

# Interlimb Coordination During Locomotion: What Can be Adapted and Stored?

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**Reisman, Darcy S., Hannah J. Block, and Amy J. Bastian.** Interlimb coordination during locomotion: what can be adapted and stored? *J Neurophysiol* 94: 2403–2415, 2005. First published June 15, 2005; doi:10.1152/jn.00089.2005. Interlimb coordination is critically important during bipedal locomotion and often must be adapted to account for varying environmental circumstances. Here we studied adaptation of human interlimb coordination using a split-belt treadmill, where the legs can be made to move at different speeds. Human adults, infants, and spinal cats can alter walking patterns on a split-belt treadmill by prolonging stance and shortening swing on the slower limb and vice versa on the faster limb. It is not known whether other locomotor parameters change or if there is a capacity for storage of a new motor pattern after training. We asked whether adults adapt both intra- and interlimb gait parameters during split-belt walking and show aftereffects from training. Healthy subjects were tested walking with belts tied (baseline), then belts split (adaptation), and again tied (postadaptation). Walking parameters that directly relate to the interlimb relationship changed slowly during adaptation and showed robust aftereffects during postadaptation. These changes paralleled subjective impressions of limping versus no limping. In contrast, parameters calculated from an individual leg changed rapidly to accommodate split-belts and showed no aftereffects. These results suggest some independence of neural control of intra- versus interlimb parameters during walking. They also show that the adult nervous system can adapt and store new interlimb patterns after short bouts of training. The differences in intra- versus interlimb control may be related to the varying complexity of the parameters, task demands, and/or the level of neural control necessary for their adaptation.

## INTRODUCTION

Animal locomotor patterns must constantly change to accommodate the demands of a complex world. Walking a perfectly straight line over a smooth, level surface is more commonly an exception (e.g., a roadside sobriety test) than the rule. Therefore, functional locomotion demands that limb movements be flexible enough to accommodate different terrain, speeds, and trajectories. Achieving this flexibility without sacrificing stability is no small feat; it requires continuous modulation of coordination within (inralimb) or between (interlimb) the legs. Interlimb coordination, particularly the maintenance of reciprocal, out of phase motions of the limbs, is particularly critical for stable human (bipedal) walking. As such, different interlimb coordination patterns are used for various forms of locomotion (e.g., walk, run) and for walking in curved trajectories (Courtine and Schieppati 2003, 2004).

For example, to walk in a curved path, the relative motion of the legs must change: the outer leg takes a longer step with a shorter stance time, and the inner leg does the opposite (Courtine and Schieppati 2003). However, this is accomplished effortlessly and without obvious asymmetries. Surprisingly, relatively little is known about the adaptability or plasticity of interlimb locomotor coordination patterns (Prokop et al. 1995).

The use of a split-belt treadmill, where the belt beneath each foot is independently controlled, allows for the systematic manipulation and study of interlimb coordination. Decerebrate or spinal cats can walk on a split-belt treadmill, where one hindlimb is made to go faster than the others, by prolonging stance and shortening swing on the “slow” hindlimb, and vice versa on the “fast” hindlimb (Forssberg et al. 1980; Kulagin and Shik 1970). This suggests that either sensory or motor information from one limb affects the control of the opposite limb’s movement. A one-to-one stepping pattern is predominantly seen for lower speed ratios (e.g., 2:1), although cats sometimes switch strategies at high ratios (e.g., 3:1–6:1), taking two or three steps on the fast limb for each step on the slow limb. Similar findings have been reported during supported stepping in human infants (Thelen et al. 1987; Yang et al. 2004). Human adults can also rapidly adjust stance and swing times during split-belt walking (Dietz et al. 1994) but have not been reported to produce multiple stepping on the fast leg at higher speed ratios. Collectively, these results show that both quadrupeds and bipeds can make basic adjustments in stance and swing times to maintain an alternating pattern with legs moving at different speeds. Spinal circuits are capable of generating this pattern in cats, and the one-to-one relationship between limbs can be temporarily changed under extreme situations in cats and infants.

Little is known about locomotor adaptation and storage of new patterns (as identified by the presence of aftereffects) in humans. Prokop et al. (1995) have shown that a very short (45 strides) bout of practice on a split-belt treadmill allows subjects to make more rapid adjustments to each leg’s stance and swing times on subsequent exposures to split-belt walking. This practice effect did not transfer when the slow and fast limbs were switched, suggesting a limb specific mechanism (Prokop et al. 1995). Practice on a split-belt treadmill also alters the perception of leg speed during walking (Jensen et al. 1998). Other types of locomotor adaptations are known to occur, although they do not involve alterations in interlimb coordina-

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tion. Treadmill running can cause an aftereffect of inadvertently jogging forward when asked to jog in place (eyes closed) on solid ground (Anstis 1995). Stepping in place on a rotating treadmill can cause curved trajectories on solid ground; this podokinetic after-rotation (PKAR) is thought to be caused by a recalibration of the proprioceptive relationship between the trunk and stance limb yaw rotations (Earhart et al. 2002; Gordon et al. 1995; Weber et al. 1998).

In this study, we investigated the adaptability of the locomotor pattern in adults using a single 10-min session of practice on a split-belt treadmill. We hypothesized that the pattern within each individual limb (i.e., intralimb parameters) would change rapidly to accommodate the treadmill but would not necessarily adapt or show aftereffects. Specifically, the leg on the faster belt was expected to produce a kinematic pattern identical to fast symmetric walking and vice versa for the leg on the slower belt. In contrast, we expected that the pattern between legs (i.e., interlimb parameters) would adapt and subsequently show aftereffects. Interlimb coordination might adapt to optimize the relative movement between legs, given the novel task mechanics associated with coupling a fast pattern on one leg with a slow pattern on the other. We also asked whether adaptation is influenced by the difference in training speeds between the two legs. We expected the largest adaptation and aftereffect when the speed ratio between the two legs is greatest. Preliminary results have been presented in abstract form (Reisman et al. 2004).

## METHODS

Twenty-one healthy subjects [ $30.4 \pm 8.6$  (SD) yr] participated in this study. All subjects gave approved written consent (Institutional Review Board, Johns Hopkins University School of Medicine) before participating. Subjects walked in a dimly lit room on a custom split-belt treadmill (Woodway) with belts moving together (tied) or at different speeds (split). Figure 1 shows the experimental paradigm. Briefly, during the baseline periods, subjects walked with both belts tied at a slow speed, then a fast speed, and again at a slow speed for 2 min at each speed. During the adaptation period, subjects walked for 10 min in a split-belt condition, with one leg moving fast and the other slow. During the postadaptation period, subjects walked for 6 min with both belts tied at the slow speed. Time between periods was brief (<1 min), just enough to reset the treadmill belt speeds. Three groups of seven subjects were tested at three different speed ratios, 2:1, 3:1, or 4:1, where the slower belt always moved at 0.5 m/s and the faster belt moved at 1.0, 1.5, or 2.0 m/s. The leg that was made to move faster was randomly assigned. Subjects were instructed not to look at

their feet during walking and were encouraged to look at an experimenter positioned in front of the treadmill. At the beginning of each period, subjects were asked whether their legs felt like they were moving at the same or different speeds. If they replied "different," they were asked which leg felt faster. For all testing, subjects wore comfortable walking shoes and a safety harness and held onto a bar on the front of the treadmill.

## Data collection

OPTOTRAK (Northern Digital, Waterloo, Canada) sensors were used to record three-dimensional position data from both sides of the body. Infrared emitting diodes (IREDs) were placed bilaterally (Fig. 1) on the foot (5th metatarsal head), ankle (lateral malleolus), knee (lateral joint space), hip (greater trochanter), pelvis (iliac crest), and shoulder (acromion process). Foot contacts were determined using four contact switches per foot: two placed on the forefoot and two on the heel. Voltages reflecting treadmill belt speeds were recorded directly from treadmill motor output. Marker position and analog data (foot switches and treadmill speed) were synchronized and sampled simultaneously using OPTOTRAK software at 100 and 1,000 Hz, respectively.

## Data analysis

Three-dimensional marker position data were low-pass filtered at 6 Hz. Custom software written in MATLAB (Mathworks) was used for all analyses. Stride time was determined from the foot switches and is defined as the period from one foot contact to the next on the same limb. A stride contains both stance (foot contact to lift-off) and swing (lift-off to next foot contact) phases. We refer to the limb on the slow belt in the split-belt period as the "slow limb" and the limb on the fast belt as the "fast limb." Joint angles were calculated such that flexion was positive and extension was negative (Fig. 1). Limb orientation angle (Bosco and Poppele 2002) was calculated as the angle between the vertical and the vector from the hip marker to the fifth metatarsal marker.

We calculated intralimb (i.e., those measured from a single leg) and interlimb (i.e., those where the measurement depended on both legs) kinematic variables. Intralimb parameters were as follows. 1) *Stride length*—a modified version of stride length for the treadmill was calculated as the distance traveled by the ankle marker in the anterior-posterior direction from initial contact to lift-off of one limb; a *stride length ratio* (fast/slow) was also calculated to assess symmetry. 2) *Percent stance time*—the duration of stance phase expressed as a percentage of the stride time; a *stance time ratio* (fast/slow) was also calculated to assess symmetry. 3) *Relative timing of peak joint angles*—the latency between peak angles occurring for all combinations of hip, knee, and ankle joint pairs. We found peak hip extension, knee flexion, and ankle extension (plantar-flexion) within a limb and

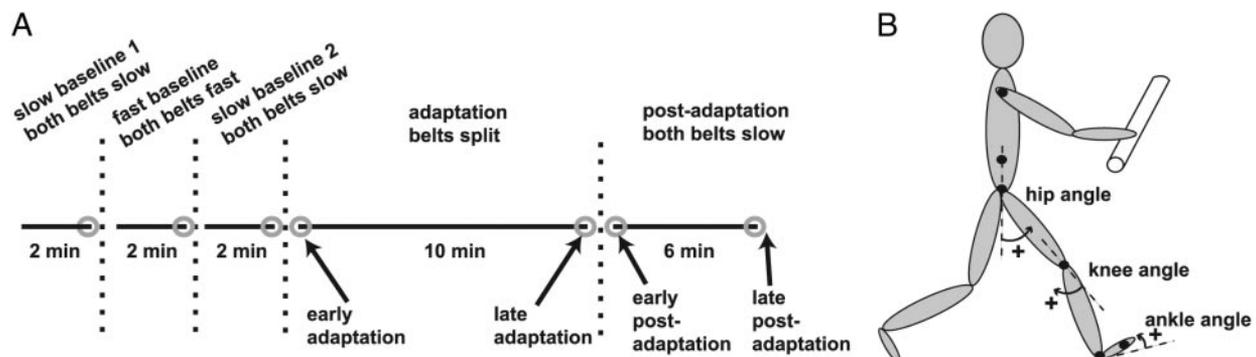


FIG. 1. A: experimental paradigm showing each period of split-belt walking. Gray circles show general location in the period over which averages were taken. B: illustration of marker locations and joint angle conventions.

calculated the relative timing between peaks. These peaks were chosen because they were the most salient peaks within a stride time (foot contact to foot contact). All times are expressed as a percent of stride time.

