Motor adaptation following split-belt treadmill walking

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UNDER NORMAL CONDITIONS in healthy human populations, the nervous system is easily able to provide optimal interlimb coordination between the lower limbs during locomotion. It has been proposed that this optimal coordination is due to areas in the brain or spinal cord named central pattern generators (CPGs), providing the onset, offset, and relative contribution of agonists and antagonists both within (intralimb) and between limb (interlimb) coordination. Under ideal circumstances, the presumed CPG is able to control human walking with relative ease. However, following central nervous system lesions, central and peripheral adaptations can disrupt intra- and interlimb coordination resulting in asymmetric gait and reduced stability. In addition, peripheral feedback and the central integration of peripheral feedback during locomotion is impaired, causing inappropriate responses to changes in the external environment, such as colliding with an object or walking over uneven terrain.

Recent work by Bastian and colleagues has investigated locomotor adaptation using split-belt paradigms. Through this methodology, the walking pattern of the legs can be altered so the two legs (positioned on 2 separate belts) are moving at different speeds and sometimes different directions. This enables a controlled disruption of the normal walking pattern and produces asymmetrical walking. Therefore, the effects of short-term pattern disruption together with carry-over effects/retention of newly learned patterns can be investigated. This may provide insight into the control of normal movement, but also the ability to change walking patterns, which may have implications to the return of symmetrical gait in patient populations.

The work by Malone et al. (2011) addresses how different training strategies affect day-to-day learning and retention of the adapted walking pattern following split-belt training. The main parameter used to evaluate relearning between consecutive days was step symmetry, defined as the difference between the step length of the fast leg and slow leg, normalized to the combined step length (i.e., fast leg + slow leg). Step symmetry can be altered by adjustments in temporal and/or spatial coordination (Malone and Bastian 2010). Phasing (used to assess temporal coordination) was defined as the time lag of peak correlation between the time series of limb angles for each leg. Center of oscillation difference (used to assess spatial coordination) was defined as the difference between the midpoints of the angle between the ankle to hip vector in the sagittal plane between heel strike and toe off. Variations in these parameters were evaluated on the first stride, an average of strides 2–30 (defined as the early changes) and on the last 30 strides (defined as the final plateau).

For the first experiment during the split-belt condition, the belt of the dominant leg moved at 0.7 m/s, and the belt of the non-dominant leg moved at 1.4 m/s. Prior to the experiment, on the first day, all subjects were exposed to 1 min of tied-belt walking (i.e., treadmill belts moving at the same speed), 10 s of split-belt walking, and a further 1 min of tied-belt walking. The 10-s split-belt exposure was to allow the subject to experience the new (split-belt) walking paradigm thereby reducing the first step variability during testing. The final 30 s of the second pre-experimental tied belt condition was used as the baseline to compare the experimental parameters on the first day. As the mean baseline values were used as the reference for the parameters, the variables of interest were subtracted to attain the day 1 “asymmetry values.”

Groups of subjects participated in the following training paradigms: No Washout, No Switch, Switch, and Switch Control. The No Washout and No Switch groups were given 15 min of split-belt treadmill training. The Switch group alternated between three cycles of split-belt walking and two cycles of tied-belt walking (each lasting 5 min). The Switch control group alternated between three cycles of split-belt walking and two cycles of sitting (each lasting 5 min). Twenty-four hours following the first session, the No Washout group walked only on split-belts for 15 min, whereas the other groups performed 15 min of tied-belt walking before again being exposed to the split-belt condition. The tied-belt walking period on the second day was used as the baseline for comparing the parameters on the second day. In the No Washout group, as no tied-belt was recorded on the second day, the baseline of the first day was used to compare parameters on the second day.

While no significant differences in adaptation following split-belt training were observed between groups on the first day, on the second day, during the early changes, both the No Washout and Switch groups regained the step symmetry more quickly than the other groups. Similar results were obtained for the center of oscillation difference. Moreover, the phasing was relearned significantly more quickly in the No Washout group. The first stride and the final plateau showed no significant
differences between groups for any of the measured parameters. Thus, the findings from experiment 1 were that relearning on the second day was faster when the adapted pattern was not washed out between days and when repeatedly switching between learning and delearning on the first day and that the training paradigms only affected the early changes and not the final plateau symmetry.

