

University of Groningen

## Adaptive control of dynamic balance in human walking

Buurke, T. J. W.

DOI:  
[10.33612/diss.108473590](https://doi.org/10.33612/diss.108473590)

**IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.**

*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2020

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Buurke, T. J. W. (2020). *Adaptive control of dynamic balance in human walking*. [Thesis fully internal (DIV), University of Groningen]. University of Groningen. <https://doi.org/10.33612/diss.108473590>

### Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

### Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

*Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.*

# 5

## **HANDRAIL HOLDING DURING TREADMILL WALKING REDUCES LOCOMOTOR LEARNING IN ABLE- BODIED PERSONS**

Tom J.W. Buurke, Claudine J.C. Lamoth, Lucas H.V. van der Woude, Rob den Otter

IEEE Transactions on Neural Systems and Rehabilitation  
Engineering. (2019) 27(9): 1753-1759

**ABSTRACT**

Treadmills used for gait training in clinical rehabilitation and experimental settings are commonly fitted with handrails to assist or support persons in locomotor tasks. However, the effects of balance support through handrail holding on locomotor learning are unknown. Locomotor learning can be studied on split-belt treadmills, where participants walk on two parallel belts with asymmetric left and right belt speeds, to which they adapt their stepping pattern within a few minutes. The aim of this study was to determine how handrail holding affects the walking pattern during split-belt adaptation and after-effects in able-bodied persons. Fifty healthy young participants in five experimental groups were instructed to hold handrails, swing arms freely throughout the experiment or hold handrails during adaptation and swing arms freely during after-effects. Step length asymmetry and double support asymmetry were measured to assess the spatiotemporal walking pattern. The results showed that holding handrails during split-belt adaptation reduces magnitude of initial perturbation of step length asymmetry and reduces after-effects in step length asymmetry upon return to symmetric belt speeds. The findings of this study imply that balance support during gait training reduces locomotor learning, which should be considered in daily clinical gait practice and future research on locomotor learning.

## INTRODUCTION

Relearning to walk is an important aspect of rehabilitation after traumatic injury, as it increases a person's mobility and functioning, and thereby quality of life [1]. Locomotor learning, i.e. (re-)learning a gait task, is often done on a treadmill, allowing for longer walking sessions with more step repetitions. The addition of handrails to a treadmill allow a person to walk more safely but without the need of a walking aid or a therapist's physical support. Consequently, holding handrails enables people to start locomotor rehabilitation early, and facilitates treadmill walking for people with impaired gait function [2]. In treadmill walking post-stroke, handrail holding reduces step width and lower leg muscle co-activation, while it increases step lengths [3]. This suggests that balance support immediately enhances walking performance. However, research indicates that provision of external support or guidance in a motor learning task may ultimately reduce motor learning [4,5]. For instance, in a beam-walking experiment with a physically guided and an unguided group, the unguided group showed greater improvements than the group that received physical guidance [5]. Similarly, when behavioral performance during the learning of a visuomotor rotation task is optimized by providing full haptic guidance, the resultant learning is substantially smaller than during unguided learning [4]. This indicates that external support may decrease locomotor learning. However, the effects of balance support through handrail holding on learning a locomotor task are currently unknown [6].

A suitable paradigm to study locomotor learning in a controlled environment is split-belt treadmill walking [7,8]. During split-belt walking people are exposed to asymmetric left and right belt speeds, by which they are initially perturbed, and in response to which they adapt their step lengths, double support times [8] and balance control [9,10]. After approximately ten minutes of split-belt walking, the perturbation is removed by setting the belts at symmetric belt speeds. In this washout phase, after-effects in stepping parameters are observed in the opposite direction of the adaptations of stepping parameters that were observed in the initial split-belt phase [8]. These after-effects are considered indicative of locomotor learning [11]. Previous research has shown that split-belt walking may enforce changes in balance control [9,10,12,13]. Holding on to handrails stabilizes the body, as it increases the base of support, allows the generation of corrective forces [14], and increases somatosensory input through touch of the handrails [15]. Arguably, in split-belt walking side-mounted handrails can provide balance support by allowing the participant to slightly lift him/herself of the treadmill by pushing on the handrails with both arms, whereas front-mounted handrails may stabilize the participant by pushing and pulling the handrails to alter braking forces [16] and reduce fore-aft angular momentum [17]. This makes it easier to control dynamic balance, thereby reducing the perturbation effect of split-belt walking. By assessing how handrail holding affects split-belt adaptation and after-effects, we can empirically test if and how the imposed balance support affects locomotor learning.

The aim of this study is to determine how handrail holding affects locomotor learning during split-belt adaptation and after-effects in able-bodied persons. To appreciate the variety of

handrails used in different gait laboratories and clinics, we assess one group holding handrails on the lateral sides of the treadmill, and one group holding handrails mounted on the front of the treadmill. To control for the possibility that differences between handrail holding and unsupported walking are due to a lack of arm swing rather than balance support, we assess an extra group in which arm swing is restrained. We hypothesize that holding on to handrails will reduce the perturbation of gait symmetry in early split-belt walking. In addition, we hypothesize that handrail holding will reduce locomotor learning, as visible by reduced after-effects in gait symmetry upon return to tied-belt walking (washout phase) [11]. To control for the possibility that the hypothesized lack of after-effects in the groups that hold on to handrails is due to balance support in the washout phase rather than reduced locomotor learning, we assess a fifth group. This group will hold handrails during split-belt adaptation, but not during the washout phase. We hypothesize that this group will also show reduced after-effects in gait symmetry during the washout phase.