Interlimb parameters were as follows. 1) *Step length*—a modified version of step length for the treadmill was calculated as the anterior-posterior distance between the ankle marker of each leg at heel strike of the leading leg; *fast step length* refers to the step length measured at fast leg heel strike and *slow step length* refers to step length measured at slow leg heel-strike. 2) *Percent double limb support time*—the time when both feet are in contact with the floor expressed as a percentage of the stride time for each leg. There are two periods of double support per stride cycle and we define *slow double support* as occurring at the end of the slow limb's stance (i.e., the time from fast leg foot contact to slow leg lift-off), and *fast double support* at the end of the fast limb's stance (i.e., the time from slow leg foot contact to fast leg lift-off). A *double support ratio* (fast/slow) was also calculated to assess symmetry. 3) *Limb orientation at weight transfer*—the angle of the leading limb at opposite limb lift-off. 4) *Limb angle phase*—the point in the slow limb cycle (i.e., time from peak limb extension to the subsequent peak limb extension) at which the fast limb reaches peak extension. We chose to calculate limb angle phasing because the limb angle represents the entire orientation of the limb, which is particularly important for foot placement and weight transfer in bipedal gait. We used a dual referent analysis method for phase calculations (Berkowitz and Stein 1994). This is superior to single referent techniques in situations where the duty cycle of the referent (i.e., slow) leg changes (e.g., peak flexion time varies within the extension-flexion cycle). It ensures that changes in the referent duty cycle will not produce shifts in phase values obtained (Berkowitz and Stein 1994); this is of issue if the percent stance and swing time change over experimental periods (thus varying the relative duration of flexor and extensor phases). We defined a phase of 0.0 and 1.0 for subsequent peaks in slow limb extension and 0.5 for peak slow limb flexion (see Fig. 7A). The following equations were used to calculate the phase of fast limb extension with respect to the slow limb (Berkowitz and Stein 1994)

$$(F_e - S_{e1})/2*(S_f - S_{e1}), \text{ if } F_e \text{ occurred between } S_{e1} \text{ and } S_f$$

$$[(F_e - S_f)/2*(S_{e2} - S_f)] + 0.5, \text{ if } F_e \text{ occurred between } S_f \text{ and } S_{e2},$$

where  $F_e$  = fast limb peak extension,  $S_{e1}$  = first peak extension of slow limb,  $S_f$  = slow limb peak flexion, and  $S_{e2}$  = second peak extension of slow limb. Here we studied when fast limb extension occurs in the slow cycle; using these conventions, a value of 0.5 means that the limbs are exactly out of phase (e.g., fast limb peak extension occurs simultaneously with slow limb peak flexion).

We also calculated the time course of adaptation during the split-belt period using an exponential decay function:  $y = a - b \times e^{-s/c}$  where  $c$  is the number of strides that it would take to obtain  $(1 - e^{-1})$  or  $\sim 63\%$  of the final adaptation. Thus our measure of the rate is an estimation of the number of strides for a subject to proceed approximately two-thirds of the way through the adaptation process.

Statistical analyses were completed using the averages of the first five strides baseline, the first and last five strides of the adaptation period (*early* and *late adaptation*, respectively), and the first and last five strides of the postadaptation period (*early* and *late postadaptation*, respectively). We will refer to the baseline period when both belts are tied at the slow speed as *both slow* and the period when the belts are tied at the fast speed as *both fast*. For all kinematic variables except phasing, we used a repeated measures ANOVA with condition (2:1, 3:1, or 4:1) as the between-subjects variable and testing period (both slow baseline, early adaptation, late adaptation, early postadaptation, and late postadaptation) as the within-subjects variable. When the ANOVA yielded a significant effect, post hoc analyses were completed using a Tukey HSD test. For phasing, we calculated the mean vector and the angular deviation (circular equivalent of the SD)

and used the Watson's  $U^2$  test (Batschelet 1981) to test for significant differences between testing periods. Statistica (StatSoft, Tulsa, OK) and MATLAB were used for all statistical analyses.

## RESULTS

Qualitatively, subjects had a symmetric gait pattern during the both slow or both fast baseline conditions. They showed a pronounced limp (asymmetric step lengths and transitions from one limb to the other) in early adaptation (belts split) that improved by late adaptation and showed a robust aftereffect with the opposite limping pattern postadaptation (belts tied; see supplementary video<sup>1</sup>). All 21 subjects reported a perceived asymmetry in leg speeds in early adaptation when the belts were split, and then felt the reverse asymmetry postadaptation, even though the belts were tied at the same speed.

Subjects maintained a one-to-one stepping pattern (i.e., alternating steps with 2 double support periods and no airborne periods) during all experiments, regardless of speed ratio. Only one subject took one double step in mid-air at the very beginning of the split-belt period in the 4:1 speed condition. To maintain one-to-one stepping, the stride times (i.e., stance + swing) of each leg were equivalent for all phases of the experiment ( $P = 0.931$ ). Stride times of both legs shortened during the both fast period and during split-belt walking ( $P < 0.05$  for both).

Although stride times were equivalent for all periods, the percent time in stance, swing, and double support changed in different ways. Figure 2 shows a Hildebrand style time plot, with time on the  $x$ -axis and stride number increasing vertically along the  $y$ -axis. At baseline, stance, swing, and double support times were equal for both legs. Early in adaptation the stride times were shorter overall, and the fast leg had a shorter stance time, longer swing time, and a shorter double limb support time compared with the slow leg. In late adaptation, double limb support times became equal, but stance and swing times did not change appreciably. In early postadaptation, there was a substantial aftereffect in double limb support times, opposite of that seen in early adaptation. However, stance and swing times switched back to baseline values rapidly. In the late postadaptation period, the temporal pattern returned to baseline values, with equal stance, swing, and double limb support times for both legs.

For all speed conditions (2:1, 3:1, and 4:1), intralimb parameters, those calculated using values from an individual leg, changed immediately and showed no appreciable aftereffect postadaptation. Figure 3 shows stride-by-stride plots of stride length and percent stance time for the group walking in the 3:1 condition (percent swing time is not shown). Subjects increased stride length and decreased stance time symmetrically when switching from the both slow to both fast periods (Fig. 3, A and C). During adaptation, there was an immediate increase in stride length and decrease in stance time on the fast limb (and vice versa for the slow limb; Fig. 3, B and D). These parameters subsequently changed very little during adaptation, and there was no aftereffect in the postadaptation period. Figure 3, E and F, shows group data for stride length and stance time ratios (a value of 1 reflects symmetry). There was a significant main effect of experimental period for both

<sup>1</sup> The Supplementary Material for this article (a video) is available online at <http://jn.physiology.org/cgi/content/full/00089.2005/DC1>.

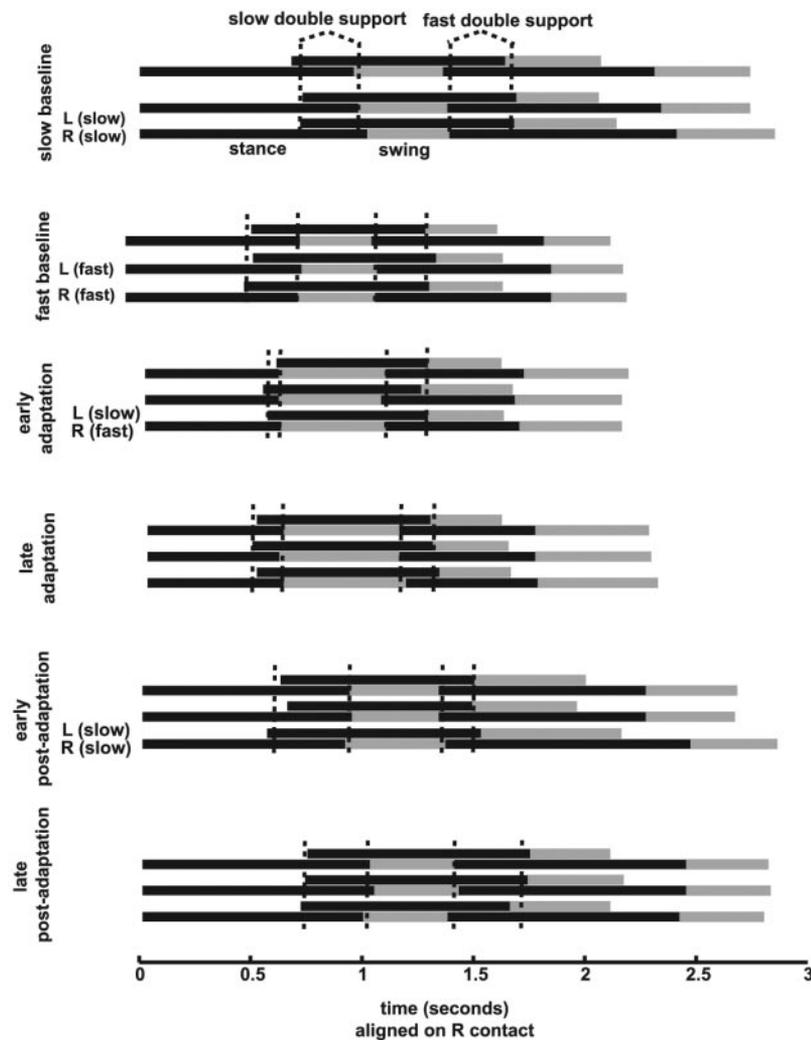


FIG. 2. Duration of stance (dark bars) and swing (pale bars) from a single subject walking in the 3:1 condition. Three consecutive strides are plotted for each period from *bottom* to *top* in each period. Dotted lines approximate double limb support time. In baseline and postadaptation periods, belts were tied at 0.5 m/s. In adaptation periods, belts were split at 0.5 and 1.5 m/s. In early adaptation, overall stride time shortens. There are also asymmetries, with shorter stance and longer swing times on the fast limb relative to the slow limb. Double support times are also markedly unequal. Stance and swing times do not change throughout adaptation, and there is no aftereffect in these parameters. However, double limb support time changes from early to late adaptation (becoming more symmetric) and there is an aftereffect with the opposite asymmetry in early postadaptation.

parameters (both  $P < 0.0001$ ). There was also a significant interaction between experimental period and speed ratio tested (both  $P < 0.05$ ), with subjects showing progressively greater asymmetries in stride length and stance time when walking at higher speed ratios with the belts split. Post hoc testing showed that subjects changed from the both slow period to the early adaptation period, but not from early to late adaptation (i.e., no adaptation, both  $P > 0.90$ ) nor from the both slow to early postadaptation periods (i.e., no aftereffect, both  $P > 0.90$ ).

