliac crests, great trochanters, knees (lateral femoral epicondyles), ankles (below the lateral malleolus, so that the foot angle was 90 degrees when a subject's shank was perpendicular to the belt), and the head of the 5th metatarsal bones. Position data was collected using the Optotrak system (Northern Digital, Inc., Waterloo, Ontario, Canada) at 100 Hz.

The motion was also recorded with digital video (JVC Evrio GZ-MG330HV) for verification that the participant was following the experimenter's instruction (i.e., watching the video and not looking at his/her feet). A custom–made digital counter that generated 5V pulses at 1 Hz synchronized the video and Optotrak data. The 1 Hz signals were forwarded to an LED display (resolution 10 ms) in view of the camera. The 1 Hz signals were also recorded on computer with a commercial A/D software (Axoscope, Molecular Devices) together with an output pulse from the Optotrak system, which indicated the timing of the first and last frame from that system. These two timing devices allowed us to synchronize the events of the video camera with the data on from the Optotrak system.

2.7 Data analysis

By convention, the limb on the fast belt was referred to as the fast leg and the limb on the slow belt as the slow leg, even when both legs were moving at the same speed during the baseline and tied-post periods (Bastian et al. 2006). Using the custom software written by Dr. Susan Patrick in MATLAB (The MathWorks, Natick MA), marker position data was analyzed. The custom software quantified a spatial measure, a temporal measure, and a global measure that includes both spatial and temporal aspects. The spatial measure used was called center of oscillation (CO). Center of oscillation is the midpoint of the limb angle between heel strike and toe off for each leg. The temporal measure used was phase shift (Phase). Phase shift is obtained by calculating the cross-correlation function between the limb angle trajectory for the left and right limb (Choi et al. 2007). Possible phasing values range from 0 to 1 stride cycle. If the left and right steps are exactly alternating during walking, the value would be 0.5, which means the two legs are 50% out-of-phase (Malone et al. 2010). The reference leg was the slow leg. When the phase shift value is over 0.5, that means the fast leg is advanced relative to the slow leg (Choi et al. 2007). The global measure, step length, represents both spatial and temporal coordinates, and is the anterior-posterior distance between the ankle markers of each leg at heel strike. Step length changes can be achieved by shifting CO and/or phase (Malone et al. 2010) (Figure 3). Fast step length refers to the step length at fast leg heel strike and slow step length refers to the step length at slow leg heel strike (Reisman et al. 2005).