## METHODS

### Participants and ethics statement

Fifty healthy young adults participated in this study and were assigned to five height-matched groups (to reduce confounding effects of leg length or body height [18]), which differed in the type of handrail support or no support. The participant characteristics are shown in Table 1. Participants were excluded from the study if they had prior experience with split-belt walking, or if they had any known impairments that may affect gait. The procedures of this study were approved by the ethics committee of the Center for Human Movement Sciences, University Medical Center Groningen, the Netherlands (ECB/2018.01.15\_1), and were in line with the Declaration of Helsinki [19]. Participants gave written informed consent prior to the experiment.

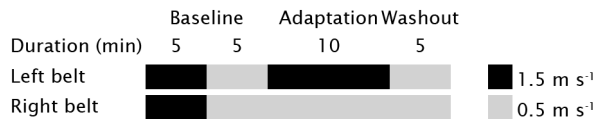
**Table 1 – Participant characteristics.**

Group	N (males)	Age (years)	Height (m)	Weight (kg)
Side	10 (5)	21.7 ± 1.7	1.80 ± 0.11	69.8 ± 11.8
Front	10 (5)	22.4 ± 2.0	1.82 ± 0.10	72.3 ± 13.9
Control	10 (5)	21.8 ± 1.7	1.79 ± 0.08	65.2 ± 10.5
Restrained arms	10 (5)	23.6 ± 2.8	1.82 ± 0.13	73.6 ± 13.6
Switch	10 (5)	22.3 ± 1.3	1.80 ± 0.06	70.5 ± 08.8

### Experimental protocol

Participants were assigned to five different groups and instructed to: Move their arms freely (Control group); Hold handrails mounted on the lateral sides of the treadmill (Side group); Hold handrails mounted on the front of the treadmill (Front group); Cross their arms across the chest (Restrained arms group); Hold handrails mounted on the lateral sides of the treadmill during

baseline and split-belt adaptation, and move their arms freely during washout (Switch group). In the Switch group, the experimenter counted down from five during the last five seconds of the adaptation phase, after which participants had to let go of the handrails, exactly on the transition from split-belt to tied-belt walking.



**Figure 1** – Split-belt treadmill protocol. The upper bar shows left belt speed, the lower bar shows right belt speed. Phase name and duration are shown above the bars. All groups walked the same treadmill protocol.

All groups completed the same treadmill walking protocol (Figure 1). Participants walked five minutes fast tied-belt baseline ( $1.5 \text{ m s}^{-1}$ ), five minutes slow tied-belt baseline ( $0.5 \text{ m s}^{-1}$ ), ten minutes split-belt adaptation ( $1.5 : 0.5 \text{ m s}^{-1}$ ), and five minutes slow tied-belt washout ( $0.5 \text{ m s}^{-1}$ ) [8,20,21]. Participants were instructed to look straight ahead and were not informed about the duration of phases or changes in belt speed. Participants' gazing behavior was monitored during the experiment and corrected if necessary. For safety, participants wore a harness that was attached to the ceiling; however, this did not provide body weight support or restrain movement.

### Data acquisition

Participants walked on an instrumented split-belt treadmill (Motek, Amsterdam, NL). Embedded force plates measured 3D ground reaction forces (N) and 2D Center of Pressure (CoP) positions (m). Data were recorded with D-Flow software (Motek, Amsterdam, NL) at 1000 Hz and saved on an encrypted drive for off-line analysis.

### Data analysis

All analyses were performed in MATLAB (version r2018b, The MathWorks Inc., Natick, MA, USA). Ground reaction forces and CoP data were filtered with a 15-hz 2<sup>nd</sup> order Butterworth filter. Gait events were defined as the point at which the vertical ground reaction force crossed a threshold of 50 N. Step length (m) was defined as the difference in fore-aft CoP position at heel-strike. Double support time (s) was defined as the period between ipsilateral heel-strike and contralateral toe-off. To assess spatiotemporal gait symmetry, Step Length Asymmetry (SLA) and Double Support Asymmetry (DSA) were calculated using Equations 1 and 2 [8].

$$SLA(i) = \frac{Step\ length_{left}(i) - Step\ length_{right}(i)}{Step\ length_{left}(i) + Step\ length_{right}(i)} \quad (1)$$