There was also little or no change in timing of intralimb joint kinematics. Figure 4, *A* and *B*, shows examples of hip, knee, and ankle angles plotted as a percentage of stride time. In Fig. 4*A*, we overlaid traces from early and late in split-belt adaptation. For comparison, we also include a trace from the slow leg when it walked slowly at baseline (i.e., both legs slow) and from the fast leg when it walked fast at baseline (i.e., both legs fast). Note that the intralimb joint timing (differences between vertical lines marking joint peaks) is very similar for all traces, with no appreciable adaptation effect and no clear difference from the both slow and both fast periods. Figure 4*B* shows overlaid traces from the both slow baseline period and the postadaptation period and shows no difference (i.e., no aftereffect). Group data for timing differences between joint pairs are shown in Fig. 4, *C–E*, for each leg across all periods of adaptation in all speed conditions. There was no difference in

knee relative to hip timing for either the fast or slow leg in any speed ratio and in any period. There was an effect of experimental period for both ankle relative to hip and ankle relative to knee timing (both  $P \leq 0.05$ ), with a post hoc difference between the both slow and early adaptation periods (both  $P \leq 0.05$ ). There was a small change from early to late adaptation that did not reach statistical significance, but no difference between the both slow baseline and early postadaptation periods (i.e., no aftereffect). We concluded that intralimb timing was only slightly changed by split-belt practice but showed no evidence of an aftereffect. The aftereffects are very important because they show that the subject was actually learning and storing a new pattern versus just changing the pattern in response to the treadmill.

In contrast, the interlimb walking parameters, those calculated using values from both legs (e.g., step length, double support, limb phasing, limb orientation), changed slowly during adaptation and showed robust aftereffects. Figure 5*A* shows an overhead view of step length for an individual subject in the 3:1 condition. During early adaptation, there was an asymmetric step length, with a shorter step on the fast leg. This asymmetry was reduced through the adaptation period and in early postadaptation there was an aftereffect such that the slow leg step length was shorter. This asymmetry gradually returned to baseline during the postadaptation period (Fig. 5*B*). Figure

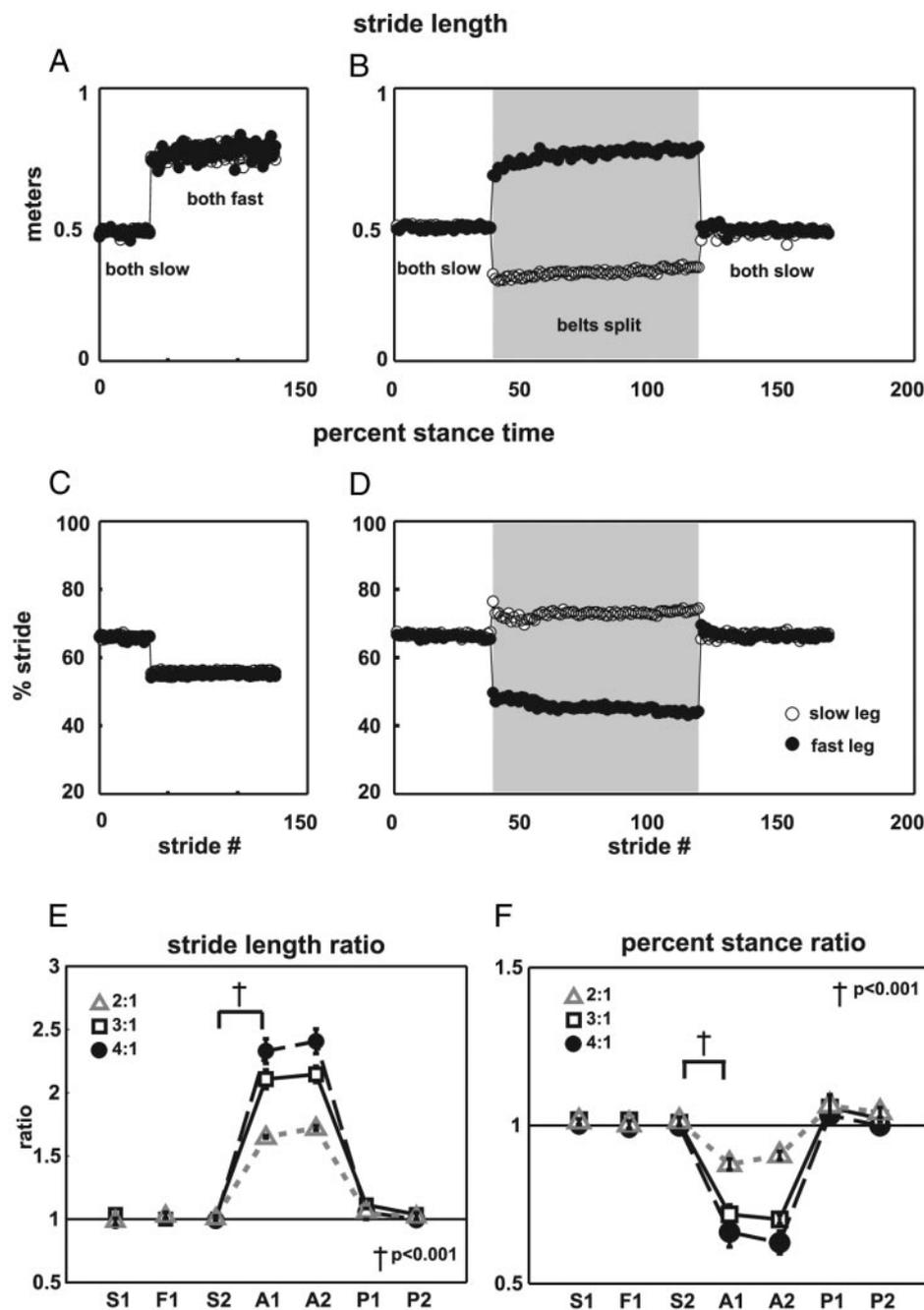


FIG. 3. Stride by stride plots of (A and B) stride length and (C and D) percent stance. Group data for subjects walking in the 3:1 experiment are shown. A and C: 1st slow and fast baseline periods (belts tied). B and D: 2nd slow baseline (belts tied), adaptation (shaded gray, belts split), and postadaptation (belts tied) periods. ○, slow limb; ●, fast limb. Data in the adaptation period are truncated to the 1st 80 strides for display purposes; this is beyond the point that behavior plateaus and represents approximately the 1st 20% of the adaptation period. Data in the postadaptation period is truncated to the 1st 50 strides. E and F: averages over the 1st 5 strides (S1, F1, S2, A1, P1) or last 5 strides (A2, P2) of an experimental period are shown for stride length ratio (fast/slow) and percent stance time ratio (fast/slow) in each speed ratio condition. Values equal to 1 represent perfect symmetry of these variables for the 2 legs. △, □, and ● represent the results for the 2:1, 3:1, and 4:1 conditions, respectively. During adaptation, there was a rapid increase in stride length and decrease in stance time on the fast limb (and vice versa for the slow limb). These parameters became more asymmetric at higher speed ratios. However, they changed little during adaptation and showed no sign of an aftereffect in the postadaptation period. S1, 1st slow baseline; F1, fast baseline; S2, 2nd slow baseline; A1, early adaptation; A2, late adaptation; P1, early postadaptation; P2, late postadaptation. Error bars, ±SE.

5C shows the step length difference (slow-fast) averaged over the five strides taken from each period. There was a significant main effect of experimental period ( $P < 0.001$ , Fig. 5C), with post hoc tests showing that subjects changed step length from the both slow period to the early adaptation period ( $P < 0.001$ ), adapted from the early to late adaptation period ( $P < 0.001$ ), and stored an aftereffect (compare 2nd both slow and early postadaptation periods,  $P < 0.001$ ).

Figure 6 shows stride-by-stride plots for double support for the three speed ratios tested. During the both slow and both fast baseline periods, double support was approximately equal across the legs. During early adaptation, there was an asymmetry that was greatest in the 4:1 speed condition (Fig. 6, A–C). The asymmetry was reduced through the adaptation through changes in both the slow and fast legs. In early postadaptation there was an

aftereffect such that the reverse pattern was observed; this gradually returned to baseline. Figure 6D shows the double support ratio (fast/slow) averaged over the five strides taken from each period. Data were collapsed across legs, because the leg that was made to walk fast (left or right) did not significantly influence the magnitude of the adaptation ( $P = 0.289$ ) or aftereffect ( $P = 0.349$ ). There was a significant main effect of experimental period ( $P < 0.001$ , Fig. 6D), with post hoc tests showing that subjects changed behavior from the both slow period to the early adaptation period ( $P < 0.001$ ) adapted (changed) from early to late adaptation ( $P < 0.001$ ) and stored an aftereffect (compare 2nd both slow and early postadaptation periods,  $P < 0.01$ ). There was an effect of speed ratio on the asymmetry of the double support periods in early adaptation: the larger the speed ratio, the greater the asymmetry ( $P < 0.01$ ).

