## RESEARCH ARTICLE

# Mode-dependent control of human walking and running as revealed by split-belt locomotor adaptation

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## ABSTRACT

Here, we investigate the association of neural control between walking and running, and in particular, how these two gait modes at different velocities are controlled by the central nervous system. The subjects were fully adapted by acquiring modified motor patterns to either walk or run on a split-belt treadmill driven in split mode (asymmetry in the velocities of two belts at 1.0 and 2.0 m s$^{-1}$). Subsequently, we tested how the adaptation affected walking and running at three different velocities in the tied mode (equal belt velocities). At 0.75 m s$^{-1}$, we found a preference to walk, at 1.50 m s$^{-1}$, there was a preference to both walk and run, and at a velocity of 2.25 m s$^{-1}$ there was a preference to run. Both walking and running on the split belt resulted in the emergence of a significant aftereffect (asymmetrical movement) at all of the velocities tested when walking after adapting to walk and running after adapting to run. However, for contrasting modes (i.e. running after adapting to walk and walking after adapting to run), such aftereffects were far less evident at all velocities; thus showing only limited transfer across gait modes. The results demonstrate a clear mode dependency in the neural control of human walking and running. In addition, only for walking, was there a degree of velocity dependency.

KEY WORDS: Walk, Run, Adaptation, Split belt, Transfer

## INTRODUCTION

In human walking and running, one gait is preferred over the other at a given velocity: walking is preferred at slower velocities and running at faster velocities. This has been well elucidated with traditional walk-to-run transition paradigms. With a subject walking comfortably on a treadmill at a given velocity, a gradual increase in the treadmill velocity results in a discrete behavioral change from walking to running, and vice versa for decreasing velocity (Thorstensson and Roberthson, 1987; Diedrich and Warren, 1995; Ivanenko et al., 2011; Hagio et al., 2015).

Regarding the neural control of human locomotion, it was demonstrated that the adaptation (i.e. an acquisition or storage of novel movement patterns) that took place in a specific task or context was not shared with other tasks/contexts; thus, a limited transfer occurs (Choi and Bastian, 2007; Vasudevan and Bastian, 2010). In animal locomotion, such as swimming in larval zebrafish (McLean et al., 2008) and stepping in mice (Talpalar et al., 2013),

there are specific groups of spinal interneurons that are responsible for different modes and in particular, different movement frequencies. These findings suggest the existence of different neural functional networks underlying different locomotion tasks.

In human walking and running, Ogawa et al. (2012), based on locomotor adaptation on a split-belt treadmill, demonstrated that the adaptation that took place in one gait mode transferred to the other mode to only a limited degree, showing the specificity of neural control being capable of each gait mode. However, the result was based on walking and running at a single velocity at which the subjects could both walk and run comfortably despite the fact that humans can both walk and run for certain ranges of velocity and the difference in the preferred velocity of the two gaits. It is therefore, necessary to further consider the possible influence of gait velocity.

On the basis of their locomotor adaptation study of human walking, Vasudevan and Bastian (2010) suggested the specificity of neural control for walking at different velocities. They observed that the degree of adaptation transfer was dependent on the velocities of walking and that this dependency was most significant under the velocities used for the adaptation. Given the results of this velocity-dependent control of walking, there is a further possibility that not only walking but also the human gaits (walking and running) as a whole may be controlled by the central nervous system (CNS) in a velocity-dependent manner (an alternative to the mode specificity of walking and running described by Ogawa et al., 2012).

In the present study, we therefore addressed how walking and running at different velocities are controlled by the CNS; that is, we investigated whether the two modes are dependent on the gait mode or on the velocity. This question was addressed by using the same split-belt adaptation paradigm as in our previous study (Ogawa et al., 2012). Briefly, subjects adapt to walk or run on a split-belt treadmill (driven in 'split' mode, with differing velocities on two belts of the treadmill). This adaptation results in the emergence of asymmetrical movements (an aftereffect) upon return to the normal belt condition (the 'tied' mode, with the treadmill's two belts at the same velocity). We then addressed the degree of adaptation transfer between walking and running at different velocities (three velocities, each reflecting a preference to walk, to walk and run, and to run) by assessing the magnitude of asymmetry in each gait under the respective velocities.