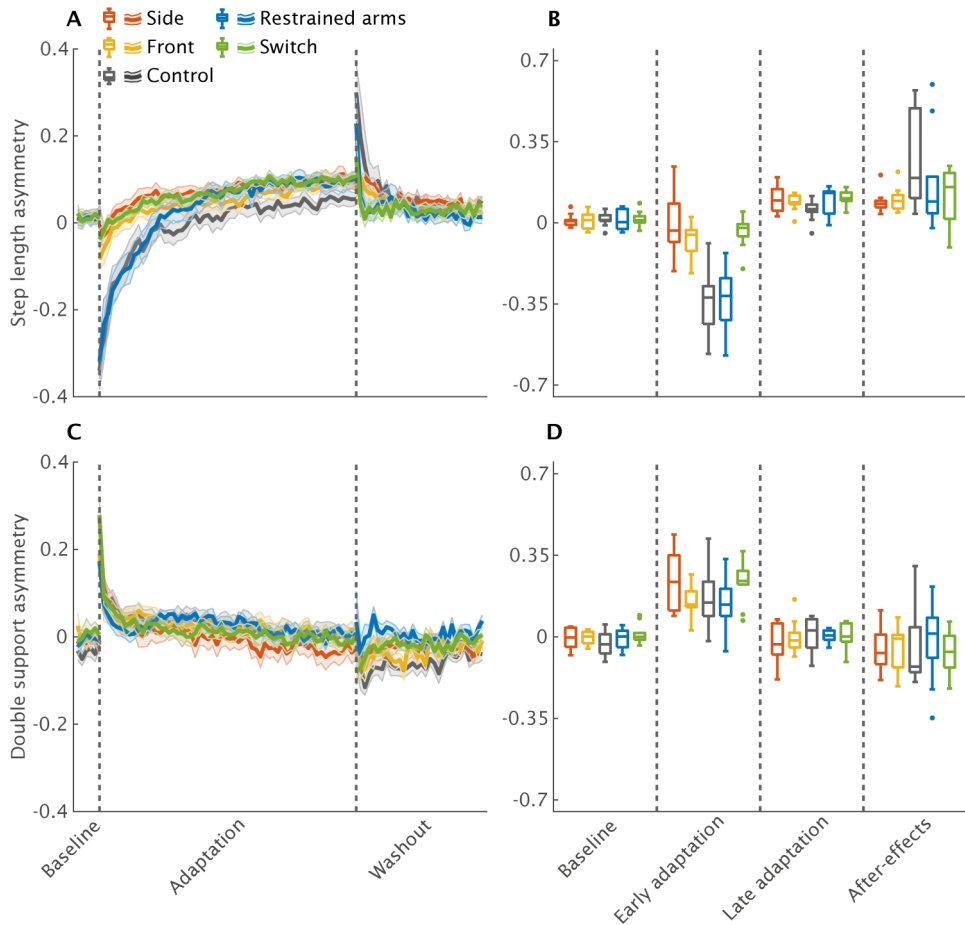
$$DSA(i) = \frac{Double\ support\ first(i) - Double\ support\ second(i)}{Double\ support\ first(i) + Double\ support\ second(i)} \quad (2)$$

### Statistical analysis

Statistical analysis was performed in IBM SPSS Statistics for Windows (Version 24, 64-bit edition, IBM Corporation, Armonk, NY, USA). Statistical significance was set at an alpha of 5 %. Step length asymmetry and double support asymmetry were averaged over the last 10 steps of baseline, first 10 steps of adaptation (early adaptation), last 10 steps of adaptation (late adaptation) and first 10 steps of washout (after-effects). The individual average baseline value was subtracted from early adaptation, late adaptation and after-effects for each participant for statistical analysis to control for baseline differences, from here on indicated as  $\Delta$ . A MANOVA with two dependent variables (baseline step length asymmetry and baseline double support asymmetry), and between-subjects factor Group (Control, Side, Front, Restrained arms, Switch) was conducted to test whether the five groups differed from one another during baseline walking. To examine whether the Side, Front, Restrained arms and Switch groups differed from the Control group during early adaptation, late adaptation and after-effects, we performed a MANOVA. The MANOVA had two dependent variables 1) step length asymmetry and 2) double support asymmetry, in three phases relative to baseline ( $\Delta$ ) 1)  $\Delta$  early adaptation, 2)  $\Delta$  late adaptation and 3)  $\Delta$  after-effects, resulting in six variables for statistical testing (two variables in three relative phases). The between-subjects factor Group had five levels: Control, Side, Front, Restrained arms and Switch. If multivariate results were significant, one-sided Dunnett's tests were assessed to compare each of the six dependent variables of the Side, Front, Restrained arms and Switch group to the Control group.

## RESULTS

No significant main effect of Group on baseline step length asymmetry and baseline double support asymmetry was found ( $F(8,90) = 0.584, p = 0.788, \eta^2 = 0.049$ ). A significant main effect of Group on step length asymmetry and double support asymmetry in  $\Delta$  early adaptation,  $\Delta$  late adaptation and  $\Delta$  after-effects was found ( $F(24, 172) = 2.249, p = 0.001, \eta^2 = 0.239$ ), therefore Dunnett's test were assessed (Table 2). Group averaged time-series and boxplots are shown in Figure 2, individual data of Figure 2 panels B and D are shown in supplementary files.



**Figure 2** – Group averaged step length asymmetry (A,B) and double support asymmetry (C,D) for the Side (N = 10), Front (N = 10), Control (N = 10), Restrained arms (N = 10) and Switch (N = 10) Groups. **A, C**) Group averaged time-series for the baseline phase (final minute), adaptation phase (10 minutes) and washout phase (5 minutes). Dotted vertical lines indicate transition from one phase to the next. Shaded areas indicate standard error. **B, D**) Boxplots of the 10 step bins that were used for statistical analysis. Individual data points of panels B and D are shown in supplementary files.

**Table 2** – Dunnett’s tests results of step length asymmetry and double support asymmetry of all phases relative to baseline ( $\Delta$ ), for all groups compared to the Control group.