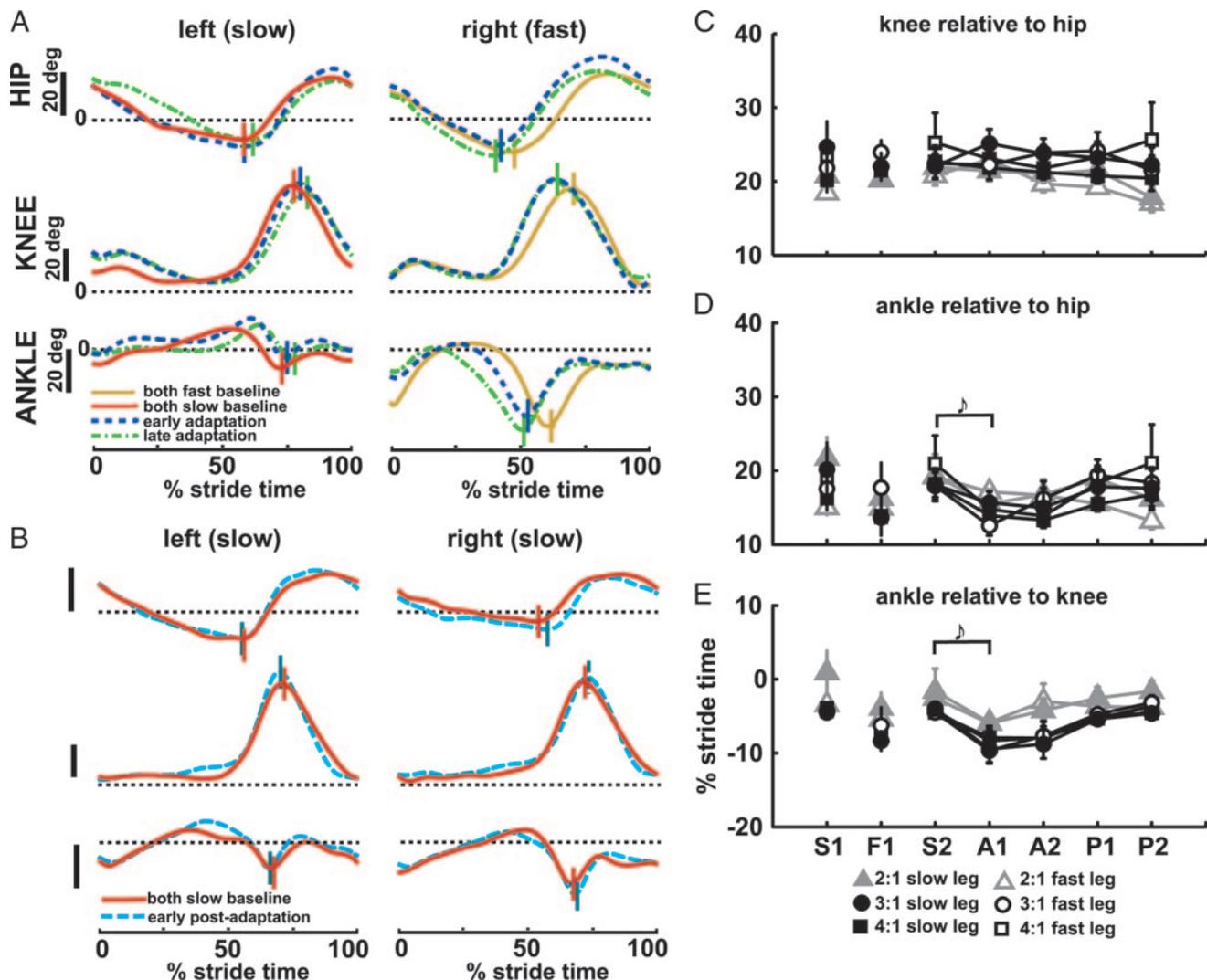


FIG. 4. Relative timing of intralimb joint kinematics. *A*: hip, knee, and ankle angles plotted as a function of stride time for a single subject walking early and late in the split-belt condition. Additionally, joint angles for the slow (left) leg when it walked in the *both slow* baseline are overlaid for comparison to the slow leg in the split-belt condition; the same is done for the fast leg. For all plots, flexion angles are (+) and extension angles are (-). Vertical lines mark the time and position of peak hip extension, peak knee flexion, and peak ankle extension. Note very little change in intralimb timing from baseline to early or late adaptation period for each leg. *B*: joint angles for the *both slow* baseline and early postadaptation show no difference, indicating no aftereffect. *C*: group averages ( $\pm$ SE) over the 1st 5 strides (S1, F1, S2, A1, P1) or last 5 strides (A2, P2) for peak knee flexion timing relative to peak hip extension for slow and fast legs in all speed ratio conditions. *D*: group averages for peak ankle extension timing relative to peak hip extension. *E*: group averages for peak ankle extension timing relative to peak knee flexion. \* $P < 0.05$ .

Because stance and swing times did not change over the course of adaptation, but double support did, we expected that limb phasing would be altered. Figure 7, *A* and *B*, shows an example of limb angle phasing traces and a stride-by-stride plot for a subject walking in the 3:1 speed ratio condition. Gray shaded boxes in Fig. 7*A* indicate the time between slow leg peak flexion and fast leg peak extension. A dual-referent phase analysis was used to calculate limb angle phasing, with a value of 0.5 indicating that the legs are exactly out of phase and 0 or 1 indicating that the legs are exactly in phase. Figure 7*B* shows that during the both slow period, the phase was  $\sim 0.66$ , with fast peak extension after slow peak flexion. During early adaptation, limb phasing values were reduced (i.e., closer to being exactly out of phase). By late adaptation, limb phasing increased, but not fully to the baseline level, and in early postadaptation, the opposite shift in phasing occurred. Circular statistical analysis of group data revealed significant differ-

ences between the both slow and early adaptation periods ( $P < 0.05$ , Fig. 7*C*) and between the both slow and early postadaptation periods ( $P < 0.05$ , Fig. 7*C*).

Another important feature of walking is the orientation of the limbs at different points in the cycle. We measured limb orientation at weight transfer (i.e., when the opposite leg just lifts off) because this is a critical point in the cycle for stability. If the limb is too flexed at weight transfer, the body may be too far behind the limb, and if it is too extended, the body may move too far forward of the limb; either can lead to instability. We found adaptive alterations in each limb's position at weight transfer during split-belt walking. Figure 8*A* shows a stick figure of the limb orientations at weight transfer from a subject walking in the 4:1 condition. During the both slow period, the slow and fast limbs accept weight in a similar position (Fig. 8*A*, cf. *top* and *bottom*). In early adaptation, the slow limb accepts weight in slightly more flexion (Fig. 8*A*, *top*), and the fast limb

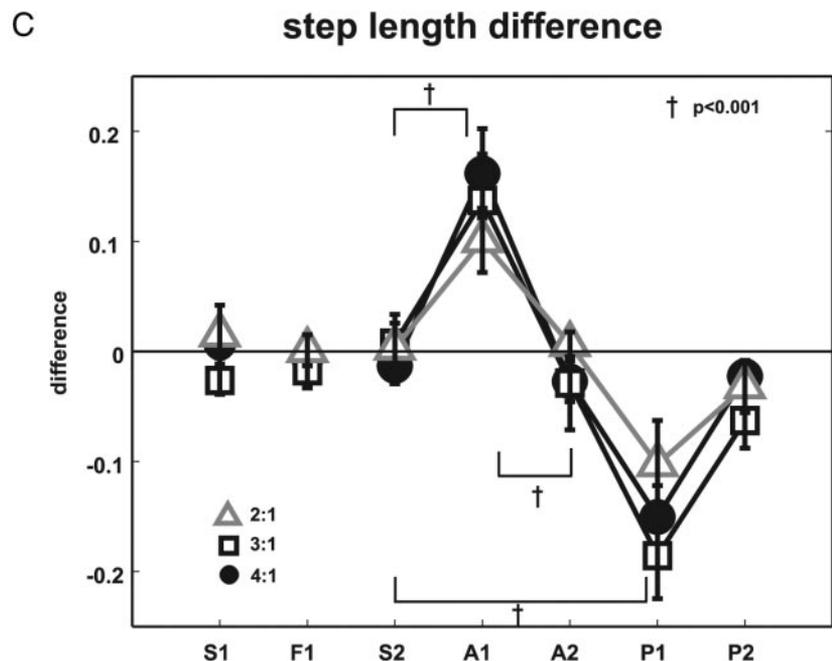
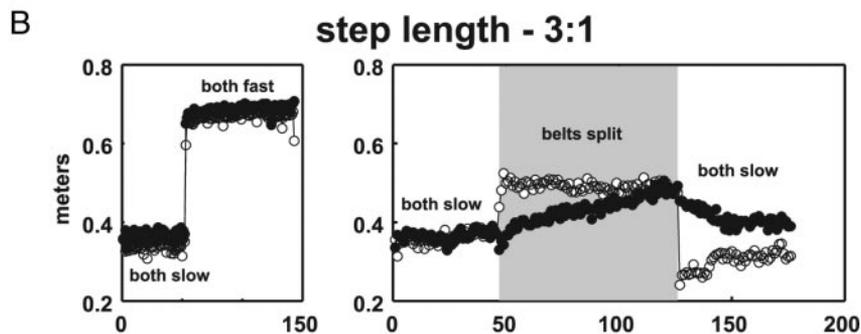
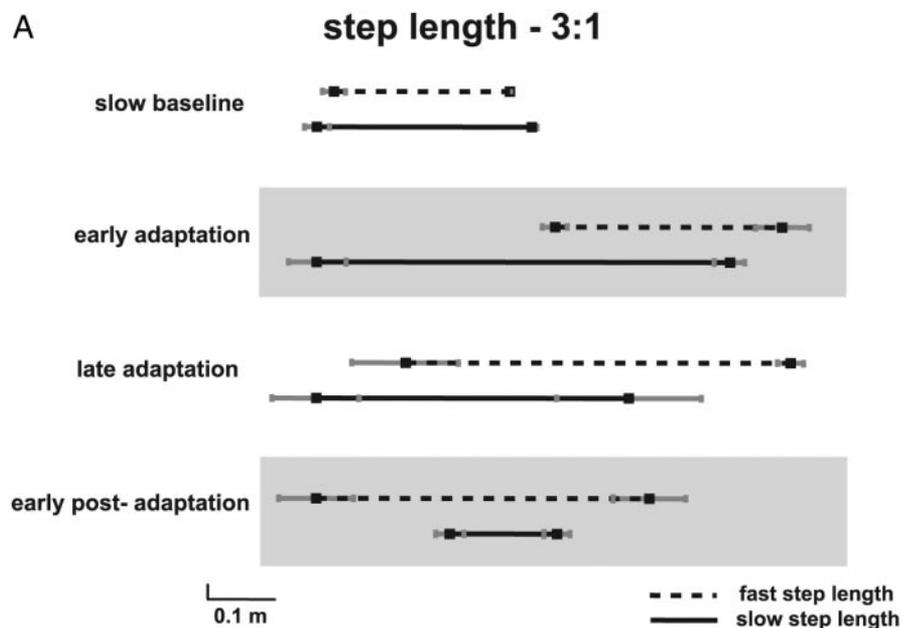