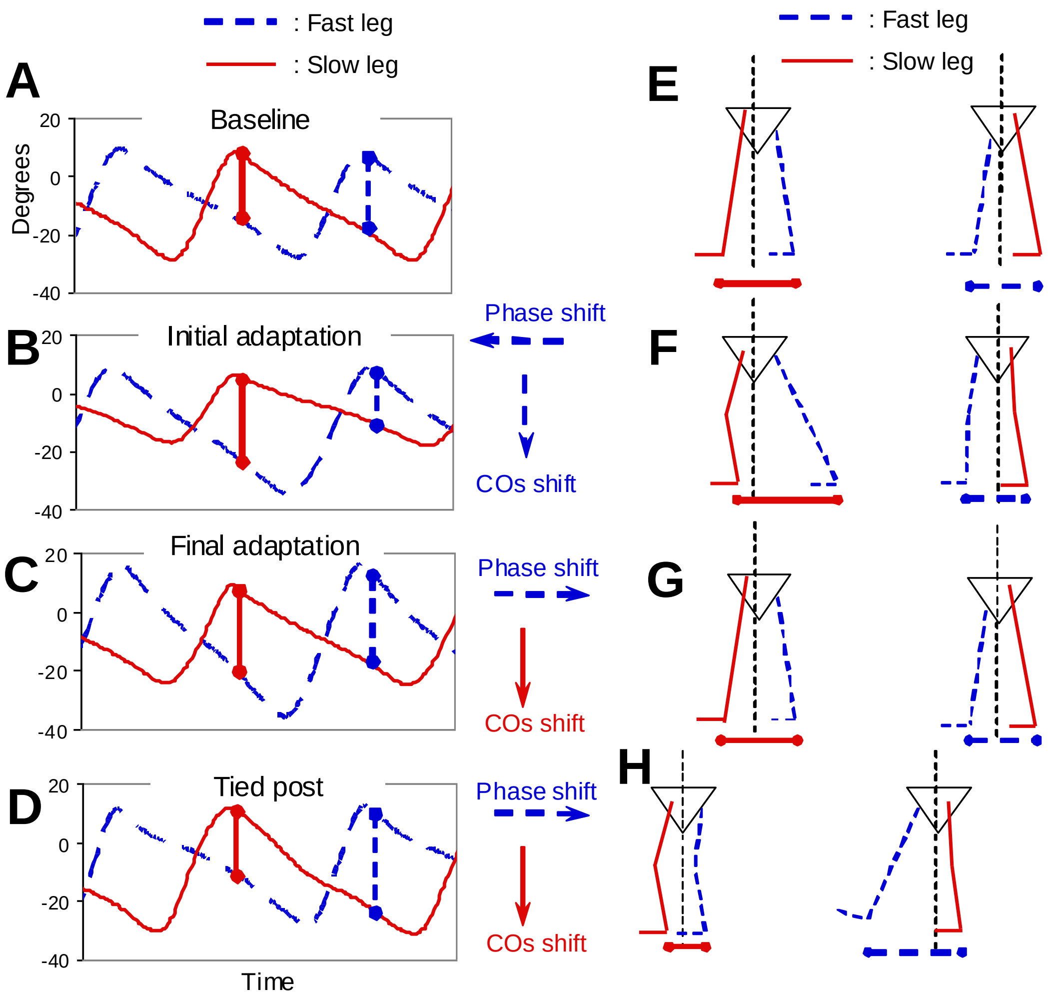

Figure 3. Limb angle trajectories and stick figures of steps at each experimental period. Dashed lines represent the fast leg, while solid lines represent the slow leg. A-D: Limb angles for two cycles are shown at baseline (A), initial adaptation (B), final adaptation (C), and early tied-post (D). Vertical lines represent step length of each step. They are proportional to the step lengths shown in E-H (the lines at the bottom). At the beginning of the adaptation period (B), limb angle trajectories were shifted, reflecting the asymmetry of the walking. Throughout the adaptation period (B-C), participants equalized step lengths by shifting both Center of Oscillation (spatial parameter) and Phase (temporal parameter). A shift in the center of oscillation and/or phase equalized the step length at the end of the adaptation period (C). In the tied post period (D), the belts speed was the same as those of the baseline; however, shifts were evident in CO symmetry and SL symmetry resulting in an aftereffect. E-H: The stick figure diagram of two consecutive steps in each period. The lines at the bottom represent the step lengths.

In order to study the symmetry of the center of oscillation and the step length, each measure of the slow leg was subtracted from the measure of the fast leg. For the step length, the difference was normalized by dividing the difference by the total of fast and slow leg length (Malone et al. 2009) as shown below:

$$\text{step length symmetry} = (\text{Fast SL} - \text{Slow SL}) / (\text{Fast SL} + \text{Slow SL})$$

where Fast SL and Slow SL represent fast step length and slow step length, respectively. Following the calculation of the symmetry, consecutive three-step average values of each measurement were generated from the symmetry measures in order to study the time course of adaptation and deadaptation (i.e., tied-post). These values were calculated from every three steps without using the same numbers again (i.e., not a running average) to smooth the adaptation and deadaptation curve of each subject. Then, they were averaged across the subjects. To remove the variability between participants due to the different baseline-symmetries, the mean asymmetry during the baseline trial was subtracted from each participant's measure prior to averaging.

2.8 **Statistics**

In order to identify the change in the symmetry while the participant was walking, three measurements for each of center of oscillation, phase shift, and step length were defined: 1) initial error, which is a difference in symmetry between the last 10 steps of the baseline trial and the first 10 steps of the adaptation period, 2) final error, which is a difference between the last 10 steps of the baseline trial and the last 10 steps of the adaptation period, 3) aftereffect, which is a difference between the last 10 steps of the baseline trial and the first 10 steps of the tied-post period. To determine if each subject showed a significant aftereffect, a paired one tail t-test was used to determine if there was a difference between the last 10 steps of baseline and the first 10 steps of tied-post. In order to test the difference between groups in the above measures, a mixed-design 2-way ANOVA was used with factors time (within-subject) and groups (between-subject) using SPSS ver. 19 (IBM). Post-hoc pairwise comparison was used in order to explore the change in symmetry at each time point (EA: early adaptation, FA: final adaptation, EP: early post adaptation) from baseline within a group. 3 pairwise comparisons were made for each group. For between group comparison, independent one tail t-test was used to determine if there was difference between abrupt and gradual groups in 1) initial error, 2) final error, and 3) aftereffect for Center of Oscillation, Step Length, and Phase. $p < 0.05$ was considered statistically significant. As for the ANOVA, Bonferroni adjustment was used for the correction of the p value for post-hoc pairwise comparisons.

CHAPTER 3. **Results**

3.1 Changes in symmetry of walking in single subject

Complete data sets have been obtained from 32 participants. Figure 4 shows an example of symmetry in step length over time from represientive subjects. Three-step averaged values are plotted. During the second baseline trial, which was after the surprise trial, walking was symmetric. In the abrupt condition (Figure 4 A), the split-belt configuration made the steps asymmetric at the onset of the adaptation period. By the end of the adaptation period, the asymmetry returned close to the level of the baseline period. In the gradual condition on the other hand, the symmetry did not change a lot in the beginning of the adaptation period, and remained relatively stable during that period (Figure 4 B). During the tied-post period, the subject showed aftereffect in both abrupt and gradual conditions. The aftereffect attenuated with time. Because we used short trials and let the subjects have rest periods between each trial, they might forget some of their adaptation with each rest period. To elucidate this, we extracted the beginning 10 steps of each adaptation trial of each subject. Then took averages across the subjects. However, we did not find systematic pattern among them (data not shown).