Group	Step length asymmetry			Double support asymmetry		
	$\Delta$ Early adaptation	$\Delta$ Late adaptation	$\Delta$ After-effects	$\Delta$ Early adaptation	$\Delta$ Late adaptation	$\Delta$ After-effects
Side	$p < 0.001$	$p = 0.058$	$p = 0.011$	$p = 0.231$	$p = 0.984$	$p = 0.740$
Front	$p < 0.001$	$p = 0.132$	$p = 0.020$	$p = 0.911$	$p = 0.908$	$p = 0.714$
Restrained arms	$p = 0.723$	$p = 0.061$	$p = 0.195$	$p = 0.934$	$p = 0.879$	$p = 0.889$
Switch	$p < 0.001$	$p = 0.073$	$p = 0.026$	$p = 0.418$	$p = 0.957$	$p = 0.442$



### **The effects of handrail holding on perturbation magnitude during early split-belt adaptation**

First, we assessed whether handrail holding affects the perturbation magnitude of gait symmetry during early split-belt adaptation. To this end, we tested whether step length asymmetry and double support asymmetry during  $\Delta$  early adaptation in the Side, Front, Restrained arm and Switch groups differed from the Control group. The results (Figure 2 and Table 2) show a significantly smaller step length asymmetry in  $\Delta$  early adaptation in the Side ( $p < 0.001$ ), Front ( $p < 0.001$ ) and Switch ( $p < 0.001$ ) groups, but not in the Restrained arms compared to Control group ( $p = 0.723$ ). No differences were found in double support asymmetry for the Side ( $p = 0.231$ ), Front ( $p = 0.911$ ), Restrained arms ( $p = 0.934$ ) and Switch ( $p = 0.418$ ) groups compared to the Control group. These results indicate that handrail holding significantly decreases the perturbation magnitude of step length asymmetry, but not double support asymmetry during early adaptation.

### **The effects of handrail holding during late split-belt adaptation**

Second, we assessed whether handrail holding affects the level of gait symmetry during late split-belt adaptation. Therefore, we tested whether step length asymmetry and double support asymmetry in  $\Delta$  late adaptation for the Side, Front, Restrained arms and Switch groups differed from the Control group. The results (Figure 2 and Table 2) show no significant difference in step length asymmetry in  $\Delta$  late adaptation in the Side ( $p = 0.058$ ), Front ( $p = 0.132$ ), Restrained arms ( $p = 0.061$ ) and Switch ( $p = 0.073$ ) groups compared to the Control group. No significant differences were found in double support asymmetry for the Side ( $p = 0.984$ ), Front ( $p = 0.908$ ), Restrained arms ( $p = 0.879$ ) and Switch ( $p = 0.957$ ) groups compared to the Control group. This indicates that holding handrails does not affect spatiotemporal gait symmetry during late split-belt adaptation.

### **The effects of handrail holding on after-effects during washout**

Finally, we assessed whether handrail holding reduces locomotor learning. Therefore, we tested whether the magnitude of  $\Delta$  after-effects in step length asymmetry and double support asymmetry in the Side, Front, Restrained arms and Switch groups differed from the Control group. The results (Figure 2 and Table 2) show significantly smaller after-effects in step length asymmetry for the Side ( $p = 0.011$ ), Front ( $p = 0.020$ ) and Switch ( $p = 0.026$ ) groups, but not the Restrained arms group ( $p = 0.195$ ) compared to the Control group. No differences were found in double support asymmetry for the Side ( $p = 0.740$ ), Front ( $p = 0.714$ ), Restrained arms ( $p = 0.889$ ) and Switch ( $p = 0.442$ ) groups compared to the Control group. This indicates that handrail holding decreases after-effects in step length asymmetry, which indicates that handrail holding reduces locomotor learning.

## DISCUSSION

In both clinical and experimental settings, treadmills are often equipped with handrails to support a person during gait training. However, the effects of handrail holding on locomotor learning are unknown. Here, we determined how handrail holding affects split-belt adaptation and after-effects in able-bodied persons. Although the groups in this study had a small sample-size ( $N = 10$ ), the results unambiguously show that holding handrails during split-belt adaptation reduces the perturbation magnitude of spatial, but not temporal gait symmetry. Furthermore, upon return to tied-belt walking, i.e. during washout, no after-effects in spatial gait symmetry were observed in the groups that held on to handrails. These results were not due to a lack of arm swing, or balance support in the washout phase. This indicates that balance support simplifies the task of split-belt adaptation, as seen in early adaptation, and thereby reduces locomotor learning, as seen by the lack of after-effects in washout.

### Balance support reduces locomotor learning

Motor learning occurs when long-lasting adjustments in movement control are made in response to discrepancies between intended and actual task performance [22,23]. During split-belt walking, a control problem emerges because of an inefficient, asymmetric gait pattern [9,20]. This study shows that altered balance demands are an important aspect of this control problem, as the asymmetry that is typically seen in early split-belt adaptation [8,9,20] was reduced when participants were externally supported. Arguably, external support altered the task demands or simplified the task of split-belt walking, as seen by the reduced perturbation magnitude during early split-belt walking in the supported groups. In addition, continuous exposure to split-belt walking resulted in a marginal change in step length asymmetry over time in supported groups compared to the Control and Restrained Arms groups, although this could also be due to the reduced initial perturbation in the supported groups. This indicates that the amount of adaptation was reduced in the supported groups. The consequences for locomotor learning became clear upon return to tied-belt walking, when the magnitude of after-effects in the supported groups was substantially lower than in the Control group. These findings are in line with previous work on upper extremity motor learning, where the authors showed that assistance through haptic guidance in a visuomotor task directly enhanced performance, and reduced visuomotor adaptation [4]. In the current study, this suggests that groups with the largest control problem during early adaptation, i.e. the Control and Restrained arms groups, also show the largest changes in locomotor control, which enhances locomotor learning [11].