FIG. 5. *A*: mean (over 5 strides) step length for a subject in the 3:1 condition in the *both slow*, early and late adaptation, and postadaptation periods. Black squares represent the mean foot position (over 5 strides) with gray error bars representing  $\pm$ SD. Dashed lines, fast leg step length; solid lines, slow leg step length. Asymmetries of step length are found in early adaptation, symmetry is largely restored by late adaptation, and the opposite asymmetry is observed in early postadaptation. *B*: stride-by-stride plot of step length from the same subject as in *A* with the same conventions as in Fig. 3. A clear adaptation effect is present, with a postadaptation aftereffect. *C*: average step length differences over the 1st 5 strides (S1, F1, S2, A1, P1) or last 5 strides (A2, P2) of an experimental period for the group in each speed ratio condition. Values equal to 0 represent perfect symmetry. Step length symmetry is significantly different from baseline in early adaptation (S2 vs. A1) and changes significantly from early to late adaptation to restore symmetry (A2 vs. A1). There is a significant aftereffect consisting of opposite asymmetry early postadaptation (S2 vs. P1).

accepts weight in much more extension (Fig. 8*A*, bottom). By late adaptation, both limbs accept weight in a similar position. There is a robust aftereffect postadaptation, with slow and fast limbs showing the opposite effect as seen in early adaptation.

Group data showing the difference between the two limbs' position at weight transfer is shown in Fig. 8*B*. There was a significant main effect for period ( $P < 0.001$ , Fig. 8*B*), and post hoc testing revealed that the slow limb was significantly

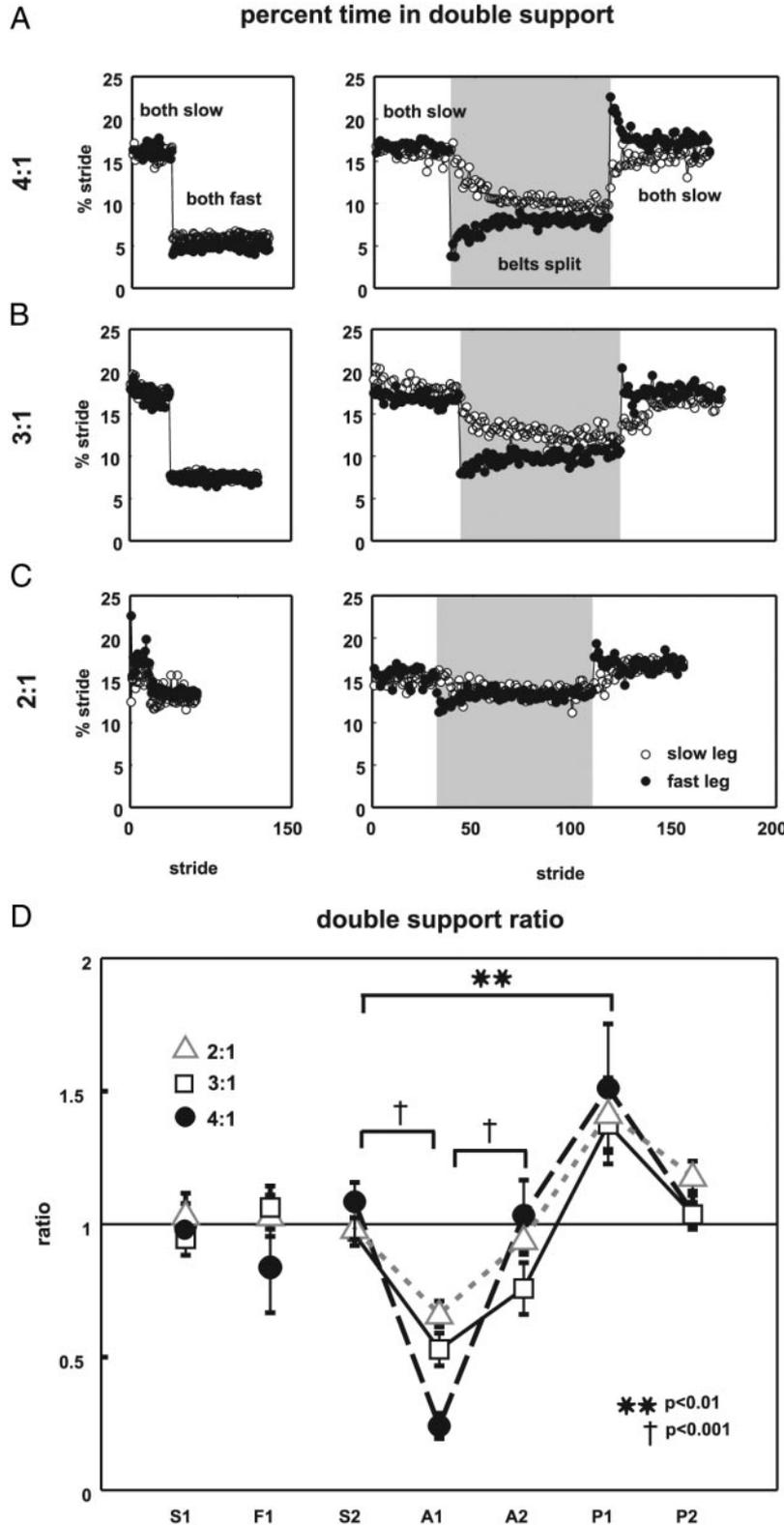


FIG. 6. Group stride-by-stride plots of double support time for (A) 4:1, (B) 3:1, and (C) 2:1 conditions. All conventions are the same as in Fig. 3. Double support is symmetric when switching from walking with both belts tied at slow versus fast speeds (*left*). It is asymmetric early in split-belt adaptation, with greater asymmetries for larger speed ratios, but moves toward symmetry throughout the adaptation period. There is an aftereffect with the reverse asymmetry in the postadaptation period. *D*: double support ratio (fast/slow) averaged for 5 strides from each period across all subjects (as in Fig. 3, *E* and *F*). Values equal to 1 represent perfect symmetry. Symmetry is significantly different from baseline in early adaptation (S2 vs. A1) and changes significantly from early to late adaptation to restore symmetry (A2 vs. A1). There is a significant aftereffect consisting of opposite asymmetry early postadaptation (S2 vs. P1).

more flexed than the fast limb at weight transfer in early adaptation compared with the both slow period ( $P < 0.001$ ). This difference diminished during adaptation ( $P < 0.001$ ) and reversed in early postadaptation such the fast limb was significantly more flexed than the slow limb at weight transfer ( $P < 0.001$ , Fig. 8*B*). There was no effect of the speed ratio on this measure.

Last, we quantified the rate of adaptation. We used double support times for this analysis because they showed robust adaptation and postadaptation effects and had the least stride-to-stride variability, producing the best curve fitting results. However, inspection of other parameters revealed a similar time course of adaptation. Curve fits were done on the double

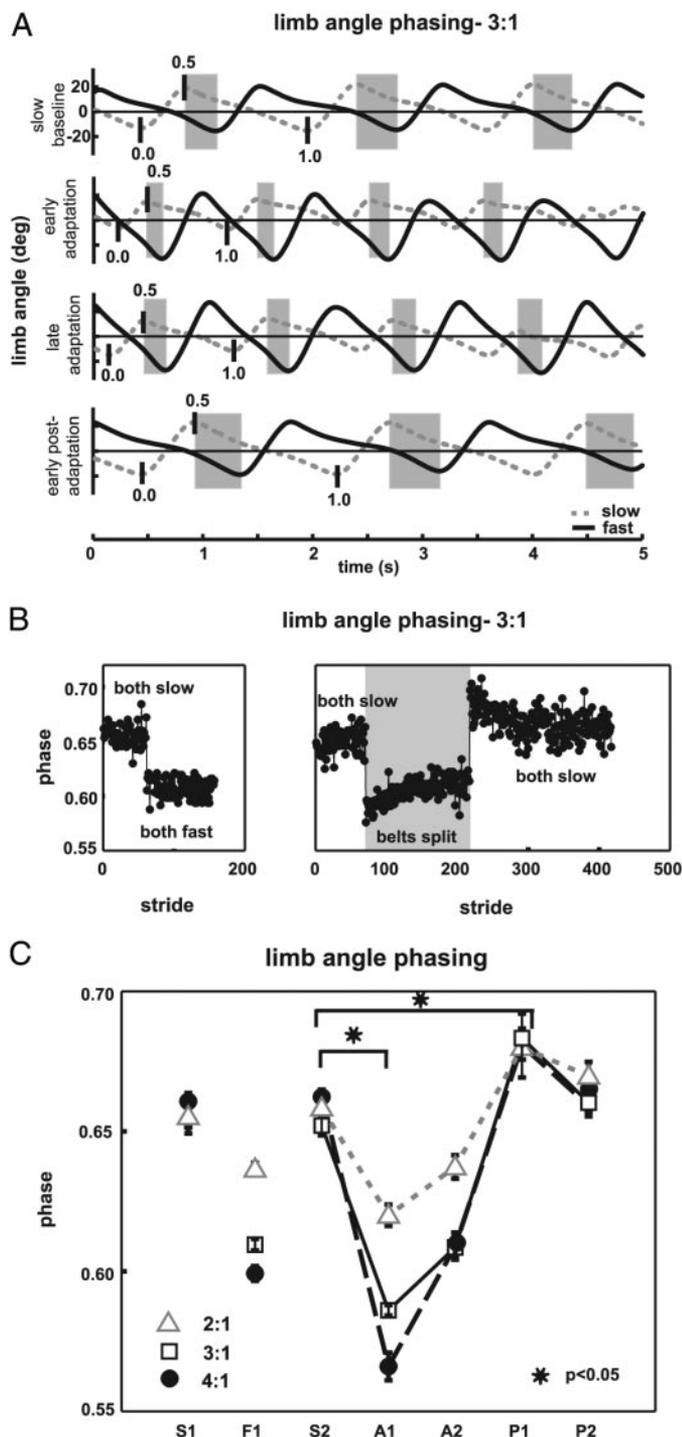


FIG. 7. *A*: limb angle plotted against time for the slow (gray dashed) and fast (solid) limbs during the 2nd slow baseline, early adaptation, late adaptation, and early postadaptation experimental periods. Data are from an individual subject in the 3:1 speed condition. Positive values indicate limb flexion angle, and negative values indicate limb extension angle. Events marked by 0, 0.5, and 1.0 indicate events of the slow limb used for the dual referent phase analysis. Gray shaded areas represent phasing of peak fast limb extension relative to slow limb flexion. Note that limb phase shortens in early adaptation but lengthens by late adaptation. There is an aftereffect with longer limb phasing postadaptation. *B*: stride-by-stride plot of limb extension phasing from the same subject as in *A* with the same conventions as in Fig. 3. A clear adaptation effect is present, with a postadaptation aftereffect. *C*: averages over the 1st 5 strides (S1, F1, S2, A1, P1) or last 5 strides (A2, P2) of an experimental period for the group in each speed ratio condition. Larger phase shifts occur for the greater speed ratios. There is a significant aftereffect during early postadaptation.