The purpose of experiment 2 was to investigate if increasing the duration of training or inverting the speed of the split-belt (i.e., non-dominant leg at 0.7 m/s and dominant leg at 1.4 m/s) would change or interfere with the learning effect. No significant differences were observed in any of the parameters between the longer and shorter duration training paradigms or when training with inverted speeds was introduced. Thus, increasing the time of training did not increase the ability to learn on the second day, and inverting the split-belt speeds did not undo the learning effect of the first split-belt condition.

Subjects retained the ability to remember the learned walking pattern as shown by the retention of this pattern from the first step. Although this is a promising finding, as it demonstrates immediate retention, no differences were observed between groups (also for strides 2–5). A possible reason for the lack of differences between groups and the large variability could be the nature of the perturbation. The phase in the gait cycle when the belts changed speed may vary between subjects that may produce a different perturbation and thus different reactions/retention. If the perturbation was normalized between subjects, differences between the groups may have been observed.

The No Washout group showed the fastest relearning on the second day. A possible reason for this was that the parameters recorded on day 2 were normalized to the baseline recorded on day 1, while for all the other groups, the parameters were normalized to the baseline recorded on day 2. If the two baselines were significantly different, the measurements of the No Washout group may be affected by the different normalization procedure. Indeed, this may change the relative difference in the parameters compared with the other groups. If the two baselines were not significantly different, the conclusion stated by the authors, that faster relearning was more effective with this type of training, would be upheld.

It should be noted that the No Washout group had no washout of the effects even though there was 24 h between testing sessions (and during that time the subjects walked overground). Therefore, the relearning effect may only be specific to treadmill walking and may not transfer to normal overground walking. This could indicate that the findings have limited applications to the regaining locomotor function during, for example, patient rehabilitation. Despite this, Reisman et al. (2009) demonstrated that healthy subjects and stroke patients differed in their ability to transfer the effects (step length and double support time) of split-belt treadmill walking to overground walking. Healthy subjects demonstrated less marked short-term post-split-belt carry-over effects than stroke patients. This indicates that the results of the current study may have greater implications and carry-over effects to overground walking in stroke patients, and possibly other patient populations. However, carry-over effects may not necessarily lead to an increase in movement function. In spinal cord-injured patients, Houldin et al. (2011) demonstrated that following the removal of an artificially produced resistance to the legs during walking, patients with larger adaptations (greater hip extension) had lower locomotor function. Additionally, the type of adaptation differed between patients (increased stride length and healthy controls [increased hip flexion (higher step)] regardless of the locomotor function. Also, the capacity to generate anticipatory locomotor commands was not related with the recovery of overground locomotor function. Therefore, Houldin et al. (2011) concluded that the better locomotor function was weakly correlated with the size of aftereffect. Furthermore, the study also showed that adaptation from similar training protocols may lead to different aftereffects in patients and healthy subjects and that an ability to produce anticipatory locomotor commands may not increase walking ability. These findings may reduce the implications and the transferability of the findings from Malone et al. (2011) to patient rehabilitation.