### Implications for split-belt adaptation studies

The split-belt adaptation paradigm has inspired many locomotor learning and adaptation studies, with multiple studies using different set-ups [7-9,20,21,24-34]. For a better

understanding of locomotor control and learning, we need to be able to compare and interpret results from different studies, and therefore research methodologies. The current study shows that handrail holding reduces the adaptation and after-effects of step length asymmetry in split-belt walking. For a good assessment of split-belt adaptation, handrail holding should be avoided or restricted throughout the experiment, provided that a participant's balance control is sufficient for unsupported walking. Furthermore, it can be argued that it should always be mentioned whether participants were allowed or instructed to hold on to handrails, and if not, how they held their arms. It should be noted that in the current study all five experimental groups show a positive step length asymmetry in late adaptation, as noted before [35]. Recent work explains this phenomenon by showing that split-belt walking with asymmetric step lengths is more mechanically efficient than symmetric step lengths, as participants learn to take advantage of the asymmetric belt speeds [36]. Finally, holding on to handrails may not only provide external balance support, but also change the kinetics of split-belt walking, i.e. participants may generate different kinetic walking patterns when split-belt walking, which should be taken into account in future work.

### **The role of arm swing in locomotor adaptation**

The reduced perturbation magnitude and lack of after-effects in the stabilized groups were not due to a lack of arm swing in this study, as shown by the Restrained arms group. Research has shown that arm movement is coupled to contralateral leg movement in symmetric and asymmetric human walking [37], and that restraining elbow movements in split-belt walking changes inter-limb temporal coordination [38]. The effect of arm movement on dynamic stability in human gait is the theme of an ongoing discussion [39]. Some authors argue that that arm swing enhances dynamic stability [40], whereas others argue that arm swing is a passive movement that does not affect dynamic stability [41,42]. If arm swing were to enhance dynamic stability in the current study, one would expect the Restrained arms group to show larger step length asymmetries than the Control group during early split-belt adaptation and after-effects. However, the Restrained arms group did not differ from the Control group in any of these phases.

### **Inter-limb temporal gait symmetry is not affected by balance support**

The present results provide clear evidence that external support of dynamic balance selectively affects the spatial, but not the temporal characteristics of stepping on a split-belt treadmill. While double support asymmetry is often reported to reflect inter-limb temporal coordination in split-belt adaptation studies [8,9,24], it appears to be unaffected by the differences in balance support offered in the current study. Given the role of temporal regulation in control of dynamic stability, especially in split-belt walking [9], it is remarkable that a substantial reduction of the balance control problem in split-belt walking does not result in altered adaptation of temporal

stepping parameters. Previously, it was also shown that double support asymmetry is insensitive to repeated split-belt treadmill training in people post-stroke [43]. The possibilities to alter double support asymmetry are limited in bipedal walking, as only ten percent of the gait cycle is spent in double support [44], which could explain previous [43] and current findings.

### **Clinical implications**

This study shows that balance support through handrail holding reduces locomotor learning, which has important implications for clinical gait rehabilitation practice. Maintaining dynamic stability is one of the most important obstacles in functional walking after neurological trauma, and balance assistance is often used to relearn people to walk, e.g. physiotherapists supporting the trunk, body weight support systems, exoskeletons and the use of handrails [3,6]. Walking performance in people post-stroke can be increased by both treadmill training [45], and balance assistance [3,46]. However, while handrail holding enables people to start treadmill training at an earlier point in rehabilitation, clinicians should take into account that this may reduce learning effects once balance control is at a safe enough level for unassisted walking, i.e. in ambulant patients with less severe impairments. Furthermore, a reduction in acute adaptation effects due to external balance support, may lead to reduced retention of the learned gait pattern in rehabilitation practice [22,23]. As an alternative, fall protection systems without body-weight support could be used to guarantee participant safety during gait training, ultimately benefiting the patient.