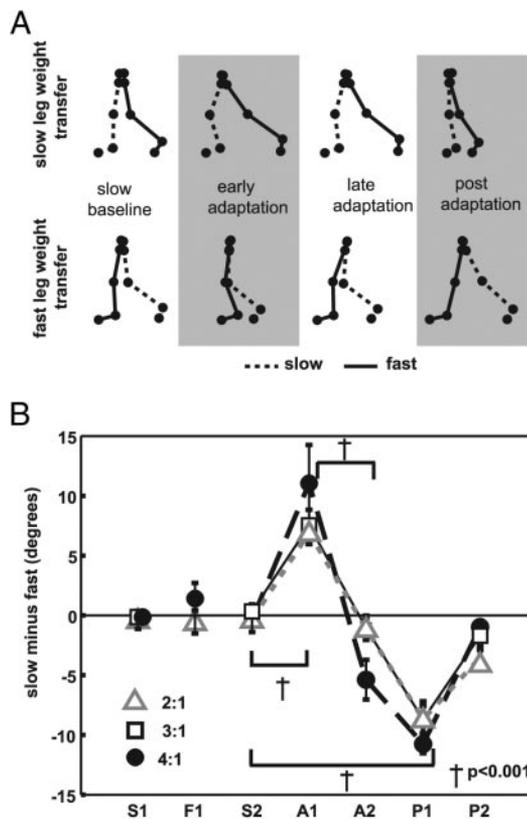


FIG. 8. *A*: limb orientations at weight transfer (i.e., trailing leg lift-off). Dots mark the toe, ankle, knee, hip, and pelvis. *Top*: weight transfer to the slow leg (dotted). *Bottom*: weight transfer to the fast leg (solid). The 1st stride from experimental periods S2–P1 is shown for a subject in the 4:1 condition. Note that the limbs are configured similarly at baseline (cf. *top* and *bottom*). Asymmetry occurs in early adaptation (1st gray shaded), but symmetry is largely re-established by late adaptation. There is an aftereffect in postadaptation (2nd gray shaded region). *B*: averages over the 1st 5 strides (S1, F1, S2, A1, P1) or last 5 strides (A2, P2) of an experimental period for the different groups. Here we show the difference between the leading limb angles at the time of each weight transfer. A value of 0 indicates that the 2 leading limbs were in the same position; a positive value indicates that the slow limb was more flexed; and a negative value indicates that the fast limb was more flexed at weight transfer. There is a significant change in symmetry in early adaptation (A1 vs. S2) and in late adaptation (A1 vs. A2). There is also a significant aftereffect postadaptation (P1 vs. S2), showing the opposite asymmetry as was produced in early adaptation. Note that similar to what is shown in *A* for an individual subject, the slow limb was markedly more flexed at weight transfer in early adaptation and the opposite was true in early postadaptation. Conventions are as in Fig. 3.

support ratio (fast/slow), which includes data from both legs in a single parameter. An example curve fit is shown in Fig. 9A from the 3:1 condition. Group results from this analysis revealed that the rate of adaptation of the double support ratio increased as the speed ratio increased (Fig. 9B). This was true even when differences in stride times between the conditions were accounted for. However, subject-to-subject variation was still relatively high in this small sample size, so that these differences did not reach statistical significance.

DISCUSSION

We have shown that adaptive changes in interlimb coordination occur after short bouts of training on a split-belt treadmill (10 min) and that these changes are stored and expressed as aftereffects. In contrast, intralimb parameters do not adapt

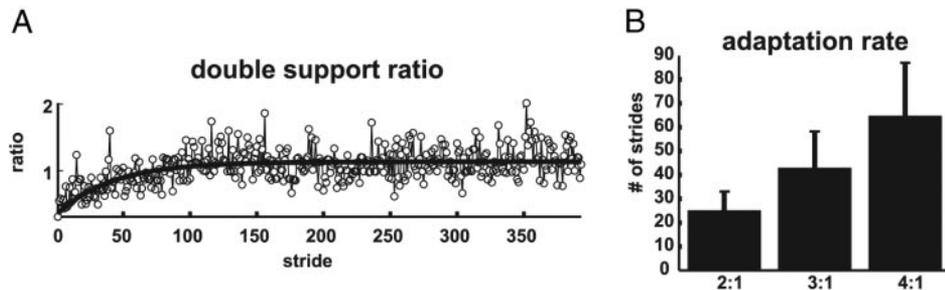


FIG. 9. An example of a curve fit for the double support ratio for a subject in the 3:1 condition is shown in A. Solid line is the curve fit to the stride-by-stride value of the double support ratio. Time constant of this curve fit is 43 strides. B: average (over subjects) number of strides required to proceed two-thirds of the way through the adaptation process for each speed ratio condition. Error bars represent  $\pm$ SE. Adaptation of double support takes increasingly more time as the speed ratio increases.

and do not show aftereffects when the belts are returned to the same speed. Similar to previous studies (Prokop et al. 1995), our subjects also had a perceptual aftereffect from walking on the split-belt treadmill, such that they felt that the legs were moving at different speeds when they were, in fact, moving at the same speed. This could be caused by a change in proprioceptive sense of the legs, or perhaps more likely, a mismatch in the expected versus actual sensory input from each leg for a given set of motor commands.

Previous studies of cats, human infants, and adults have focused on basic temporal and spatial features of split-belt walking, without addressing inter- versus intralimb differences or adaptation and storage of a new pattern (Dietz et al. 1994; Forssberg et al. 1980; Jensen et al. 1998; Kulagin and Shik 1970; Prokop et al. 1995; Thelen et al. 1987; Yang et al. 2004). All studies have shown speed appropriate changes in intralimb parameters such as stance and swing times on the split-belt treadmill, similar to what we report here. Adult humans have also been shown to require several strides to change stance (and swing) times when they first encounter the split-belt treadmill (Prokop et al. 1995). In contrast, we found that these parameters changed almost immediately, and further showed no aftereffects in them after split-belt training. One difference between the studies is that we stopped and started the treadmill between each period (i.e., belts tied vs. split), whereas they switched from tied to split-belt walking midstream; this midstream transition may have required a few strides to switch to the split-belt pattern. Only one study in cats has looked for the presence or absence of motor aftereffects after split-belt walking and found adaptive changes in double support times (Ito et al. 1998). Here we show for the first time that there are differences between the adaptability of intra and interlimb coordination during human bipedal gait.

Similar adaptation studies have been done for arm movements, although fewer exist for walking. Adaptation occurs for changes in load during catching (Lang and Bastian 1999), altered dynamics during reaching (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994), and altered gaze direction from prisms during reaching and walking (Martin et al. 1996b; Morton and Bastian 2004b). These processes are similar to the split-belt adaptation in that they occur within a single session of practice and they result in aftereffects when the perturbation is removed. They are different from the split-belt adaptation in that adapted parameters are intralimb and are related to another perturbation like altered dynamics or gaze direction. Of interest is that lesion studies have shown that all of these adaptations seem to require the cerebellum (Lang and Bastian 1999; Martin et al. 1996a; Maschke et al. 2004; Smith and Shadmehr 2004), with the exception of Coriolis perturbations (Lackner and Dizio 1994), for which patient performance has not been

tested. Another type of locomotor adaptation has been reported when walking on a rotating treadmill (Gordon et al. 1995; Weber et al. 1998). Similar to our results, this adaptation occurs within a short time (15 min) and results in a robust aftereffect. One important difference is that podokinetic adaptation is thought to alter the relationship between the trunk and stance limb yaw rotations with no change in interlimb coordination; split-belt adaptation alters interlimb relationships. It may be that very different systems are involved in these processes: one that alters body orientation relative to the feet versus one that alters phase between the legs.

Adaptations such as these require error information to drive the changes that take place. As error is reduced, the adaptation is complete. We expect that the error signal for split-belt should reflect some difference between the limbs. Errors in limb phasing or relative orientation might drive this process. We think it is less likely that kinematic parameters at single joints drive the process because they change very little during adaptation and show minimal aftereffects, which are needed to drive the readaptation process.

#### Pattern generation and split-belt walking

There are three results from this study that speak to the organization of putative pattern-generating circuits in adult humans. First, we see relatively invariant patterns of intralimb joint motion timing, regardless of whether the two legs walk at the same or different speeds. This result is present for all joint pairs within a limb, but strongest for timing between hip and knee, probably because of greater biomechanical coupling, but possibly because of greater neural coupling, of these two joints. This shows that there are circuits that can drive intralimb kinematics in an invariant way, independent of changes in interlimb coordination. One interpretation is that there are separate pattern-generating circuits for each of the two legs, although these can be coupled somewhat flexibly. Consistent with this, other animals seem to show preservation of basic intralimb patterns (e.g., rostral and pocket scratch in turtle), even when they are performed as a mixed-form interlimb pattern, where one limb makes a rostral scratch and the other a pocket scratch (Field and Stein 1997).

