Split-belt walking: adaptation differences between young and older adults

Sjoerd M. Bruijn¹,², Annouchka Van Impe¹, Jacques Duysens¹,³, Stephan P. Swinnen¹
¹Motor Control Laboratory, Research Center for Movement Control and Neuroplasticity, Dept. of Kinesiology, K.U.Leuven, Belgium
²Department of Orthopedics, First Affiliated Hospital of Fujian Medical University, Fuzhou, Fujian, P.R. China
³Department of Research, Development and Education, Sint Maartenskliniek, Nijmegen, The Netherlands

Corresponding author: Sjoerd M. Bruijn
Motor Control Laboratory
Research Center for Movement Control and Neuroplasticity
Dep. of Biomedical Kinesiology
K.U.Leuven
Tervuurse Vest 101
3001 Leuven
s.m.bruijn@gmail.com

Number of pages: 23
Number of figures: 7
Word count:
Abstract: 220
Introduction: 644
Discussion: 1490

Conflict of interest: none

Acknowledgements

SMB was funded by a visiting postdoctoral fellowship from the FWO (GP.030.10.N).
AVI was funded by a PhD fellowship of the FWO Vlaanderen. JD was supported by a grant from ‘Bijzonder Onderzoeksfonds’ KU-Leuven (OT/08/034). SPS was supported by the Research Fund K.U.Leuven (OT/11/071) and FWO Vlaanderen (G.0483.10; G.0721.12).
Abstract
Human walking is highly adaptable, which allows us to walk under different circumstances. With ageing, the probability of falling increases, which may partially be due to a decreased ability of older adults to adapt the gait pattern to the needs of the environment. Literature on visuomotor adaptations during reaching suggests however that older adults have little problems in adapting their motor behavior. Nevertheless, it may be that adaptation during a more complex task like gait is compromised by ageing. In this study, we investigated the ability of young (n=8) and older adults (n=12) to adapt their gait pattern to novel constraints using a split-belt paradigm. Findings revealed that older adults adapted less and more slowly to split-belt walking, and showed fewer aftereffects than young adults. While young adults showed a fast adjustment of the relative time spent in swing for each leg, older adults failed to do so, but instead they were very fast in manipulating swing speed differences between the two legs. We suggest that these changes in adaptability of gait due to ageing stem from a mild degradation of cortico-cerebellar pathways (reduced adaptability), and cerebral structures (decreased ability to change gait cycle timing). However, an alternative interpretation may be that the observed reduced adaptation is a compensatory strategy in view of the instability induced by the split-belt paradigm.
Introduction

Human walking is highly adaptable, which allows us to walk under different circumstances, such as on different surfaces, with or without backpack, etc. (Choi and Bastian 2007). With ageing however, the probability of falling increases (Rubenstein 2006). Apart from a reduced ability to respond to sudden perturbations (Weerdesteyn et al. 2005a), this could be due to a reduced capability to adapt gait to the needs of the environment (Bierbaum et al. 2010; Bierbaum et al. 2011).

The use of a split-belt treadmill, in which subjects walk with their two legs on two different belts that run at different velocities, has been used in several studies to assess adaptability of gait (Choi and Bastian 2007; Choi et al. 2009; Dietz et al. 1994; Marques et al. 2007; Prokop et al. 1995; Reisman et al. 2005; Reisman et al. 2007; 2009; Yang et al. 2005; Zijlstra and Dietz 1995; Zijlstra et al. 1996). In this paradigm the two belts of the apparatus are set to run at different speeds. Initially, subjects will display a step length asymmetry (see figure 1 A), which typically disappears with exposure to splitbelt walking; subjects become adapted to the new situation (see figure 1B). The fact that after prolonged exposure, subjects show aftereffects (that is, a step length asymmetry in opposite direction, see also figure 1C) suggests that this is truly a process of adaptation, rather than simple feedback. The inability to show an increase of symmetry during splitbelt walking, and the absence of aftereffects after a period of splitbelt walking are considered signs of a reduced ability to adapt the gait pattern.