### **CONCLUSION**

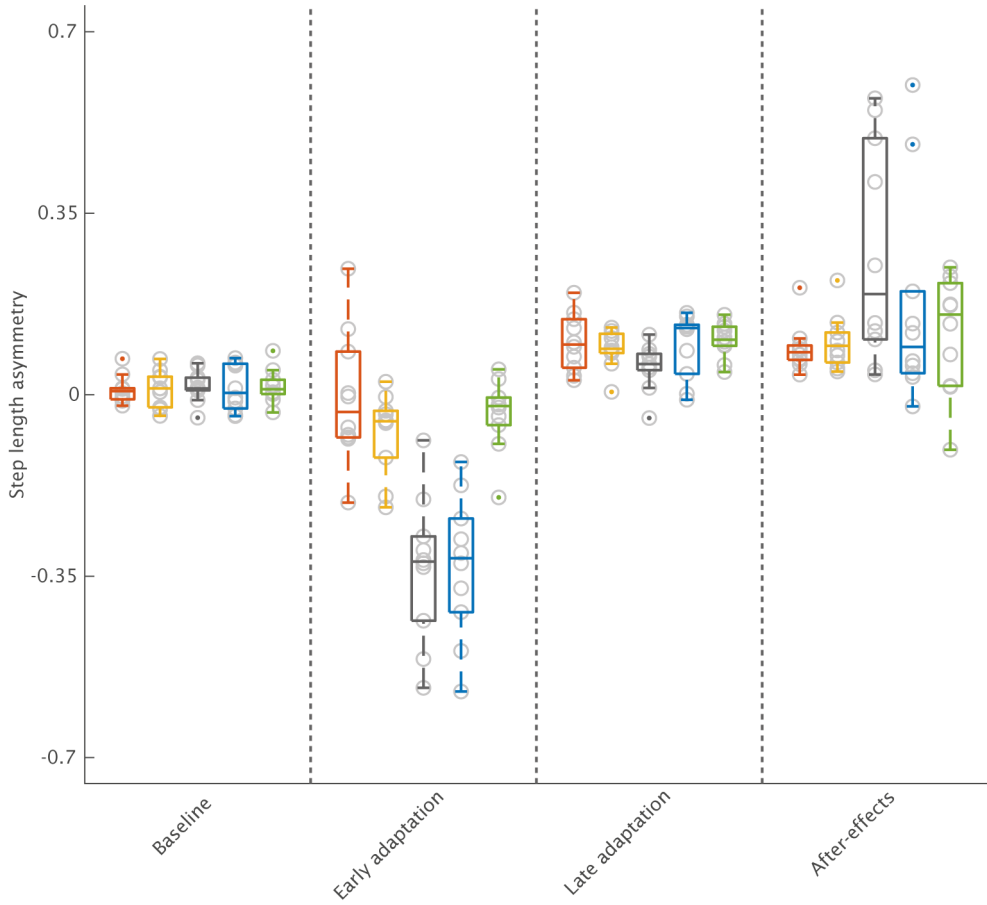
We studied the effects of handrail holding on split-belt adaptation and after-effects in able-bodied persons. The results indicate that balance support reduces locomotor learning. This reduction in locomotor learning may be due to task simplification or altered task demands, as split-belt walking poses a major challenge for balance control, which is no longer present when a person is externally supported by handrails. The findings of this study should be taken into account in future research on locomotor learning and split-belt adaptation, as well as daily clinical gait practice.