Second, our subjects maintain a 1:1 interlimb stepping pattern on the treadmill, regardless if the speeds were 2:1, 3:1, or 4:1. Only one subject took one 2:1 "air" step on the first step in the 4:1 speed condition. This finding is different from that for split-belt treadmill walking in spinal walking cats or supported infant stepping; both spontaneously produce multiple stepping on one limb relative to the other at the speed ratios that we tested (Forssberg et al. 1980; Thelen et al. 1987; Yang et al. 2004). Other animals, such as spinal turtle, also produce

2:1 interlimb coordination patterns during scratching and swimming movements (Field and Stein 1997). It is possible that our results are different because of a mechanical need to have a 1:1 ratio for better stability and balance during adult bipedal walking. It should be noted, however, that our subjects did hold onto a safety bar that was more than sufficient to reduce balance demands (Jeka and Lackner 1994), so they theoretically were not required to produce this pattern to maintain upright stability. We have also found (unpublished observations) that subjects can make themselves adopt a 2:1 stepping pattern, although they comment that this requires conscious effort and “doesn’t feel as much like walking, more like trying to learn a dance step.” Therefore we suspect that there is a strong bias toward 1:1 interlimb neural coupling between circuits that control the two legs during walking in adults.

Third, our main finding is that interlimb motor parameters gradually adapt during split-belt walking. Changes in interlimb parameters paralleled the behavioral observation of a limp in early adaptation, a reduced limp in late adaptation, and the opposite limp postadaptation (after training). This adaptation took longer for larger speed ratios and is in line with the subjective experience of the participants, who all felt like their gait became more natural during adaptation and felt the opposite asymmetry postadaptation. Thus in the adult human nervous system, interlimb coordination can be independently controlled and modified without necessarily altering many aspects of intralimb coordination. This also suggests that neural elements that control interlimb coordination are dissociable from those that control intralimb coordination during human bipedal walking.

#### *Why adapt interlimb coordination?*

Adaptation of the interlimb parameters largely restored symmetry to the gait cycle. There are several reasons why this might occur. First, symmetry has inherent advantages for stability. Even though subjects held onto the safety bar, which greatly improves balance (Jeka and Lackner 1994), they still may optimize gait parameters to reduce the likelihood of becoming unstable. For example, equalizing double support during adaptation allows for comparable transition times between stance and swing on each leg. Adapting the angle of the leading limb at weight transfer is critical; this is the time when the body’s center of mass is propelled forward toward the forefoot (Perry 1992). If the weight-accepting limb is too extended, the body’s center of mass may be propelled too far forward of the foot and if it is too flexed, the center of mass may lie too far behind the foot; both situations reduce stability and could lead to falling. Second, symmetric walking patterns are probably more efficient than asymmetric patterns. For example, it is known that in amputees and persons with hemiparesis, the greater the gait asymmetry, the slower the walking speed (Brandstater et al. 1983; Donker and Beek 2002; Roth et al. 1997; Titianova et al. 2003), and slower walking is associated with greater energy costs (Zampano et al. 1995). Third, neural interlimb coupling mechanisms might be biased toward producing symmetric patterns for walking. It is known that there are phase-dependent responses in one leg based on the activity of the contralateral leg during other reciprocal leg movements like cycling (Ting et al. 2000). In this task, it is

possible that similar phase-dependent influences of one leg on the other lead to the changes observed in the interlimb parameters. This may be a direct consequence of the organization of circuits that generate interlimb patterns.

Note that the interlimb parameters that adapt are not necessarily independent, but can be simultaneously altered by phase shifting one limb’s movement relative to the other. In our experiments, limb angle phasing changed in early adaptation because of altered stance and swing times. Specifically, there were earlier peaks in the limb extension angle on the fast leg because of a shorter stance time and later peaks in the limb extension angle on the slow leg because of a longer stance time. Limb angle phasing adapted slowly and showed aftereffects in the postadaptation phase. Theoretically, even small shifts in phase can produce robust changes in interlimb parameters that are comparable with what we see in the early split-belt condition of our experiments (i.e., early adaptation). This is shown in Fig. 10, which shows the right and left limb angles for both legs moving at the same speed (0.5 m/s, Fig. 10A); the phase is 0.63, with symmetric double support times and limb angles at weight transfer. Figure 10B shows the same data after we manually introduced a phase shift similar to what we saw early in 3:1 walking (double referent shift of  $-0.06$  to produce a phase of 0.57). This manipulation makes the double support times and limb angles at weight acceptance asymmetric, and the pattern is similar to early split-belt walking. In addition, this example also shows that asymmetric gait patterns may exist, even when stance/swing times are symmetric.

#### *What CNS regions could adapt interlimb coordination?*

We predict that the nervous system should have a means to estimate and adjust phase between the limbs and detect errors in this relationship. We expect that sensory information or motor command information from both of the limbs is necessary for this process. Sensory information about hip angle and loading from the ipsilateral limb affects transitions from stance to swing (Duysens and Pearson 1980; Grillner and Rossignol 1978; Pang and Yang 2000). Afferent feedback from a given limb also strongly affects the contralateral limb in spinal cat (Giuliani and Smith 1987), human pedaling movements (Ting et al. 1998, 2000), and walking (Verschuere et al. 2002). The motor state of one limb, even under isometric conditions, can also alter contralateral limb activity during cyclic movements like human pedaling (Ting et al. 2000).

It is possible that spinal networks could be used to adaptively adjust phasing between the limbs. In spinal turtle, removal of hemisegments of the spinal cord changes bilateral patterns that occur during fictive scratching (Stein et al. 1995), with deletions of contralateral extensor activity. Thus interlimb flexion–extension phasing is disrupted by a lesion of only one side of the spinal cord. Stein et al. (1995) suggested that the neural elements that coordinate interlimb phase are embedded in pattern generators in a bilateral shared core of the spinal cord.

Another possibility is that supraspinal centers are involved. More specifically, there is good evidence to suggest that the cerebellum could be important for this adaptation. It receives information about the state of spinal pattern generating circuits (through ventral spinocerebellar pathways) and the sensory state of the limbs bilaterally (through dorsal spinocerebellar

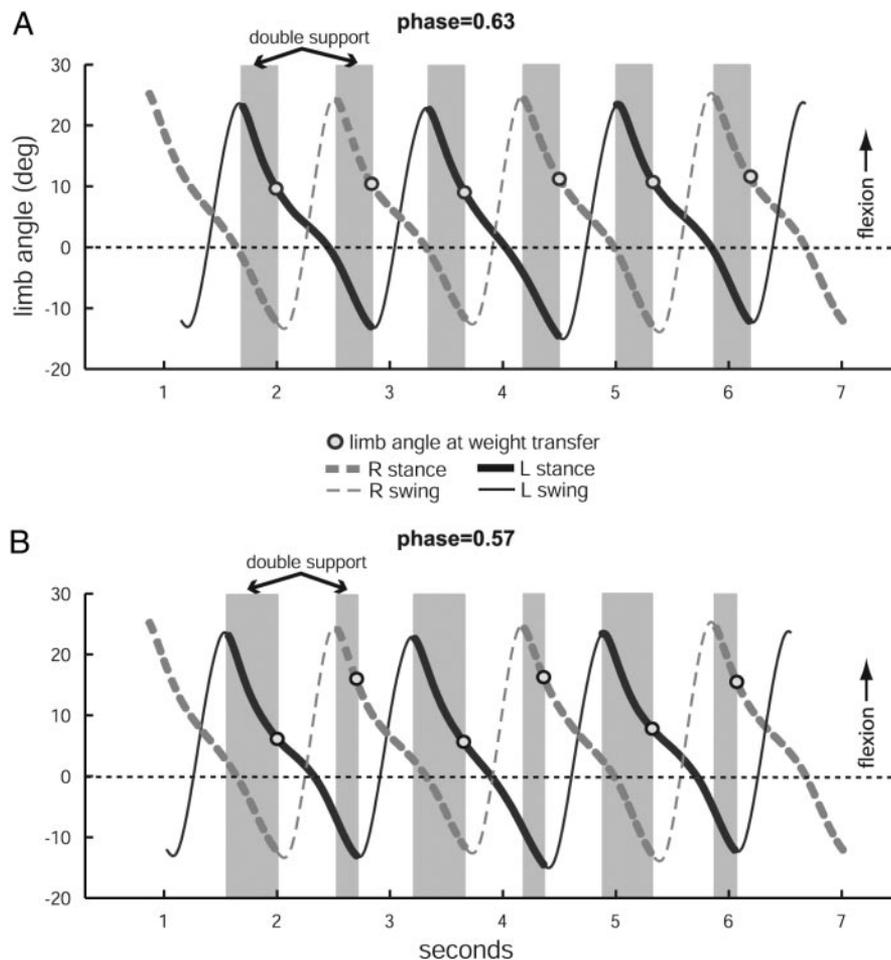


FIG. 10. *A*: example of limb angles plotted against time for right and left legs walking at 0.5 m/s (belts tied). Phase is 0.63 using the double referent calculation. Gray shaded regions show double support times and open circles show the limb angles at weight transfer; both are symmetric. *B*: same data with left leg limb angle trace shifted 150 ms earlier in time. This results in a phase of 0.57, which is comparable with the shift observed in 3:1 walking experiments. This phase shift makes the left leg similar to the fast leg in our split-belt experiments and the right leg similar to the slow leg. Note the double support times become unequal, with a shorter double support at the end of left leg stance vs. longer double support at the end of right leg stance. Limb angles at weight transfer also became asymmetric, with the left leg more extended during weight transfer and the right leg more flexed. These results parallel observations seen during early adaptation and suggest that phase shifts can explain changes in the other parameters.

pathways), allowing it to compare intended leg movements with actual leg motions and elicit corrections. Dorsal spinocerebellar neurons also carry information about limb angles (Bosco and Poppele 2002) and respond to ipsi- or contralateral stepping (Poppele et al. 2003). A large percentage of dorsal spinocerebellar neurons also showed bipedal interactions, modulating with movement of both limbs (Poppele et al. 2003); these cells could theoretically carry information about interlimb phasing, although this was not specifically tested. Brain stem neurons of the vestibulospinal and reticulospinal pathways of cats are also active with extensor and flexor phases of locomotion, and the modulation of these neurons with the locomotor cycle is disrupted with cerebellar damage (Orlovsky 1972a,b). It is also known that decerebrate cats that can normally adapt double support times to the split-belt treadmill cannot do so after disruption of activity in the cerebellar vermis through NO deprivation (Yanagihara and Kondo 1996). Finally, our preliminary studies in humans with cerebellar damage show that they do not adapt interlimb parameters during split-belt walking and show little or no aftereffects from practice (Morton and Bastian 2004a).