A schematic overview of our hypothesis is presented in Fig. 1. One possibility is 'mode-dependent control'. This possibility would be supported by limited or no transfer of the adaptation (and therefore, significantly larger aftereffects in the adapted mode) irrespective of the velocity (Fig. 1A). Another possibility is 'velocity-dependent control'. This second possibility would be supported if the aftereffect size were rather similar for walking and running under each velocity setting, each reflecting preferences to execute the particular gait mode. Since walking is preferred to move slower, greater aftereffects are evident irrespective of the mode when moving 'slow' (0.75 m s$^{-1}$) after adapting to walk. In contrast,

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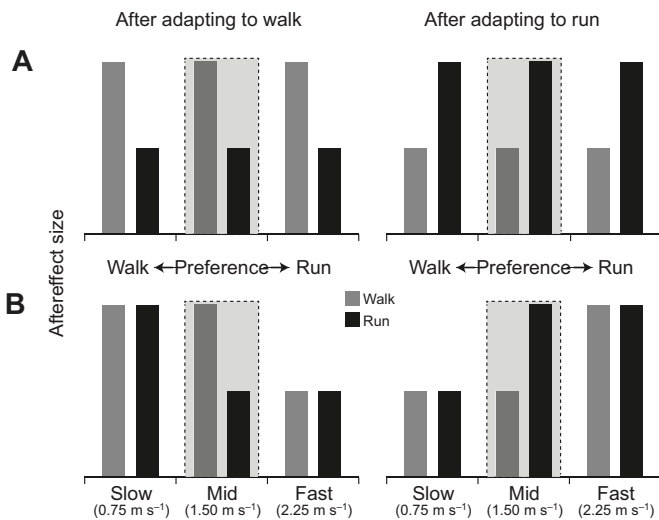
**Fig. 1. Predicted aftereffect sizes based on hypothesized mode and velocity dependency of the neural control of walking and running.** With significantly greater aftereffects in the 'mid' condition (1.50 m s$^{-1}$, gray) in the adapted mode (as previously demonstrated in Ogawa et al., 2012), (A) mode dependency shows greater aftereffects under all velocities in the adapted mode. Aftereffect sizes in (B) velocity dependency are dependent on the velocities and reflect preferences to velocities in the respective modes. Since walking is preferred to move slower, greater aftereffects are evident irrespective of the modes when moving 'slow' (0.75 m s$^{-1}$) after adapting to walk. In contrast, since running is preferred to move faster, greater aftereffects are evident irrespective of the modes under 'fast' (2.25 m s$^{-1}$) conditions after adapting to run.

since running is preferred to move faster, greater aftereffects are evident, irrespective of the mode, under the 'fast' condition (2.25 m s$^{-1}$) after adapting to run.

## RESULTS

Sixteen subjects underwent experimental protocols that were aimed to test: (1) their preference to either walk or run at given velocities,

and (2) the degree of adaptation transfer between walking and running at different velocities after adaptation on a split-belt treadmill; that is, how the acquisition or storage of modified movement patterns in one gait mode affects the subsequent task execution in the other mode (see the Materials and methods for details).

Each subject was first tested to determine their preferred velocity to spontaneously transit their gait from walking to running in accord with changing velocity of the treadmill. The mean (±s.d.) of the preferred walk-to-run transition velocity for all 16 subjects was 1.681±0.183 m s$^{-1}$.

Fig. 2 portrays the representative examples of the anteroposterior ground reaction forces (GRFs) for five consecutive gait cycles (for both left and right sides) at different time points for Experiment 1 (adaptation to walk) and Experiment 2 (adaptation to run), respectively. As shown by the GRFs, there are slight differences in the peak anterior breaking forces between the sides (even during the baseline periods) because of the natural gait patterns of the subjects. As noted earlier, these slight differences are the reason why normalizing the data is necessary in order to avoid potentially overestimating or underestimating the magnitude of the aftereffects.