Recently, this paradigm has been used to assess the adaptability of gait in young children (Musselman et al. 2011; Vasudevan et al. 2011). Findings revealed that younger children are less able to adapt step length symmetry to the altered gait
Split-belt walking and ageing

pattern required by the two belts moving at different speeds, and showed smaller aftereffects in step length symmetry.

Such a reduced ability to adapt step length symmetry during split-belt walking, and decreased aftereffects in step length symmetry following split belt walking were also found for patients with cerebellar ataxia (Morton and Bastian 2006). Moreover, the amount of adaptation (i.e. increase in step length symmetry) to split-belt walking has been shown to be positively correlated with the depression of cerebellar excitability (as determined using Transcranial Magnetic Stimulation, TMS) (Jayaram et al. 2011), highlighting the role of the cerebellum in adapting the gait pattern to split-belt walking. Lastly, a recent study showed that transcranial direct current stimulation (tDCS) of the cerebellum could lead to increased ability to increase step length symmetry during split-belt walking, thereby further strengthening the relationship between adaptability of gait and cerebellar function (Jayaram et al. 2012). These findings have led to the suggestion that the decreased ability to adapt the gait pattern in children might be linked to immaturity of the cortico-cerebellar pathways (Musselman et al. 2011; Vasudevan et al. 2011).

In ageing, there may be a reduction in the structural integrity of these pathways (Hogan 2004), as has been demonstrated for several other white matter pathways (Sullivan et al. 2010; Sullivan et al. 2009; Zahr et al. 2009), which could potentially also lead to degradation in adaptability of the gait pattern. Nonetheless, studies on visuomotor adaptation during reaching show that sensorimotor adaptation is preserved or only moderately degraded in old age (Bock and Schneider 2002; Heuer and Hegele 2008). In contrast, adaptations of gait may be more complex than the above-mentioned visuomotor adaptations in reaching, as the former require a reorganization of the movements of all body segments. Thus, in the current study the
Split-belt walking and ageing

effect of ageing on gait adaptability was tested using the split-belt paradigm. It was hypothesized that older adults would show a reduced adaptability of the gait pattern (i.e. a slower increase in step length symmetry, and smaller step length symmetry aftereffects).

Methods

Subjects

Eight young healthy adults (4 males, age 22.1 ± 3.6 years, mass 68.8 ± 6.5 kg, height 1.77 ± 0.07 m), and 12 healthy older adults (9 males, age 73.1 ± 4.7 years, mass 78.1 ± 14.9 kg, height 1.71 ± 0.09 m) were measured. Apart from gait testing, all subjects performed the Montreal Cognitive Assessment (MOCA), to obtain a measure of general cognitive function. Subjects were required to score at least 26 points. All subjects had normal or corrected to normal vision and were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield 1971). Before measurement, all subjects signed an informed consent form. The protocol was in agreement with the Helsinki convention, and was approved by the local ethical committee of the K.U. Leuven.

Procedure

Before actual measurement started, subjects were first fitted with retro reflective markers on the lateral malleoli for movement registration using an optoelectronic system (Vicon Nexus, Oxford Metrics, Oxford, UK). Throughout all conditions, kinematics were sampled at 100 samples/second. Moreover, in order to accurately assess temporal parameters, 3D ground reaction forces and torques were sampled at
1000 samples/second using the sensors built in the treadmill (Custom built by Forcelink Culemborg, The Netherlands).

