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 aging, 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 the gait to the needs of the environment (Bierbaum et al. 2010, 2011).

The 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, 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 Fig. 1A), which typically disappears with exposure to split-belt walking; subjects become adapted to the new situation (see Fig. 1B). The fact that after prolonged exposure subjects show aftereffects (that is, a step length asymmetry in the opposite direction; see also Fig. 1C) suggests that this is truly a process of adaptation rather than simple feedback. The inability to show an increase of symmetry during split-belt walking and the absence of aftereffects after a period of split-belt 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 pattern required by the two belts moving at different speeds and show 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 with transcranial magnetic stimulation (TMS)] (Jayaram et al. 2011), highlighting the role of the cerebellum in adapting the gait pattern to split-belt walking. Finally, 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 aging, 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. 2009, 2010; 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 present study the effect of aging on gait adaptability was tested with 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 men, 4 women; age 22.1 ± 3.6 yr, mass 68.8 ± 6.5 kg, height 1.77 ± 0.09 m) and 12 healthy older adults (9 men, 3 women; age 73.1 ± 4.7 yr, 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 KU Leuven.

Procedure. Before actual measurement started, subjects were first fitted with retroreflective markers on the lateral malleoli for movement registration with an optoelectronic system (Vicon Nexus, Oxford Metrics, Oxford, UK). Throughout all conditions, kinematics were sampled at 100 samples/s. Moreover, to accurately assess temporal parameters, three-dimensional ground reaction forces and torques were sampled at 1,000 samples/s with 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 m at their natural pace (Abellan van Kan et al. 2009). This procedure was repeated three times. Next, subjects were allowed to become familiar with the treadmill. After this familiarization procedure, the 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 min with belts tied (1 m/s, “baseline condition”), followed by 10 min with split belts (0.5 m/s and 1.0 m/s, “adaptation condition”), followed by 5 min of walking with belts tied (at 1 m/s, “aftereffects condition”). Between conditions the belt was stopped for a maximum of 30 s, 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 center of pressure trajectories using a previously described algorithm (Roerdink et al. 2008). For the 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 present 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-belt treadmill walking (Choi et al. 2009; Malone and Bastian 2011; Morton and Bastian 2006). First, step lengths were calculated as the anterior-posterior distance between the lateral malleolus markers of both legs at heel strike (Morton and Bastian 2006; Reisman et al. 2005). Fast step length referred to the step length calculated at the heel strike of the fast leg and slow step length to that calculated at the heel strike of the slow leg (see also Fig. 1).

Then step length symmetry (Choi et al. 2009; Malone and Bastian 2011) could be calculated as

\[
\text{step length symmetry} = \frac{\text{fast step length} - \text{slow step length}}{\text{fast step length} + \text{slow step length}}
\]

Moreover, for sake of completeness, we report stride length, calculated as

![Fig. 1. Definition of step and stride length of fast and slow leg during the early adaptation condition (A), late adaptation condition (B), and aftereffects condition (C). Vertical lines show the path of the lateral malleolus marker during the gait cycle; most forward positions of 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.](http://jn.physiology.org/content/journal/jn/105/6/1150/F1.large.jpg)
swing phase. This was calculated as

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

in which \( x_{\text{latmal}} \) is the \( x \) position of the lateral malleolus of the leg, \( t_{\text{heelstrike}} \) is the time of heel strike, \( t_{\text{toeoff}} \) is the time of toe off, and \( i \) is the stride index (i.e., the stride for which the calculation is done).

It may prove difficult to determine exactly what causes the adaptation processes seen during the adaptation condition, as most variables are highly interlinked. Nonetheless, we aimed at shedding some light on this process and started from the idea that the initial asymmetry in step length can be overcome by moving the fast leg more forward with respect to the slow leg. This could be done in two ways. A first way is by increasing the percentage of a gait cycle a given leg spends in swing time (while concurrently decreasing relative stance time) on the fast leg, so that the fast leg swings forward more, or decreasing relative swing time (while concurrently increasing relative stance time) on the slow leg, so that the slow leg 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, 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

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

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

\[ \text{swing speed}(i) = \frac{\text{stride length}(i)}{t_{\text{heelstrike}(i)} - t_{\text{toeoff}(i)}} \]

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 exist 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 two-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 aging 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 Fig. 2A), than young adults, although they did not exhibit longer stride times (\( P = 0.8 \); see Fig. 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 Fig. 2C). During treadmill walking in the baseline condition, older adults walked with significantly shorter stride times (\( P < 0.01 \); see Fig. 2D) and, as a consequence, with shorter stride lengths (not analyzed, but see Fig. 3B).