The mean differences in the peak anterior force between legs during the baseline periods (slow at 0.75 m s$^{-1}$, mid at 1.50 m s$^{-1}$ and fast at 2.25 m s$^{-1}$) were: 14.6±1.1, 23.7±2.4 and 33.6±2.6 N for walking and 22.7±1.3, 24.4±1.7 and 24.9±1.8 N for running, respectively. After the adaptation period to either walk or run on the split-belt treadmill, the GRF profile showed prominent differences between legs, with an evident asymmetry in the peak anterior forces (Fig. 2). As found in the GRFs, the degree of asymmetry was far more evident in the adapted modes (i.e. walking after adaptation to walk and running after adaptation to run) and not in the opposite modes (walking after adaptation to run and running after adaptation to walk) (Fig. 2).

The time series changes in the peak anterior force are plotted over the course of the experiment for the mean values of each leg separately (Fig. 3A and Fig. 4A) and the differences between legs
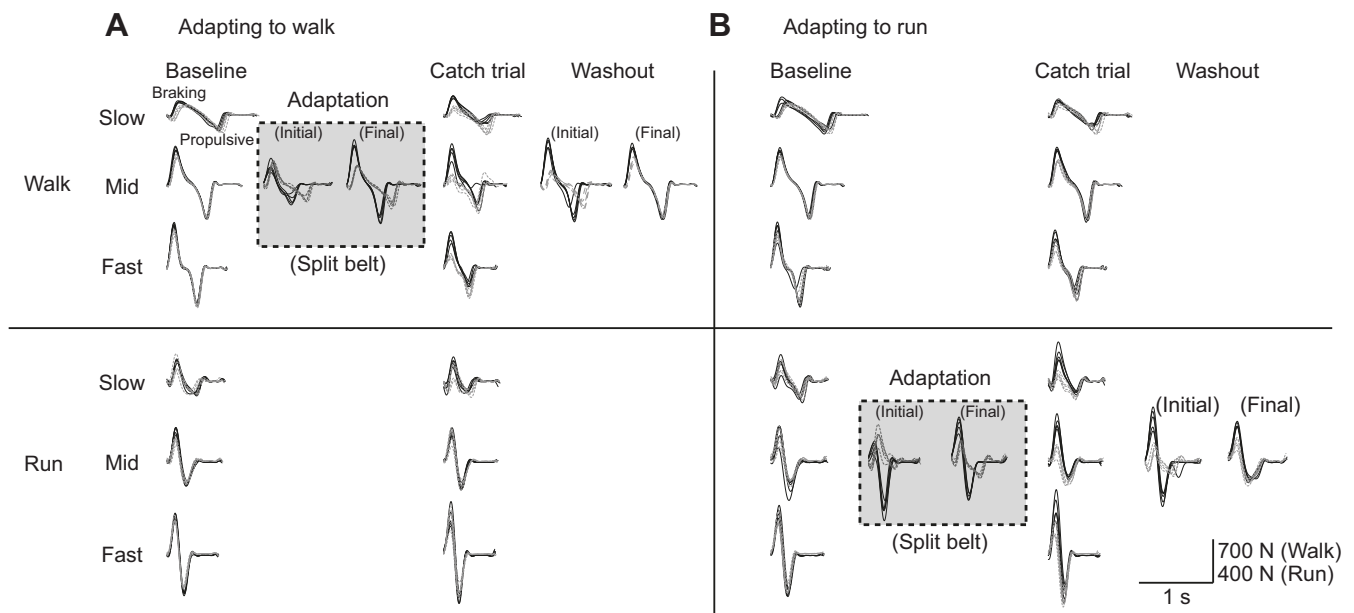