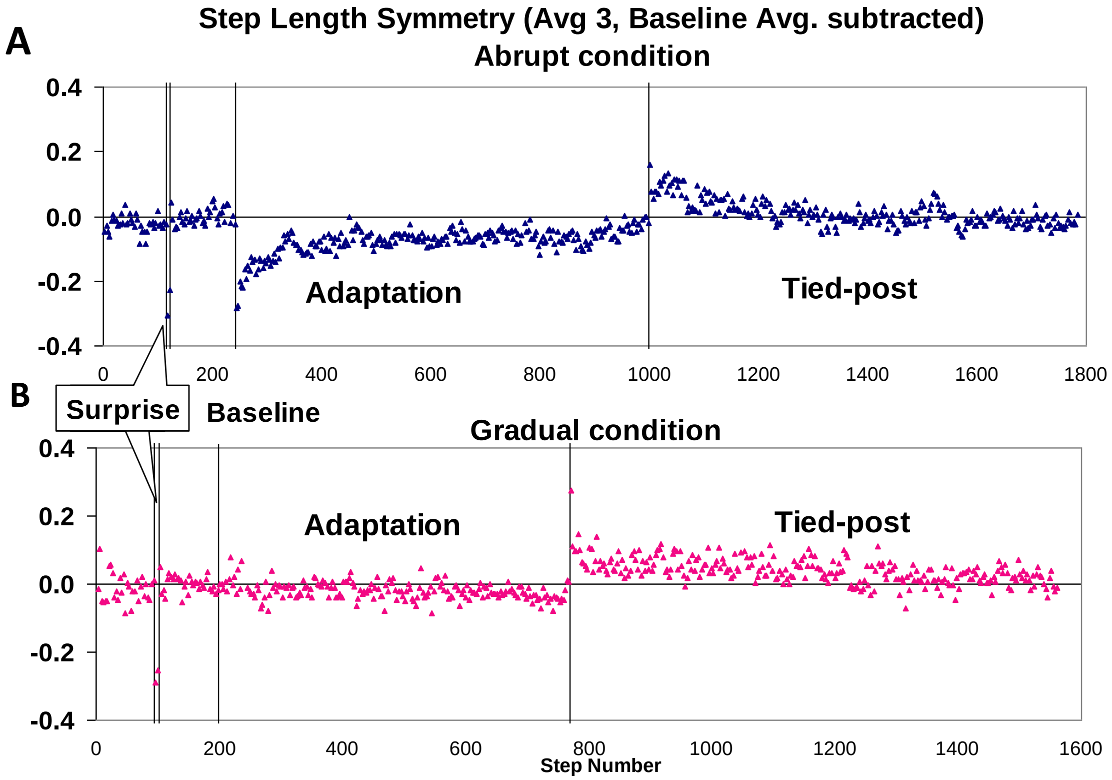

Figure 4. Step length symmetry from two representative subjects. Baseline (second baseline) average value was subtracted out from each curve. At the beginning of the adaptation period, the subject in the abrupt condition showed significant initial error (A), whereas little change was observed in the gradual condition (B). By the end of the adaptation period, symmetries were close to the level of the baseline period in both conditions (A, B). At the onset of the tied-post period, the subjects showed the aftereffects, which were in opposite direction to the asymmetry in the initial errors (A, B). During the tied-post period, aftereffect attenuated over time.

3.2 **Changes in symmetry of walking for the two groups**

Figure 5 shows the averages across the subjects for each of CO, phase, and step length at each of the time points of interest (see Methods). BL represents baseline; EA, early adaptation; FA, final adaptation; EP, early post adaptation respectively. Note that the averages are shown for subjects in the gradual and abrupt groups separately.

3.2.1 Center of Oscillation (CO)

For CO (Figure 5 A), pairwise comparisons for each condition revealed that there were significant differences between BL and other time points ($p < 0.05$). The difference between BL and EA in the gradual condition was smaller than those in the abrupt condition. Significant differences between BL and FA in both conditions ($p < 0.05$) mean that the adaptation was not complete. As for the EP, there were significant differences from BL in both abrupt and gradual conditions ($p < 0.05$), which indicates the aftereffects were significant.

3.2.2 Phase

For phase (Figure 5 B), EA and FA were significantly different from BL in the abrupt condition ($p < 0.05$). On the other hand, no significant differences were found in EA and FA from BL in the gradual condition ($p < 0.05$). Thus, in contrast to CO, adaptation was complete in the case of phase. There were significant aftereffects (i.e., difference between BL and EP) in both groups ($p < 0.05$).

3.2.3 Step length (SL)

For step length (SL), there was a significant difference between BL and EA in the abrupt condition ($p < 0.05$) (Figure 5 C), whereas no difference was found in the gradual condition. For EP, there were significant differences from BL in both groups.