## REFERENCES

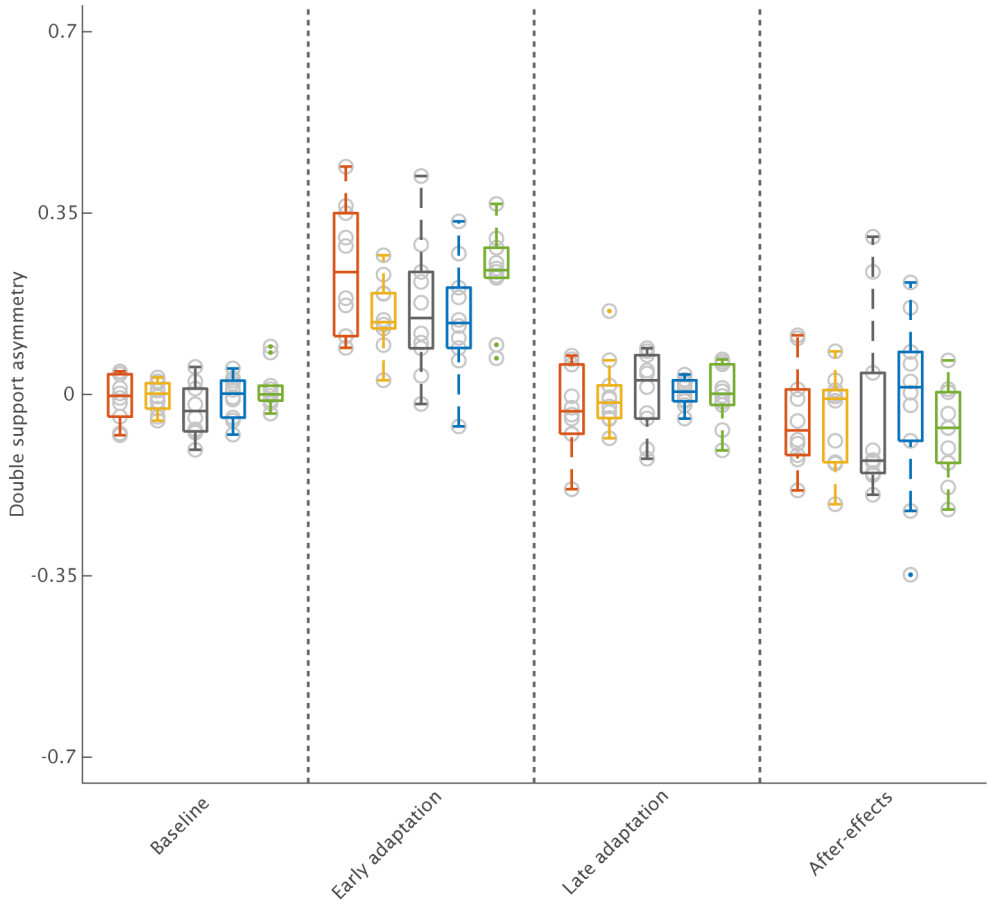
1. Clarke, P. J., Lawrence, J. M. & Black, S. E. (2000) Changes in quality of life over the first year after stroke: Findings from the sunnybrook stroke study. *J Stroke Cerebrovasc Dis.* 9(3), 121-127.
2. Kang, K. W., Lee, N. K., Son, S. M., Kwon, J. W. & Kim, K. (2015) Effect of handrail use while performing treadmill walking on the gait of stroke patients. *J Phys Ther Sci.* 27(3), 833-835.
3. Ijmker, T., Lamoth, C. J. C., Houdijk, H., Tolsma, M., van der Woude, L. H. V., Daffertshofer, A. & Beek, P. J. (2015) Effects of handrail hold and light touch on energetics, step parameters, and neuromuscular activity during walking after stroke. *Journal of NeuroEngineering and Rehabilitation.* 12, 70.
4. van Asseldonk, E. H. F., Wessels, M., Stienen, A. H. A., van der Helm, F. C. T. & van der Kooij, H. (2009) Influence of haptic guidance in learning a novel visuomotor task. *J Physiol Paris.* 103(3), 276-285.
5. Domingo, A. & Ferris, D. P. (2009) Effects of physical guidance on short-term learning of walking on a narrow beam. *Gait Posture.* 30(4), 464-468.
6. Mehrholz, J., Thomas, S. & Elsner, B. (2017) Treadmill training and body weight support for walking after stroke. *Cochrane Database Syst Rev.* 8, CD002840.
7. Dietz, V., Zijlstra, W. & Duysens, J. (1994) Human neuronal interlimb coordination during split-belt locomotion. *Exp Brain Res.* 101(3), 513-520.
8. Reisman, D. S., Block, H. J. & Bastian, A. J. (2005) Interlimb coordination during locomotion: What can be adapted and stored?. *J Neurophysiol.* 94(4), 2403-2415.
9. Buurke, T. J. W., Lamoth, C. J. C., Vervoort, D., van der Woude, L. H. V. & den Otter, R. (2018) Adaptive control of dynamic balance in human gait on a split-belt treadmill. *J Exp Biol.* 221(13), jeb174896.
10. Park, S. & Finley, J. M. (2017) Characterizing dynamic balance during adaptive locomotor learning. *EMBC.*, 50-53.
11. Krakauer, J. W. (2009) Motor learning and consolidation: The case of visuomotor rotation. *Adv Exp Med Biol.* 629, 405-421.
12. Roper, J. A., Roemmich, R. T., Tillman, M. D., Terza, M. J. & Hass, C. J. (2017) Split-belt treadmill walking alters lower extremity frontal plane mechanics. *J Appl Biomech.* 33(4), 256-260.
13. Sawers, A., Kelly, V. E., Kartin, D. & Hahn, M. E. (2013) Gradual training reduces the challenge to lateral balance control during practice and subsequent performance of a novel locomotor task. *Gait Posture.* 38(4), 907-911.
14. Bateni, H. & Maki, B. E. (2005) Assistive devices for balance and mobility: Benefits, demands, and adverse consequences. *Arch Phys Med Rehabil.* 86(1), 134-145.
15. Jeka, J. J. & Lackner, J. R. (1994) Fingertip contact influences human postural control. *Exp Brain Res.* 100(3), 495-502.
16. Ogawa, T., Kawashima, N., Ogata, T. & Nakazawa, K. (2012) Limited transfer of newly acquired movement patterns across walking and running in humans. *PLOS ONE.* 7(9), e46349.
17. Nott, C. R., Neptune, R. R. & Kautz, S. A. (2014) Relationships between frontal-plane angular momentum and clinical balance measures during post-stroke hemiparetic walking. *Gait Posture.* 39(1), 129-134.
18. Hof, A. L. (1996) Scaling gait data to body size. *Gait Posture.* 4(3), 222-223.
19. World Medical Association. (2013) World medical association declaration of helsinki: Ethical principles for medical research involving human subjects. *JAMA.* 310(20), 2191-2194.
20. Finley, J. M., Bastian, A. J. & Gottschall, J. S. (2013) Learning to be economical: The energy cost of walking tracks motor adaptation. *J Physiol (Lond).* 591(4), 1081-1095.
21. Malone, L. A. & Bastian, A. J. (2010) Thinking about walking: Effects of conscious correction versus distraction on locomotor adaptation. *J Neurophysiol.* 103(4), 1954-1962.
22. Shadmehr, R., Smith, M. A. & Krakauer, J. W. (2010) Error correction, sensory prediction, and adaptation in motor control. *Annu Rev Neurosci.* 33(1), 89-108.
23. Krakauer, J. W., Hadjiosif, A. M., Xu, J., Wong, A. L. & Haith, A. M. (2019) Motor learning. *Compr Physiol.* 9(2), 613-663.
24. Vervoort, D., den Otter, A. R., Buurke, T. J. W., Vuillerme, N., Hortobágyi, T. & Lamoth, C. J. C. (2019) Effects of aging and task prioritization on split-belt gait adaptation. *Front Aging Neurosci.* 11, 10.