We have not yet tested whether split-belt treadmill walking generalizes to other contexts. For example, it is important to know if this adaptation induces aftereffects in any parameters during overground walking, where stance speed is no longer constrained by the treadmill. Aftereffects in intralimb parameters like stride length might be expressed overground, causing

subjects to walk in a curved trajectory, which is not possible when walking on a treadmill. Overground aftereffects after treadmill training have been observed in other types of locomotor tasks, such as circular treadmill walking (Gordon et al. 1995; Weber et al. 1998) and treadmill running (Anstis 1995), although neither paradigm tests reorganization of motor patterns between the legs. The extent of generalization to other forms of locomotion, such as backward walking or running, is also important because it indicates whether the adaptation is caused by alterations of neural circuits specific for forward walking or shared circuits used for generation of multiple locomotor patterns.

In conclusion, the results of this study reveal, for the first time, that after walking on a split-belt treadmill, healthy human adults show a new motor pattern of locomotor interlimb coordination when the belts are returned to the same speed. This indicates that during split-belt walking, subjects adapted and stored new patterns of interlimb coordination. This adaptation was observed in the locomotor parameters whose values are calculated from the time and position of both limbs during the gait cycle. Adaptation of these parameters seems to restore some symmetry to the gait cycle that is important for stability and efficiency. In contrast, other parameters, like stance time, stride length, and intralimb joint timing, do not adapt slowly over training and showed no after-effect in the postadaptation period. These results are exciting because they raise the possibility that asymmetric gait patterns resulting from some types

of CNS damage could be remediated with specific adaptive rehabilitation strategies using a split-belt treadmill. These results also suggest that the adult nervous system employs separate processes to change and store different locomotor parameters. We speculate that the differences in these processes may be related to the varying complexity of the parameters, task demands, and/or the level of supraspinal control necessary for their adaptation.

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## REFERENCES

- Anstis S. Aftereffects from jogging. *Exp Brain Res* 103: 476–478, 1995.
- Batschelet E. *Circular Statistics in Biology*. New York: Academic, 1981.
- Berkowitz A and Stein PS. Activity of descending propriospinal axons in the turtle hindlimb enlargement during two forms of fictive scratching: phase analyses. *J Neurosci* 14: 5105–5119, 1994.
- Bosco G and Poppele RE. Encoding of hindlimb kinematics by spinocerebellar circuitry. *Arch Ital Biol* 140: 185–192, 2002.
- Brandstater ME, de Bruin H, Gowland C, and Clark BM. Hemiplegic gait: analysis of temporal variables. *Arch Phys Med Rehabil* 64: 583–587, 1983.
- Courtine G and Schieppati M. Human walking along a curved path. I. Body trajectory, segment orientation and the effect of vision. *Eur J Neurosci* 18: 177–190, 2003.
- Courtine G and Schieppati M. Tuning of a basic coordination pattern constructs straight-ahead and curved walking in humans. *J Neurophysiol* 91: 1524–1535, 2004.
- Dietz V, Zijlstra W, and Duysens J. Human neuronal interlimb coordination during split-belt locomotion. *Exp Brain Res* 101: 513–520, 1994.
- Donker SF and Beek PJ. Interlimb coordination in prosthetic walking: effects of asymmetry and walking velocity. *Acta Psychol (Amst)* 110: 265–288, 2002.
- Duysens J and Pearson KG. Inhibition of flexor burst generation by loading ankle extensor muscles in walking cats. *Brain Res* 187: 321–332, 1980.
- Earhart GM, Fletcher WA, Horak FB, Block EW, Weber KD, Suchowersky O, and Melvill Jones G. Does the cerebellum play a role in podokinetic adaptation? *Exp Brain Res* 146: 538–542, 2002.
- Field EC and Stein PS. Spinal cord coordination of hindlimb movements in the turtle: intralimb temporal relationships during scratching and swimming. *J Neurophysiol* 78: 1394–1403, 1997.
- Forsberg H, Grillner S, Halbertsma J, and Rossignol S. The locomotion of the low spinal cat. II. Interlimb coordination. *Acta Physiol Scand* 108: 283–295, 1980.
- Giuliani CA and Smith JL. Stepping behaviors in chronic spinal cats with one hindlimb deafferented. *J Neurosci* 7: 2537–2546, 1987.
- Gordon CR, Fletcher WA, Melvill Jones G, and Block EW. Adaptive plasticity in the control of locomotor trajectory. *Exp Brain Res* 102: 540–545, 1995.
- Grillner S and Rossignol S. On the initiation of the swing phase of locomotion in chronic spinal cats. *Brain Res* 146: 269–277, 1978.
- Ito S, Yuasa H, Luo ZW, Ito M, and Yanagihara D. A mathematical model of adaptive behavior in quadruped locomotion. *Biol Cybern* 78: 337–347, 1998.
- Jeka JJ and Lackner JR. Fingertip contact influences human postural control. *Exp Brain Res* 100: 495–502, 1994.
- Jensen L, Prokop T, and Dietz V. Adaptational effects during human split-belt walking: influence of afferent input. *Exp Brain Res* 118: 126–130, 1998.
- Kulagin AS and Shik ML. [Interaction of symmetric extremities during controlled locomotion]. *Biofizika* 15: 164–170, 1970.
- Lackner JR and Dizio P. Rapid adaptation to Coriolis force perturbations of arm trajectory. *J Neurophysiol* 72: 299–313, 1994.
- Lang CE and Bastian AJ. Cerebellar subjects show impaired adaptation of anticipatory EMG during catching. *J Neurophysiol* 82: 2108–2119, 1999.
- Martin TA, Keating JG, Goodkin HP, Bastian AJ, and Thach WT. Throwing while looking through prisms. I. Focal olivocerebellar lesions impair adaptation. *Brain* 119: 1183–1198, 1996a.
- Martin TA, Keating JG, Goodkin HP, Bastian AJ, and Thach WT. Throwing while looking through prisms. II. Specificity and storage of multiple gaze-throw calibrations. *Brain* 119: 1199–1211, 1996b.
- Maschke M, Gomez CM, Ebner TJ, and Konczak J. Hereditary cerebellar ataxia progressively impairs force adaptation during goal-directed arm movements. *J Neurophysiol* 91: 230–238, 2004.
- Morton SM and Bastian AJ. Cerebellar adaptation of locomotion: impaired adaptation during split-belt but not tied treadmill locomotion. *Soc Neurosci Abstr* 415.413, 2004a.
- Morton SM and Bastian AJ. Prism adaptation during walking generalizes to reaching and requires the cerebellum. *J Neurophysiol* 92: 2497–2509, 2004b.
- Orlovsky GN. Activity of vestibulospinal neurons during locomotion. *Brain Res* 46: 85–98, 1972a.
- Orlovsky GN. The effect of different descending systems on flexor and extensor activity during locomotion. *Brain Res* 40: 359–371, 1972b.
- Pang MY and Yang JF. The initiation of the swing phase in human infant stepping: importance of hip position and leg loading. *J Physiol* 528: 389–404, 2000.
- Perry J. *Gait Analysis: Normal and Pathological Function*. Thorofare, NJ: SLACK Inc., 1992.
- Poppele RE, Rankin A, and Eian J. Dorsal spinocerebellar tract neurons respond to contralateral limb stepping. *Exp Brain Res* 149: 361–370, 2003.
- Prokop T, Berger W, Zijlstra W, and Dietz V. Adaptational and learning processes during human split-belt locomotion: interaction between central mechanisms and afferent input. *Exp Brain Res* 106: 449–456, 1995.
- Reisman DS, Block H, and Bastian AJ. Split-belt locomotion: adaptation and after-effects from short-term training. *Soc Neurosci Abstr* 415.413, 2004.
- Roth EJ, Merbitz C, Mroczek K, Dugan SA, and Suh WW. Hemiplegic gait. Relationships between walking speed and other temporal parameters. *Am J Phys Med Rehabil* 76: 128–133, 1997.
- Shadmehr R and Mussa-Ivaldi FA. Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14: 3208–3224, 1994.
- Smith MA and Shadmehr R. Intact ability to learn internal models of arm dynamics in Huntington's disease but not cerebellar degeneration. *J Neurophysiol* 93: 2809–2821, 2004.
- Stein PS, Victor JC, Field EC, and Currie SN. Bilateral control of hindlimb scratching in the spinal turtle: contralateral spinal circuitry contributes to the normal ipsilateral motor pattern of fictive rostral scratching. *J Neurosci* 15: 4343–4355, 1995.
- Thelen E, Ulrich BD, and Niles D. Bilateral coordination in human infants: stepping on a split-belt treadmill. *J Exp Psychol Hum Percept Perform* 13: 405–410, 1987.
- Ting LH, Kautz SA, Brown DA, and Zajac FE. Contralateral movement and extensor force generation alter flexion phase muscle coordination in pedaling. *J Neurophysiol* 83: 3351–3365, 2000.
- Ting LH, Raasch CC, Brown DA, Kautz SA, and Zajac FE. Sensorimotor state of the contralateral leg affects ipsilateral muscle coordination of pedaling. *J Neurophysiol* 80: 1341–1351, 1998.
- Titianova EB, Pitkanen K, Paakkonen A, Sivenius J, and Tarkka IM. Gait characteristics and functional ambulation profile in patients with chronic unilateral stroke. *Am J Phys Med Rehabil* 82: 778–786, 2003.
- Verschueren SM, Swinnen SP, Desloovere K, and Duysens J. Effects of tendon vibration on the spatiotemporal characteristics of human locomotion. *Exp Brain Res* 143: 231–239, 2002.
- Weber KD, Fletcher WA, Gordon CR, Melvill Jones G, and Block EW. Motor learning in the “podokinetic” system and its role in spatial orientation during locomotion. *Exp Brain Res* 120: 377–385, 1998.
- Yanagihara D and Kondo I. Nitric oxide plays a key role in adaptive control of locomotion in cat. *Proc Natl Acad Sci USA* 93: 13292–13297, 1996.
- Yang JF, Lam T, Pang MY, Lamont E, Musselman K, and Seinen E. Infant stepping: a window to the behaviour of the human pattern generator for walking. *Can J Physiol Pharmacol* 82: 662–674, 2004.
- Zamparo P, Francescato MP, De Luca G, Lovati L, and di Prampero PE. The energy cost of level walking in patients with hemiplegia. *Scand J Med Sci Sports* 5: 348–352, 1995.