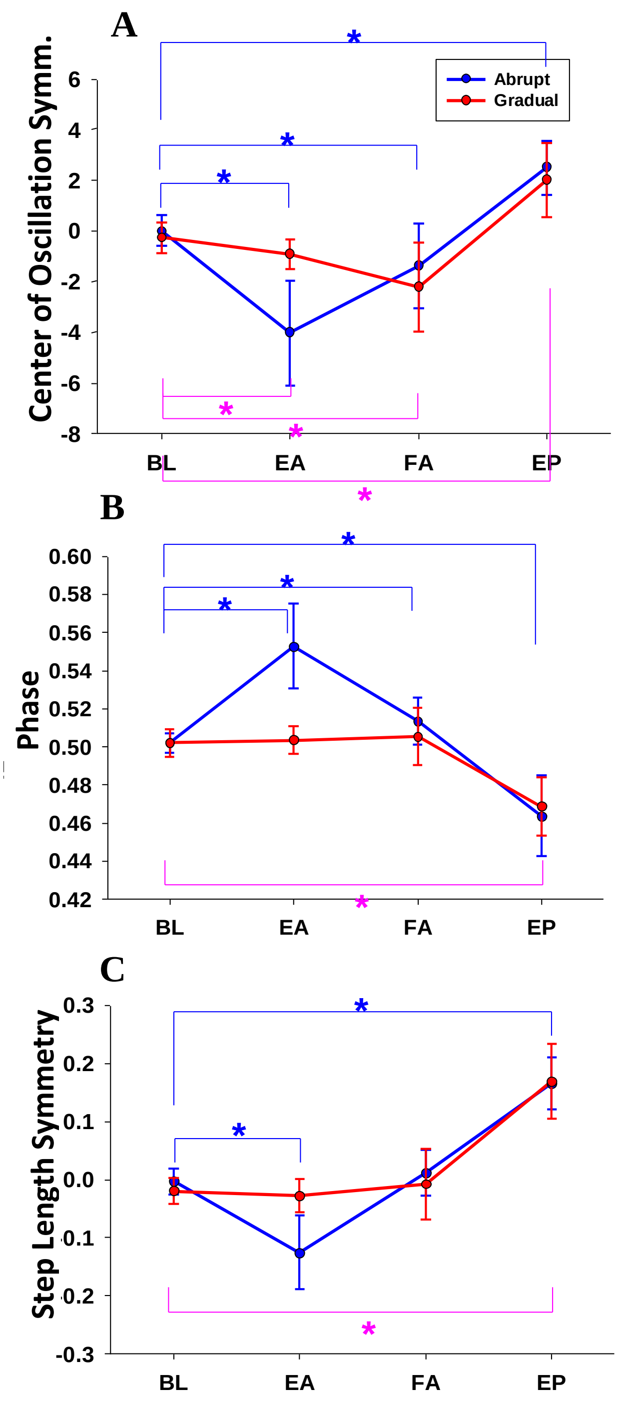

Figure 5. 10-step averages at each experimental period for three measurements. The gradual and abrupt groups are overlapping. For CO symmetry and SL symmetry (A, C), the value of zero represents the complete symmetry. For Phase (B), 0.5 represents the complete symmetry. BL, last 10 steps of the baseline period; EA, first 10 steps of the split-belt period; FA, last 10 steps of the split-belt period; EP, first 10 steps of the post adaptation period.

3.3 **Feedforward parameters between gradual and abrupt perturbations**

Comparisons between the groups were made for initial error, final error, and aftereffect.

The initial error of CO in the abrupt condition was significantly larger than that in the gradual perturbation (Figure 6 A; $p < 0.05$). No significant differences were seen between groups at the end of the adaptation period (final error; Figure 6 B; $p > 0.05$), and the beginning of the tied-post period (aftereffect; Figure 6 C; $p > 0.05$). That tells us there was no significant difference in the aftereffect between the groups.

The same data is shown for phase (Figure 6 D-F) and step length (Figure 6 G-I). Significantly larger initial error was observed in the abrupt perturbation (Figure 6 D, G; $p < 0.05$). At the end of adaptation period, the difference was attenuated. At the beginning of the tied-post period, there were no differences between gradual and abrupt perturbations (Figure 6; F, I).