25. MacLellan, M. J., Ivanenko, Y. P., Massaad, F., Bruijn, S. M., Duysens, J. & Lacquaniti, F. (2014) Muscle activation patterns are bilaterally linked during split-belt treadmill walking in humans. *J Neurophysiol.* 111(8), 1541-1552.
26. Torres-Oviedo, G., Vasudevan, E., Malone, L. & Bastian, A. J. (2011) Locomotor adaptation. *Prog Brain Res.* 191, 65-74.
27. Selgrade, B. P., Thajchayapong, M., Lee, G. E., Toney, M. E. & Chang, Y. (2017) Changes in mechanical work during neural adaptation to asymmetric locomotion. *J Exp Biol.* 220, 2993-3000.
28. Leech, K. A., Roemmich, R. T. & Bastian, A. J. (2018) Creating flexible motor memories in human walking. *Sci Rep.* 8, 94.
29. Roemmich, R. T., Stegemöller, E. L. & Hass, C. J. (2012) Lower extremity sagittal joint moment production during split-belt treadmill walking. *J Biomech.* 45(16), 2817-2821.
30. Hinkel-Lipsker, J. W. & Hahn, M. E. (2016) Novel kinetic strategies adopted in asymmetric split-belt treadmill walking. *J Mot Behav.* 48(3), 209-217.
31. Roper, J. A., Stegemöller, E. L., Tillman, M. D. & Hass, C. J. (2013) Oxygen consumption, oxygen cost, heart rate, and perceived effort during split-belt treadmill walking in young healthy adults. *Eur J Appl Physiol.* 113(3), 729-734.
32. Bruijn, S. M., Van Impe, A., Duysens, J. & Swinnen, S. P. (2012) Split-belt walking: Adaptation differences between young and older adults. *J Neurophysiol.* 108(4), 1149-1157.
33. Hoogkamer, W., Bruijn, S. M. & Duysens, J. (2014) Stride length asymmetry in split-belt locomotion. *Gait Posture.* 39(1), 652-654.
34. Helm, E. E. & Reisman, D. S. (2015) The split-belt walking paradigm: Exploring motor learning and spatiotemporal asymmetry poststroke. *Phys Med Rehabil Clin N Am.* 26(4), 703-713.
35. Hinkel-Lipsker, J. W. & Hahn, M. E. (2017) Contextual interference during adaptation to asymmetric split-belt treadmill walking results in transfer of unique gait mechanics. *Biology Open.* 6(12), 1919-1932.
36. Sánchez, N., Simha, S. N., Donelan, J. M. & Finley, J. M. (2019) Taking advantage of external mechanical work to reduce metabolic cost: The mechanics and energetics of split-belt treadmill walking. *J Physiol.* 597(15), 4053-4068.
37. MacLellan, M. J., Qaderdan, K., Kohestanie, P., Duysens, J. & McFadyen, B. J. (2013) Arm movements during split-belt walking reveal predominant patterns of interlimb coupling. *Hum Mov Sci.* 32(1), 79-90.
38. Hirata, K., Hanawa, H., Miyazawa, T., Kokubun, T., Kubota, K., Sonoo, M. & Kanemura, N. (2019) Influence of arm joint limitation on interlimb coordination during split-belt treadmill walking. *Adv Biomed Eng.* 8, 130-136.
39. Meyns, P., Bruijn, S. M. & Duysens, J. (2013) The how and why of arm swing during human walking. *Gait Posture.* 38(4), 555-562.
40. Park, J. (2008) Synthesis of natural arm swing motion in human bipedal walking. *J Biomech.* 41(7), 1417-1426.
41. Pontzer, H., Holloway, J. H., Raichlen, D. A. & Lieberman, D. E. (2009) Control and function of arm swing in human walking and running. *J Exp Biol.* 212(4), 523-534.
42. Collins, S. H., Adamczyk, P. G. & Kuo, A. D. (2009) Dynamic arm swinging in human walking. *Proc R Soc B.* 276(1673), 3679-3688.
43. Reisman, D. S., McLean, H., Keller, J., Danks, K. A. & Bastian, A. J. (2013) Repeated split-belt treadmill training improves poststroke step length asymmetry. *Neurorehabil Neural Repair.* 27(5), 460-468.
44. Perry, J. & Burnfield, J. M. (1992) *Gait analysis: Normal and pathological function*, 2nd edn, pp. 576. Thorofare, New Jersey: SLACK Incorporated.
45. Patterson, S. L., Rodgers, M. M., Macko, R. F. & Forrester, L. W. (2008) Effect of treadmill exercise training on spatial and temporal gait parameters in subjects with chronic stroke: A preliminary report. *J Rehabil Res Dev.* 45(2), 221-228.
46. Beauchamp, M. K., Skrela, M., Southmayd, D., Trick, J., van Kessel, M. V., Brunton, K., Inness, E. & Mclroy, W. E. (2009) Immediate effects of cane use on gait symmetry in individuals with subacute stroke. *Physiother Can.* 61(3), 154-160.

### SUPPORTING INFORMATION



**Supplementary Figure S1** - Expanded view of step length asymmetry box plots (Figure 2B) with individual data points.



**Supplementary Figure S2** – Expanded view of double support asymmetry box plots (Figure 2D) with individual data points.