Measurements started with overground conditions, in order to assess comfortable walking speed. Subjects were asked to walk a distance of 6 meters at their natural pace (Abellan van Kan et al. 2009). This procedure was repeated 3 times. Next, subjects were allowed to become familiar with the treadmill. After this familiarization procedure, actual conditions started. In short, we performed a classical split-belt paradigm (Choi and Bastian 2007; Morton and Bastian 2006; Reisman et al. 2005); 5 minutes with belts tied (1 m/s, ‘baseline condition’), followed by 10 minutes with split-belts (0.5 m/s and 1.0 m/s ‘adaptation condition’), followed by 5 minutes walking with belts tied (at 1 m/s, ‘aftereffects condition’). In between conditions, the belt was stopped for a maximum of 30 seconds, and during the start of all conditions, the belt had an acceleration of 0.3 m/s². Subjects (especially older adults) were allowed a break between baseline and adaptation conditions, but not between adaptation and aftereffects conditions. The fast belt was randomly assigned to the right or left leg.

Calculations

Gait events (time points at which the feet touched or left the support surface) were detected from the Centre of Pressure trajectories using a previously described algorithm (Roerdink et al. 2008). For sake of clarity, all variables calculated for the leg that was on the fast belt during the adaptation condition, are referred to as “fast leg” parameters, even for the baseline and aftereffects conditions.

Since the main goal of the current study was to assess whether or not older adults are able to adapt their gait pattern, our main outcome measure was step length symmetry, as it has been shown to most clearly display signs of adaptation in split-
Split-belt walking and ageing

152 belt treadmill walking (Choi et al. 2009; Malone and Bastian 2011; Morton and
153 Bastian 2006). First, step lengths were calculated as the anterior posterior distance
154 between the lateral malleolus markers of both legs at heel strike of each leg (Morton
155 and Bastian 2006; Reisman et al. 2005). Fast step length referred to the step length
156 calculated at the heel strike of the fast leg, and slow step length to that calculated at
157 the heel strike of the slow leg (see also figure 1).
158
159 Then, step length symmetry (Choi et al. 2009; Malone and Bastian 2011) could be
160 calculated as:
161
162 Step length symmetry = (fast step length - slow step length)/(fast step length + slow
163 step length).
164
165 Moreover, for sake of completeness, we report stride length, calculated as
166
167 \[ \text{stride length}(i) = x_{\text{latmal}}(t_{\text{heelstrike}}(i)) - x_{\text{latmal}}(t_{\text{toeoff}}(i)) \]
168
169 In which \(x_{\text{latmal}}\) is the x position of lateral malleolus of the leg, \(t_{\text{heelstrike}}\) is the time of
170 heel strike, and \(t_{\text{toeoff}}\) is the time of toe off, and \(i\) is the stride index (i.e. the stride for
171 which the calculation is done).
172
173 It may prove difficult to exactly determine what causes the adaptation
174 processes seen during the adaptation condition, as most variables are highly
175 interlinked. Nonetheless, we aimed at shedding some more light on this process, and
176 started from the idea that the initial asymmetry in step length can be overcome by
177 moving the fast leg more forward with respect to the slow leg. This could be done in
178 two ways. A first way is by increasing the percentage of a gait cycle a given leg
179 spends in swing time (while concurrently decreasing relative stance time) on the fast
180 leg, so that the fast leg swings forward more, or decreasing relative swing time (while
181 concurrently increasing relative stance time) on the slow leg, so that the slow leg
182 moves backward more. A second way is altering swing speed of both legs to attain the
goal of moving one leg in front of the other. Thus, in order to explore how and why
differences in adaptation between the younger and the older adults arose, we
calculated two “underlying variables”.
The first underlying variable was the percentage of the gait cycle each leg spent in
swing, which was calculated as:

\[ \% \text{swing}(i) = \frac{t_{\text{toeoff}(i)} - t_{\text{heelstrike}(i)}}{t_{\text{heelstrike}(i)} - t_{\text{heelstrike}(i-1)}} \times 100 \]

The second underlying variable was the swing speed of the legs, that is, the average
speed with which the legs moved forward during the swing phase. This was calculated
as:

\[ \text{swingspeed}(i) = \frac{\text{Stridelength}(i)}{t_{\text{heelstrike}(i)} - t_{\text{toeoff}(i)}} \]

It should be noted that we chose to report only on normalized step asymmetry and
swing time percentages, rather than on absolute step asymmetry and actual swing
times, as the latter may be greatly influenced by differences in stride lengths and
times that may exists between groups.