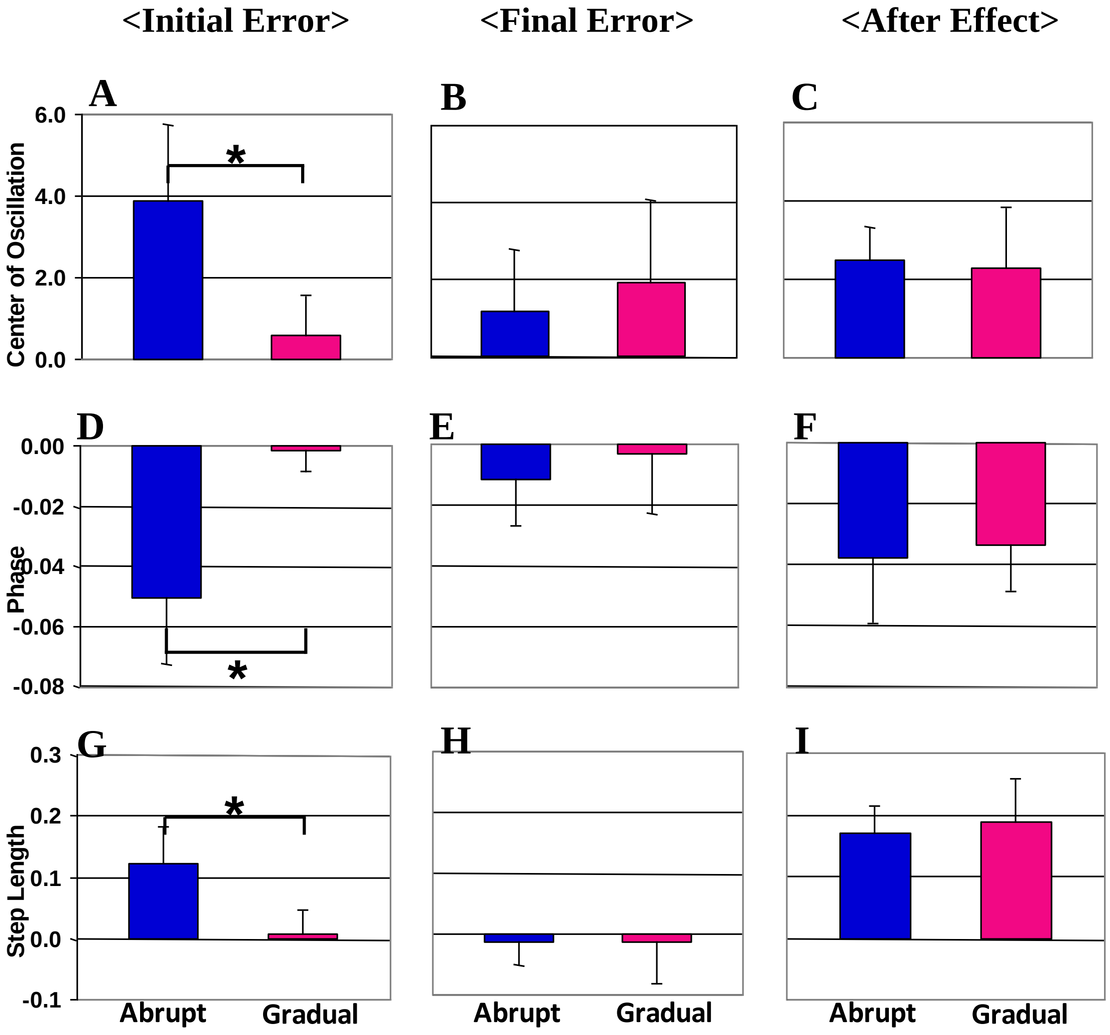

Figure 6. Comparison of error sizes and aftereffect between abrupt and gradual conditions. For the initial errors (A, D, G), the values in the gradual conditions were significantly smaller than those in the abrupt conditions. At the end of adaptation period (final errors; B, E, H), the differences decreased. For the aftereffects, two groups were similar between abrupt and gradual conditions. Although no significances were observed, the aftereffects for step length in the gradual condition was slightly larger than those in abrupt condition (I), whereas the aftereffects for CO and phase in the abrupt conditions were slightly smaller than those in the abrupt conditions (C, F).

3.4 Time courses

Time courses for each of CO symmetry, phase, and step length symmetry during the adaptation and the post adaptation period were measured in order to study the changes in symmetry over time across the groups. Figure 7 shows the superimposed curves of time courses in the gradual and the abrupt condition.

For all three variables in the adaptation period, significant asymmetry was observed in the abrupt condition, whereas there was little change in the gradual condition (Figure 7 A, C, E). At the end of the adaptation period, CO, phase, and step length approached symmetry, but both groups were significantly lower than the value of zero for CO, and the abrupt group had a residual asymmetry in phase (See figure 5 B).

For the post adaptation period, the two curves were very similar for all variables (Figure 7 B).

In summary, little difference was found during the post adaptation period between the gradual and abrupt group in each measurement of CO, phase, and step length, while the abrupt group showed large asymmetries at the beginning of the adaptation period.