**Adaptation and aftereffects.** Figure 3A shows step length symmetry during the adaptation condition. Statistical testing

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**Fig. 2.** Self-selected walking speed (A), self-selected stride times (B), self-selected stride lengths (C), and stride times during treadmill walking at 1 m/s (D) of young and older adults. Error bars represent SE.
showed a significant effect of group ($P < 0.05$) and episode ($P < 0.01$) and a group × episode interaction ($P < 0.05$). Initially, there was little difference in step length symmetry between young and older adults, but after ~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 × episode $P = 0.5$) and that the age groups still differed markedly in symmetry ($P < 0.05$). In conclusion, despite having more exposure to split-belt 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 × episode interaction). Both groups were able to quickly adapt stride lengths (see Fig. 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 (Fig. 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 × 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 Bonferroni corrections.

In contrast, similar to the adaptation condition, stride lengths (Fig. 4B) were quick to readapt, and even increased somewhat during the aftereffects 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 young adults (effect of group, for both fast and slow leg, $P < 0.01$). We also found a group × episode interaction effect ($P < 0.05$) for the slow leg, suggesting that the older adults increased stride lengths somewhat more slowly.

There was no significant correlation between the amount of adaptation and the size of the aftereffect for either of the groups (see Fig. 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 the aftereffects 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.
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 older group. Nonetheless, variability is needed for correlational analysis and the two excluded subjects cannot 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 Fig. 6B).

What defines adaptation speed and amount? Figure 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 × 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-stride 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 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, a clear identification proved more difficult in the aftereffects condition, and no statistically significant effects of group or group × episode were found (all P > 0.2). This was most likely due to the large interindividual 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 with a split-belt paradigm. We found that older adults adapted their gait pattern more slowly and tended to show fewer 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 aging 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 one hand and older adults on the other. Similar to our young adults, both cerebellar subjects and young children were less able to adapt the gait pattern in terms

![Figure 7A](http://jn.physiology.org/10.1152/jn.00018.2012.00018.2012)
of step length, but they showed an immediate increase in stance time at the slow leg and a decrease in stance time at the fast leg. Conversely, older adults lacked such a response and did 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 disease patients (Dietz et al. 1995) did fully adapt the gait pattern (in terms of step length and compared with 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 min). In this regard, the split-belt paradigm is inherently different from several other motor adaptation paradigms (Cressman and Henriques 2011; Donchin et al. 2012), 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 three 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) optimization not taking 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 aging leads to a decline in executive function (Greenwood 2000; Miller 2000), which could lead to higher computational load compared with 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 the elderly are unable to make these changes. However, our previous work on obstacle avoidance in the elderly argues against this. To avoid obstacles the most frequently used strategy in older 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 ~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 split-belt walking are 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 older adults are “speed” adapters.

It is clear that the present 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 study of 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-Oviedo et al. 2011). Their work showed that step symmetry could be altered by adapting spatial elements of coordination, temporal elements of coordination, or a combination of both (Malone and Bastian 2010). With the present data the temporal aspects were not fully explored (as they require measuring limb angle trajectories and calculations of phase shifts between the legs).

Finally, a limitation of the present 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.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

Author contributions: S.M.B., A.V.I., J.D., and S.P.S. conception and design of research; S.M.B. and A.V.I. performed experiments; S.M.B. analyzed data; S.M.B., A.V.I., J.D., and S.P.S. interpreted results of experiments; S.M.B. prepared figures; S.M.B. drafted manuscript; S.M.B., A.V.I., J.D., and S.P.S. edited and revised manuscript; S.M.B., A.V.I., J.D., and S.P.S. approved final version of manuscript.

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