**Statistical analysis**

First, time series of all variables were smoothed with a 10-point moving average
window. Next, time series of adaptation and aftereffects conditions were divided into
episodes of 50 strides, and a 2 factor repeated measures ANOVA with Group and
Episode (8 episodes for the adaptation condition, and 4 for the aftereffects condition)
as factors was performed. Whenever the interaction effect was found to be significant
without significant effects of Group, post-hoc t-tests per Episode were performed
along with Bonferroni correction. To further identify whether ageing impairs
adaptations to split-belt walking, we performed correlations between age and step length symmetry at the end of the adaptation condition, and between age and step length symmetry at the onset of the aftereffects condition. These correlations were only performed on the data from the older adults, as the younger adults had very little spread in age. Throughout, $\alpha < 0.05$ was considered as significant.

**Results**

**Overground walking and baseline gait parameters**

During overground walking, older adults were not significantly different from young adults. They walked slightly slower ($P=0.1$, see Figure 2A), than young adults, although they did not exhibit longer stride times ($P=0.8$, see Figure 2B), as would be expected when walking slower. Thus, all decreases in walking speed were caused by the fact that the older adults had somewhat shorter stride lengths ($P=0.09$, see Figure 2C). During treadmill walking in the baseline condition, older adults walked with significantly shorter stride times ($P<0.01$ see Figure 2D), and, as a consequence, with shorter stride lengths (not analysed, but see Figure 3B).

**Adaptation and aftereffects**

Figure 3A shows step length symmetry during the adaptation condition. Statistical testing showed a significant effect of Group ($P<0.05$), Episode ($P<0.01$), and a Group x Episode interaction ($P<0.05$). Initially, there was little difference in step length symmetry between young and older adults, but after about 200 strides, the difference between young and older adults increased, as the older adults did not increase their symmetry anymore beyond this point whereas the young adults did. Thus, older adults seemed to be less able to adapt their gait pattern to split-belt walking. Since not all
subjects walked the same amount of strides, we also compared symmetry at the end of
the adaptation condition with symmetry after 400 strides, using a repeated measures
ANOVA. Results showed that subjects did not further improve symmetry after 400
strides (i.e. Episode $P=0.39$ and Group x Episode $P=0.5$), and that the age groups still
differed markedly in symmetry ($P<0.05$). In conclusion, despite having more
exposure to splitbelt walking (i.e. taking more steps because of shorter stride lengths),
older adults were less able to adapt the gait pattern.

In contrast, the changes in stride length were less different between groups (i.e. no
significant Group x Episode interaction). Both groups were able to quickly adapt
stride lengths (see Figure 3B), and even increased stride lengths during the adaptation
condition (effect of Episode, for both fast and slow leg, $P<0.01$). Similar to the
baseline condition, stride lengths were significantly smaller in older adults (effect of
Group, for both fast and slow leg, $P<0.01$). It should be noted that changes in stride
length are not necessarily related to “adaptation” per se, but are simply needed in
order to be able to walk on split belts.

Aftereffects in symmetry were less pronounced in the older adults (Figure
4A), indicating that the adaptation was stored less prominently (nearly reaching
significance, $P=0.06$). It should be noted that using shorter windows (<10) of
analysis, yielded significant Group x Episode interactions (although no window
length yielded a significant Group effect alone). However, upon post-hoc testing,
differences between groups in none of the episodes survived Bonferronni corrections.

In contrast, similar to the adaptation condition, stride lengths (Figure 4B) were quick
to re-adapt, and even increased somewhat during the aftereffect condition (effect of
Episode, for both fast and slow leg, $P<0.01$). Similar to the baseline condition, older
adults walked with smaller strides than the young adults (effect of Group, for both fast
and slow leg, \( P<0.01 \). We also found a Group x Episode interaction effect (\( P<0.05 \)) for the slow leg, suggesting that the older adults increased stride lengths somewhat slower.