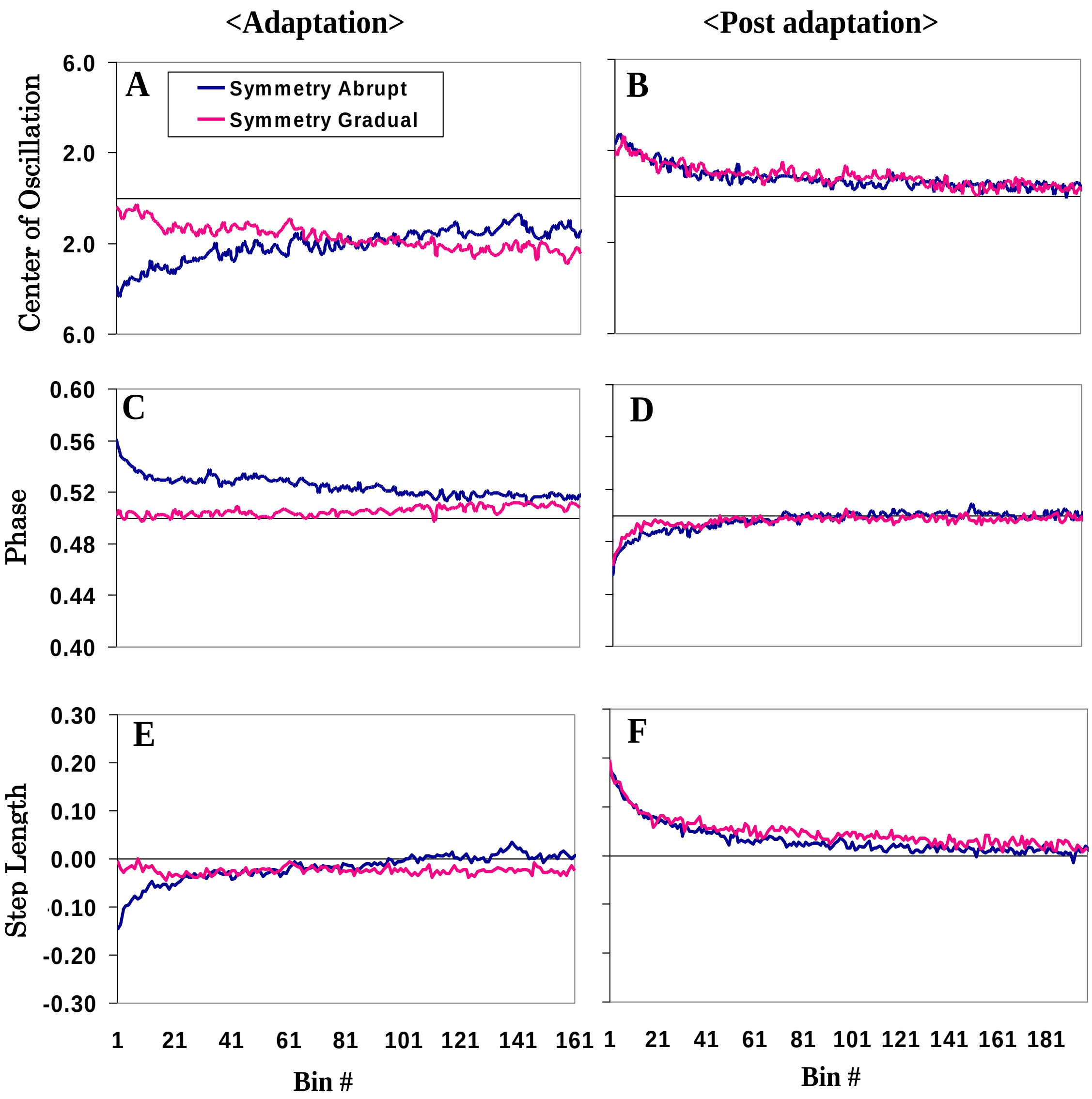

Figure 7. The group data of the time course of change in walking symmetry (the abrupt and the gradual groups were overlapped). Three consecutive-step average values are plotted. The baseline average is subtracted out from each curve. The step number of each subject was chopped into that of the shortest subject in order to make the periods the same length. For CO (A, B) and step length (E, F), the value of zero represents the complete symmetry. For phase (C, D), the symmetry appears as the value of 0.5. In general, the abrupt group in each measurement of CO, phase, and step length showed significant asymmetry during the adaptation period, while the gradual group did not show such asymmetry (A, C, E). During the post adaptation period, no significant differences between the gradual and the abrupt groups were observed (B, D, F).

CHAPTER 4. **Discussion and Conclusion**

4.1 **Size of error has little effect on the magnitude of the aftereffect in split-belt adaptation**

We investigated whether size of error affects motor adaptation during walking. Unexpectedly, the comparison in aftereffect between groups revealed that there was no significant difference between abrupt and gradual introduction of errors, in spite of the significant difference in the size of error at the start of the adaptation period. This suggests that incremental introduction of the movement error did not augment the motor adaptation during walking. This finding is inconsistent with the reports of the reaching motions of upper limbs, in which subjects experienced adaptation in either visuomotor or force field distortion. Those studies showed that the gradual introduction of the distortion enhanced the magnitude (Kargerer et al. 2008; Klassen et al. 2005; Ingram et al. 2000) and duration (Criscimagna-Hemminger et al. 2010; Huang et al. 2009; Klassen et al. 2005; Kluzik et al. 2008) of the aftereffect.