Malone et al. (2011) emphasized the role of the cerebellum in the adaptation and retention of changes observed following the split-belt paradigms. A number of studies have proposed the importance of cerebellar structures for adaptation and relearning (see Malone et al. 2011 for reference). Additionally, studies have demonstrated the importance of proprioceptive feedback from spinocerebellar pathways to the adaptation and retention of movement patterns (Arshavsky et al. 1972; Bosco et al. 2006; suggested by Houldin et al. 2011). Furthermore, Reisman et al. (2007) suggested that cerebellar networks are important for the regaining of walking symmetry and the relearning of interlimb networks in stroke patients following split-belt training. These findings are supported by research in the cat whereby the removal of the contribution of the cerebellum (through manipulation of nitric oxide concentrations) interferes with motor adaptation (Yanagihara and Kondo 1996). These studies demonstrate that the integration of information through the cerebellum is a strong candidate for motor relearning and adaptation during split-belt locomotion. Despite this, the possible role of other areas should not be ignored. Malone et al. (2011) suggested that cortical areas (and interactions between the cortex and cerebellum) may contribute to the changes in control following split-belt training. Studies investigating stroke patients suggest cortical areas are important for motor adaptation that requires task anticipation (Patton et al. 2006; Takahashi and Reinkensmeyer 2003). Furthermore, Bonnard et al. (2002) observed that motor-evoked potentials in the rectus femoris were larger during constrained walking compared with unconstrained walking, suggesting the involvement of corticospinal pathways in adaptive walking tasks. Additionally, the cortex is also involved in integrating longer latency sensory feedback to the tibialis anterior from the superficial peroneal nerve/sural nerve (Nielsen et al. 1997) and the long latency reflex response following a dorsiflexion stretch to the tibialis anterior (Christensen et al. 2000, 2001). It has been suggested that these transcortical pathways may be required to ensure the stability of the supporting leg during gait (Christensen et al. 2000, 2001; Zehr and Stein 1999). Therefore, the control of adaptations and relearning following split-belt training may be a result of such transcortical pathways.

Although it is likely that the cerebellum and the cerebrum (as stated by Malone et al. 2011) are the source of the adaptive changes, it is possible that other supraspinal areas have a role in adaptation and the relearning of interlimb networks. The reticular formation has a number of inputs from the mesen-
cephalic locomotor region, cerebellum, ipsilateral/contralateral pyramidal tract, and the ipsilateral/contralateral red nucleus and ascending tract neurons (Jankowska 2008; also see Stecina et al. 2008). Due to the large number of inputs (including the cerebellum), this region maybe a more likely source of temporal changes following a perturbation. In the cat, these have a large role in controlling hindlimb spinal commissural interneurons, intralimb and interlimb coordination (Jankowska 2008). Although this may differ in the human, some of this control maybe similar.

The work of Malone et al. (2011) did not comment on the possible role of spinal pathways and CPGs in the adaptation and relearning of split-belt locomotion. Anticipatory motor commands in response to perturbations can be produced without the involvement of cortical areas (Hodgson et al. 1994; Lou and Bloedel 1988; Patton et al. 2006), and spinalized or decerebrate animal preparations show aftereffects following sustained perturbations (Hodgson et al. 1994; Lou and Bloedel 1988). Asymmetric stepping movements can also be induced in the spinal cat (Grillner 1981), and recovery of stepping can be facilitated by daily training sessions (Belanger et al. 1996). Bouyer et al. (2001) observed recovery of movement following neuromectomy of two different limb nerves in chronic spinal cat and suggested that spinal cord must be considered capable of adaptive locomotor plasticity following motor nerve lesions. It was suggested that adaptive plasticity could occur from the reactivation of spinal networks without the influence of supraspinal areas. In the spinal man, although training effects have been observed in the locomotor pattern (Dietz et al. 1994, 1995) (supporting the argument of plasticity in spinal CPGs), completely spinalized human populations have not demonstrated independent walking and have rarely shown rhythmic pattering following peripheral stimulation (see Bussel et al. 1988, 1989 for instances of rhythmical movement). Therefore, although spinal mediated reflex pathways could influence the muscle activity and subsequent body/joint positions of limbs of the same and opposite sides of the body, it is unlikely that this will be the complete source of the changes in limb coordination. For this reason, it likely that the changes in coordination observed in Malone et al. (2011) involve supraspinal areas, spinal CPGs, and spinal reflex pathways.

In conclusion, the work of Malone et al. (2011) provides insight into control, learning, and relearning following split-belt locomotion. The findings of this study are promising and could provide a greater understanding of the control of locomotion. Despite this, as acknowledged by the authors, more work needs to be conducted to understand the full implications of the findings.

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AUTHOR CONTRIBUTIONS

Author contributions: P.W.S. and S.G. conception and design of research; P.W.S. and S.G. interpreted results of experiments; P.W.S. and S.G. drafted manuscript; P.W.S. and S.G. edited and revised manuscript; P.W.S. and S.G. approved final version of manuscript.

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