There was no significant correlation between the amount of adaptation and the size of the aftereffect for either of the groups (see Figure 5). However, when taking both groups into account, a significant correlation emerged (\( R=0.48, \ P<0.05 \)) indicating that subjects who were most symmetrical (in step length) at the end of the adaptation period were also most likely to show step asymmetry at onset of after-effect condition. However, it should be noted that when we expressed the adaptation as amount of adaptation (that is, step length symmetry at the end of the adaptation condition minus step length symmetry at the start of the adaptation condition), rather than as symmetry, no significant correlation was found (\( P>0.5 \)), suggesting that the actual symmetry at the end of the adaptation is more important than the amount adapted.

**Correlations with age**

Figure 6A shows the effects of age on step length symmetry at the end of the adaptation condition. As can be seen from this figure, age negatively affected the degree of symmetry reached at the end of the adaptation condition (\( R=-0.68, \ P=0.01 \)). Stated differently, the older the subjects were, the lower their ability to reach symmetry during split-belt walking. It should however be noted that this correlation disappeared when excluding the youngest and the oldest subject from the old group. Nonetheless, variability is needed for correlational analysis, and the two excluded subjects can not be qualified as outliers, as their age was within 2.5 SD from the mean of the population, and thus, we render it valid to include these subjects. For the effects
of age on step length symmetry at the onset of the aftereffects condition, no such
effects could be found (see Figure 6B).

**What defines adaptation speed and amount?**

Figures 7A shows the percentage of time spent in swing phase for both legs. From this figure, it can be seen that the younger adults almost immediately responded to the adaptation condition by shortening relative swing times on the slow leg, and lengthening them on the fast leg. The older adults however, seemed to be lacking this initial response although later on, they did decrease relative swing times on the slow leg. Statistical analyses showed a significant Group x Episode interaction for both legs ($P<0.001$ for both legs), although post-hoc testing showed only a significant difference between young and older adults for the first 50 strides episode of the slow leg. For the fast leg, a significant effect of Episode ($P<0.01$) was also present, most likely caused by the initial increase and later decrease of the younger adults only.

Figure 7B shows the swing speeds of fast and slow legs during the adaptation condition. As can be seen, at the start of the adaptation condition, the young adults exhibited slower swing speeds at their fast, and faster swing speeds at their slow legs than the older adults. Hence, at onset of adaptation, the older adults had a much larger difference in swing speed between the two legs than the young adults. However, after some period, these differences more or less disappeared, which was probably why the younger adults were able to adapt more than the older adults. Statistical analyses showed results similar to those for percentage swing time; a significant Group x Episode effect for both legs ($P<0.01$ for both legs), with post-hoc testing showing only a significant difference between young and older adults for the first 50 strides episode of the slow leg. Again, for the fast leg, a significant effect of Episode
(P<0.01) was present, most likely caused by the initial decrease and later increase in swing speeds of the younger adults only.

**Some remarks on aftereffects**

Although we could clearly identify to what extent young and older adults differed in how they adapted to the adaptation condition, such a clear identification proved more difficult in the aftereffects condition, and no statistically significant effects of Group or Group x Episode were found (all P>0.2). This was most likely due to the large inter-individual differences, and the relatively small aftereffects may have been caused by the fact that we tested at the fast walking speed, which has been shown to induce smaller aftereffects than walking at the slow walking speed (Vasudevan and Bastian 2010).