4.2 **Why does the size of error affect motor adaptation in walking differently than adaptation of arm movements?**

4.2.1 Methodological reasons

There are possibilities that our methodology that did not allow for the expression of the difference between abrupt and gradual groups. First, we used 2:1 speed differential ratio for the adaptation period. A larger differential may have resulted in a more intense aftereffect. Reisman et al. (2005) measured the magnitude of aftereffect at different speed ratios in split-belt adaptation. They found that the larger speed differentials resulted in larger aftereffects. A larger aftereffect might have revealed differences between the two groups more easily.

Also, in the present study, the gradual group experienced the full strength of perturbation (2:1 speed differential ratio) only for 3 minutes, while the abrupt group experienced it for 15 minutes from the onset of the adaptation period. This could make the aftereffect of the gradual group smaller than that of the abrupt group, because of a smaller “dose” of the 2:1 belt-speed ratio. In upper limb reaching motions, Klassen et al. (2005) showed that when the perturbation is introduced incrementally, the retention of the adaptation is similar or better than that when the perturbation is introduced instantaneously even if the full strength of the perturbation is shorter for the incremental group than the instantaneous group. However, it is still unclear whether the amount of the experience with the full strength perturbation affects the split-belt adaptation.

Finally, we used short trials of 3 minutes each, interspersed with 1 minute breaks, because we wanted to use this data to compare with both healthy children and adults with injury to the central nervous system. Both these groups require shorter trials with rest breaks (Reisman et al. 2010; Musselman et al. 2011). Breaks after adaptation allow the subjects to forget what they learned (Criscimagna-Hemminger et al. 2008), and because of the difference in adaptation rate, the forgetting could be different for the two groups. Torres-Oviedo et al. (in press) tested split-belt adaptation for the gradual group and the abrupt group, with only one short break in the adaptation trial. In their study, the abrupt group showed larger aftereffects than that of the gradual group. In our study, on the other hand, the aftereffects of the two groups were very similar. There is the possibility that the breaks between the adaptation trials allowed the subjects to forget, and that the forgetting could be greater in the group with abrupt perturbation.

Visual information could also affect the adaptation. For reaching tasks, subjects cannot know whether the distortion is applied or not before they start the trial. As for walking on a split-belt treadmill, in contrast, subjects were allowed to watch the belts at least when they start walking for safety reasons. By watching a change in the belt speed prior to the trial, subjects can rely on the visual information before walking rather than the error they experience during actual walking for anticipation of the desirable leg trajectories and rhythms of gait. They might even estimate what the examiners expect. Certainly there are some studies that tested over ground walking with subjects blindfolded (Anstis et al. 1995; Weber et al. 1998; Gammon et al. 2002). However, because we allowed the subjects to see the belt during the experiment, there is the possibility that visual information affected the adaptation even though subjects were instructed not to look down.

In the present study, subjects held a handrail in front of them during walking. This might also affect their walking. Holding onto a handrail during walking requires less effort for trunk stability (Jeka et al. 1994). Although it would not affect the changing of the magnitude of the adaptation within the subject as long as the experimental protocol is kept consistent across the periods, it should be noted that split-belt walking with a handrail is different from without a handrail, which requires more effort for trunk stability. Indeed, in the video analysis, we observed that several subjects blocked their trunk sway that occurred in the sagittal plane as the consequence of the larger trajectory of the fast-side leg at the onset of the post adaptation period with their upper limbs. Although it is not clear whether this phenomenon is common, walking without holding handrail is more preferable because the trials without the effort for trunk stability could affect the adaptation during walking.

4.2.2 Neurophysiological reasons

Emken et al. (2005) pointed out the existence of the common processes that the nervous system uses in order to adapt the motion of the leg during gait and the arm during reaching to the novel environments. The nervous system forms the internal models that fit the novel environments by anticipating the imposed perturbation, and creates the preferable movements. Moreover, the cerebellum has a crucial role for motor adaptation in both arm movement (Galea et al. 2010; Jayaram et al. 2011) and split-belt walking (Choi et al. 2009; Morton et al, 2006). However, motions of legs during walking and arm during reaching are controlled by different neural networks respectively. For instance, in the motor cortex, arm and leg movements have distinct representations (Schott et al. 1993). Further, although both of these kinds of movements are thought to be controlled through the spinal circuitry, the segmental level for each movement is situated is different locations (Tantisira et al. 1996; Alstermark et al. 2000; Barriere et al. 2008). In cats, Alstermark et al. (2000) and their group showed that the supraspinal neural systems innervate forelimb motoneurons through the propriospinal neurons at the C3-C4 level (Tantisira et al.

1996; Alstermark et al. 2000). On the other hand, movements of lower limb are controlled by more caudal regions of the spinal neuron system. Barriere et al. (2008) showed that cats can generate a bilateral hindlimb pattern of locomotion even though they were completely transected their spinal cord at the level of L1. This finding suggests that alternate motions of legs are controlled by the regions lower than L1 level. Although, it is still unclear where and how the differential response of the distinct neural circuits that control upper limb reaching and lower limb walking reside.