**Discussion**

We investigated the ability of older adults to adapt their gait pattern to novel constraints using a split-belt paradigm. We found that older adults adapted their gait pattern more slowly, and tended to show less aftereffects than young adults. This reduced ability to adapt the gait pattern was correlated with age for the group of older adults, further suggesting that ageing decreases the ability to adapt the gait pattern to split-belt walking. Furthermore, older adults were less able to change their relative timings of swing within the gait cycle, but instead showed fast changes in swing speed at the onset of the adaptation.
Possible Neural mechanisms of reduced adaptation in older adults

With respect to life span changes in adaptation to split-belt walking, all efforts so far have been directed to the early stages of development. In young children, adaptation of step length symmetry to split-belt walking is also slower, and aftereffects in step length symmetry are less present (Musselman et al. 2011; Vasudevan et al. 2011). Adaptations to split-belt walking have also been shown to be diminished in patients with cerebellar ataxia (Morton and Bastian 2006). Moreover, the amount of adaptation during split-belt walking has been shown to be proportional to the depression of cerebellar excitability (with higher adaptation rates coinciding with higher depression of cerebellar excitability), as determined by means of TMS (Jayaram et al. 2011), and tDCS of the cerebellum has been shown to improve split-belt adaptation (Jayaram et al. 2012). Taken together, these findings have resulted in the suggestion that adaptive learning is mediated by the cerebellum. More specifically, the reduced ability to adapt the gait pattern in younger children is argued to stem from underdeveloped cortico-cerebellar pathways (Musselman et al. 2011; Vasudevan et al. 2011).

Following this line of reasoning, the reduced ability to adapt the gait pattern (in terms of step length) in older adults may equally have arisen from a degradation of cortico-cerebellar pathways (Hogan 2004; Woodruff-Pak et al. 2010). However, there is one interesting difference between the reduced ability to adapt the gait pattern to split-belt walking in young children and cerebellar patients on the one hand, and older adults on the other hand. Similar to our young adults, both cerebellar subjects and young children were less able to adapt the gait pattern in terms of step length, but they showed an immediate increase in stance time on the slow leg, and a decrease in stance time at the fast leg. Conversely, older adults lacked such a response, and did
Split-belt walking and ageing

not change their relative timings within the gait cycle. This was also reported for
children who had previously undergone hemispherectomy (Choi et al. 2009), and
stroke survivors (Reisman et al. 2007), but only when they walked with the paretic leg
on the slow belt. Moreover, similar effects have also been reported for subjects with
Parkinson’s disease (Dietz et al. 1995). These studies appear to suggest that the
reduced ability to alter the relative gait cycle timing is related to cerebral rather than
cerebellar deficits. Unlike older adults however, subjects who had undergone
hemispherectomy (Choi et al. 2009), stroke survivors (Reisman et al. 2007) and
Parkinson’s patients (Dietz et al. 1995) did fully adapt the gait pattern (in terms of
step length, and compared to age matched controls). However, it should be kept in
mind that there is a decline in the integrity of cortico-cerebellar pathways with aging,
as well as a decline in cerebral cortex thickness (Good et al. 2001; Smith et al. 2007),
which in combination, could lead to the reduced ability to adapt step length, which
may partially have been caused by the reduced ability to change the relative timing
within the gait cycle.

Possible biomechanical causes of slowed adaptation in older adults

Although the present study clearly indicates that older adults were less able to adapt
their gait pattern to split-belt walking, one has to consider that a full adaptation of step
lengths is not needed in order to successfully complete the task (that is, to keep
walking for the full 10 minutes). In this regard, the split-belt paradigm is inherently
different from several other motor adaptation paradigms (Cressman and Henriques
2011; Donchin et al. 2011), where a failure to adapt will lead to a decrease in task
performance.

For split-belt walking, this is clearly not the case, although it seems reasonable
to assume that adaptations occur in order to optimize the gait pattern to some
criterion. If this is indeed the case, this implies that this quantity is less optimized in subjects who show less or no adaptation. Theoretically, such a failure to optimize a given quantity may have at least 3 causes: 1) a failure to adequately monitor the quantity that needs to be optimized (sensory deficit in older adults), 2) a failure to adapt the motor behavior in such a way that the quantity is fully optimized and 3) the optimization does not take place because the advantages of optimizing the quantity do not outweigh the disadvantages (such as increased instability or augmented cognitive loading, or increased demands on muscle forces).

For the older adults in the present study, it may be that adapting the gait pattern (in terms of step length) will lead to a high computational load, because a normally more or less automatic pattern has to be altered, and therefore does not happen fully. In young healthy adults, adaptations to split-belt walking were found to be slower when subjects performed a cognitive dual task, and faster when they were instructed to pay attention to their gait (Malone and Bastian 2011). It is well known that ageing leads to a decline in executive function (Greenwood 2000; Miller 2000), which could lead to higher computational load compared to young adults for adaptation of the gait pattern (Woollacott and Shumway-Cook 2002).

Older adults changed relative timings within the gait cycle less, which could suggest that elderly are unable to make these changes. However, our previous work on obstacle avoidance in elderly argues against this. To avoid obstacles the most frequently used strategy in old adults is to prolong the swing phase to overcome the obstacle (“long step strategy”; see (Weerdesteyn et al. 2005b)). Older adults possibly feel uncomfortable using short stance periods on the fast leg, because of stability issues. Some support for this may be seen in the fact that gait cycle timing in older adults starts changing after about 50 strides, which also appears to be the time when
they start to make longer strides. This may possibly be interpreted as a sign of getting
“used” to the new situation. However, no data on how stable subjects feel during
splitbelt walking is currently available.

It is possible however, that the older subjects already invented another strategy
to compensate for the discomfort associated with shortened stance phases. Indeed, one
can maintain swing and stance duration as one compensates by adjusting swing speed.
This is exactly what the older subjects seemed to be doing. Hence one can state that
the young are primarily “timing” adapters while the older adults are “speed” adapters.

It is clear that the current study is but a first attempt at studying the underlying
mechanisms of changes in adaptations in the elderly. Hence the choice of parameters
was limited and did not allow studying some additional aspects of adaptation. For
example, in several studies from the group of Bastian, it was argued that there are
interesting differences between spatial and temporal parameters in the adaptation
process (i.e. Choi and Bastian, 2007; Torres et al, 2011). Their work showed that step
symmetry could be altered by adapting either spatial elements of coordination,
temporal elements of coordination, or a combination of both (Malone and Bastian,
2010). With the current data the temporal aspects were not fully explored (as they
require measuring limb angle trajectories and calculations of phase shifts between the
legs).

Lastly, a limitation of the current study is that we measured only a relatively
small number of subjects with a limited age range, and found only weak correlations
with age. Additional studies with subjects from a larger, more uniformly distributed
age range are necessary to get full insight into these correlations.
Conclusion

Older adults adapted more slowly, and showed fewer aftereffects than young adults in a split-belt paradigm. This reduced adaptation capability was linked to a decreased ability to change the relative timing within the gait cycle. The elderly compensated by introducing changes in swing speed but these adjustments were not sufficient to obtain the same symmetry levels as the young adults.

The adaptive behavior of the older adults most closely resembled that of subjects suffering from cortical pathology, possibly suggesting that the decrease in adaptation, as observed in older adults, is more linked to cortical than cerebellar deficits. It is pointed out, however, that the observed age-related changes are not necessarily pathological but instead, may reflect a deliberate strategy to choose for gait patterns that are as stable as possible.

References


Figure captions

**Figure 1:** Definition of step and stride length of fast and slow leg during the (A) early adaptation condition, (B) late adaptation condition, and (C) Aftereffects condition. The vertical lines show the path of the lateral malleolus marker during the gait cycle; most forward positions of the vertical lines indicate the anterior-posterior position of the lateral malleolus position and correspond to heel-strikes, while most backward positions correspond to toe off. Note: figure is only for illustrative purposes, and contains no actual data.

**Figure 2:** (A) Self-selected walking speed (m/s), (B) self-selected stride times (s), (C) self-selected stride lengths (m) and (D) stride times (s) during treadmill walking at 1 m/s of young (black) and older adults (white). Error bars represent standard errors, and asterisks indicate significant differences.