In addition, the differences in the results between the present study and previous ones in the upper limb could be due to the nature of the movements. Reaching motions that have been studied in motor adaptation are goal directed, voluntary, and single limb movements of arm (Buch et al. 2003, Huang et al. 2009), while walking in this study used rhythmic, alternating movement of legs. Walking movements are considerably more automatic, with the spinal cord playing an important role in the control (Grasso et al. 2004, Molinari et al. 2009). In contrast, reaching movements require visual guidance, with the visual and motor cortices playing an important role (Eisenberg et al. 2011, Thaler et al. 2011). This dissimilarity might also partly account for the different results.

4.3 Distinct adaptation profiles for spatial versus temporal symmetry suggest different neural mechanisms

For CO, asymmetry both in the abrupt and gradual group at the end of the adaptation period did not return to the level of the baseline, while Phase and SL returned to the baseline level. In the gradual condition, asymmetry in CO even got larger as step number increased. However, no significant difference was found across groups in the CO symmetry at the end of the adaptation period. Moreover, similar findings were reported by other studies on split-belt adaptation (Malone et al 2010, 2011). This supports the distinct characteristics between temporal and spatial factors in motor adaptation.

Studies with patients who have supraspinal lesions suggest that different neural structures contribute to spatial and temporal factors in adaptation. Children with hemispherectomy showed adaptation deficits in temporal but not spatial symmetry (Choi et al. 2009). In contrast, subjects with cerebellar damage showed more impaired adaptation in spatial symmetry than temporal symmetry (Morton et al. 2006). Taking these findings together, it is plausible to assume that there are at least two aspects in motor adaptation during walking: spatial, and temporal (timing), and that they are controlled by discrete neural circuits. In addition, spatial adaptation might take longer than timing adaptation.

Further, a study showed the different extent of retention for spatial and temporal symmetry in split-belt adaptation. Malone et al. (2011) explored whether the adaptation to walking on a split-belt treadmill is maintained day to day (one day apart). They demonstrated that subjects showed faster readaptation in the spatial measurement on day 2, whereas there was little difference in temporal measurement (Malone et al. 2011).

Also, Malone et al. (2010) show that spatial control of motor adaptation is more sensitive to conscious effort or distraction than temporal control. They attribute these differences to the distinct neural networks involved. In their studies, Malone et al. (2010, 2011) proposed that spatial control engages connections between the lateral hemisphere of the cerebellum and the cerebral motor cortex, whereas temporal control engages circuits that connect the midline cerebellum to the midbrain and brainstem. They conjectured that lower neural structures, such as midbrain and brainstem are less susceptible to the change of the situation during walking, which might be a reason why temporal adaptation was not influenced much by the previous exposure (Malone et al. 2010, 2011). If spatial control is more sensitive to the change of the situation than temporal control and takes more time for adaptation, it is reasonable that spatial control did not return to the baseline level within the same adaptation time period as temporal control did.

4.4 Other possible effects of gradual perturbations

Torres-Oviedo et al. (in press) explored whether size of error affected the transfer of split-belt adaptation to walking over ground. They found that when the subjects adapted to the gradual perturbation during the split-belt treadmill walking, the transfer of the aftereffect to over ground walking was larger than that of the abrupt perturbation. That means that the smaller errors (the gradual perturbation) enhanced the transfer of the adaptation across the context, even though they produced a smaller aftereffect within the same context (i.e., on the treadmill) when compared to the group with abrupt perturbation. Torres-Oviedo et al. (in press) suggest that when an individual experiences the errors that are greater than the ordinary range (i.e., normal variability of walking), the nervous system assigns the errors to the environment, and the acquired learning is related to the particular context. On the other hand, when the errors are within the natural variability, they are assigned to the body, and the acquired learning is generalized across the contexts. This finding is consistent with the study of Kluzik et al. (2008) that showed enhanced transfer to movements without the device when the subjects adapted to gradual perturbations in reaching.

Further, studies with upper limb reaching motions report that when subjects adapt to the gradual perturbation, it leads to longer-lasting aftereffects (Kagerer et al. 1997; Hatada et al. 2006) and larger retention (Klassen et al. 2005; Huang et al. 2009). These findings suggest that adaptation to gradual perturbations might have other benefits for learning even when it does not augment the aftereffect within the same task.

4.5 **Conclusion**

We examined whether size of error affected the extent of motor adaptation during walking on a split-belt treadmill. Unexpectedly, we did not find a significant difference whether the perturbation was introduced gradually or abruptly. Studies have already shown the advantages of split-belt treadmill training for improvement of walking symmetry post-stroke (Reisman et al. 2007, 2009, 2010). We have explored the differences within the single session. It remains to be explored, the extent to which the adaptation in walking is retained day to day when the errors are introduced gradually versus abruptly. Retention is different for upper limb motions when errors are introduced with a different time course (Klassen et al. 2005; Hatada et al. 2006). Further studies might reveal other effects of manipulating the error size.

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