**Figure 3:** (A) Step length symmetry (dimensionless) during stride 1-400 of the adaptation condition of young (solid line) and older adults (dash-dotted line). Shaded areas represent standard errors. Episodes over which the mean was taken for statistical testing have been indicated in alternating white and grey bars. If only the Group x Episode effect was significant, post-hoc t-tests with Bonferroni correction were performed on the difference between groups per episode, and significance per episode indicated in the corresponding episode. (B) Stride lengths (m) of the fast (young adults: solid line, older adults, dash-dotted line) and slow (young adults: dashed line, older adults: dotted line) leg during stride 1-400 of the adaptation. Shaded areas represent standard errors. Thin horizontal lines represent means of the baseline condition. Episodes over which the mean was taken for statistical testing
have been indicated in alternating white and grey bars. If only the Group x Episode
effect was significant, post-hoc t-tests with Bonferroni correction were performed on
the difference between groups per episode, and significance per episode indicated in
the corresponding episode.

Figure 4: (A) Step length symmetry (dimensionless) during stride 1-200 of the
aftereffects condition of young (solid line) and older adults (dash-dotted line). Shaded
areas represent standard errors. Episodes over which the mean was taken for
statistical testing have been indicated in alternating white and grey bars. If only the
Group x Episode effect was significant, post-hoc t-tests with Bonferroni correction
were performed on the difference between groups per episode, and significance per
episode indicated in the corresponding episode. (B) Stride lengths (m) of the fast
(young adults: solid line, older adults, dash-dotted line) and slow (young adults:
dashed line, older adults: dotted line) leg during stride 1-200 of the aftereffect
condition. Shaded areas represent standard errors. Thin horizontal lines represent
means of the baseline condition. Episodes over which the mean was taken for
statistical testing have been indicated in alternating white and grey bars. If only the
Group x Episode effect was significant, post-hoc t-tests with Bonferroni correction
were performed on the difference between groups per episode, and significance per
episode indicated in the corresponding episode.

Figure 5: Relationship between adaptation and aftereffects. Horizontal axis: step
length symmetry at the end of adaptation. Vertical axis: step length symmetry at the
onset of the aftereffect condition. black circles represent young adults, open circles
represent older adults. Text depicts correlation coefficients (p-values between brackets).

Figure 6: Relationships of age with (A) step length symmetry at the end of adaptation, and (B) step length symmetry at the onset of the aftereffect condition.

Figure 7: (A) Percentage of swing time (%) of the fast (young adults: solid line, older adults, dash-dotted line) and slow (young adults: dashed line, older adults: dotted line) leg during stride 1-400 of the adaptation condition. Shaded areas represent standard errors. Thin horizontal lines represent means of the baseline condition. Episodes over which the mean was taken for statistical testing have been indicated in alternating white and grey bars. If only the Group x Episode effect was significant, post-hoc t-tests with Bonferroni correction were performed on the difference between groups per episode, and significance per episode indicated in the corresponding episode.

(B) Average swing speed (m/s) of the fast (young adults: solid line, older adults, dash-dotted line) and slow (young adults: dashed line, older adults: dotted line) legs during stride 1-400 of the adaptation condition. Shaded areas represent standard errors. Thin horizontal lines represent means of the baseline condition. Episodes over which the mean was taken for statistical testing have been indicated in alternating white and grey bars. If only the Group x Episode effect was significant, post-hoc t-tests with Bonferroni correction were performed on the difference between groups per episode, and significance per episode indicated in the corresponding episode.
(A) After effects: symmetry

Group: 0.06
Episode: 0.00
Group X Episode: 0.77

(B) After effects: stride lengths

Fast leg:
Group: 0.00
Episode: 0.03
Group X Episode: 0.25

Slow leg:
Group: 0.00
Episode: 0.00
Group X Episode: 0.05
Adaptation Vs. Aftereffect

- **Young adults**: -0.12 (0.78)
- **Older adults**: 0.36 (0.24)
- **Overall**: 0.48 (0.03)

Symmetry at the end of adaptation (-) vs. Initial symmetry after effect.