**Fig. 2. Representative examples of the anteroposterior GRFs while walking and running for five consecutive gait cycles at different time points.** (A) Experiment 1: adaptation to walk. (B) Experiment 2: adaptation to run. Solid lines shown in black represent those of faster (right) side and dashed lines shown in gray are the slower (left) side under split-belt adaptation and re-adaptation periods, respectively.
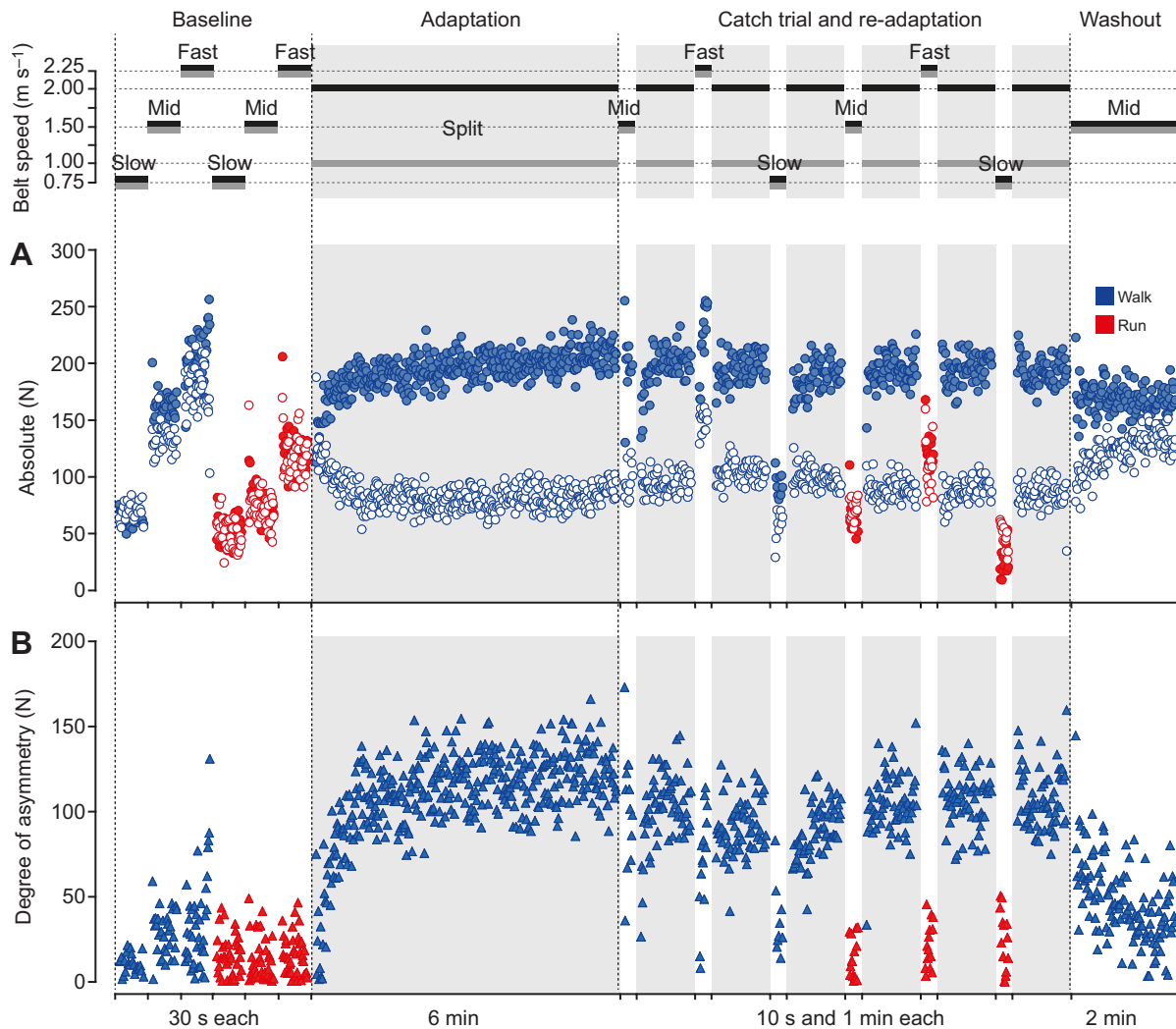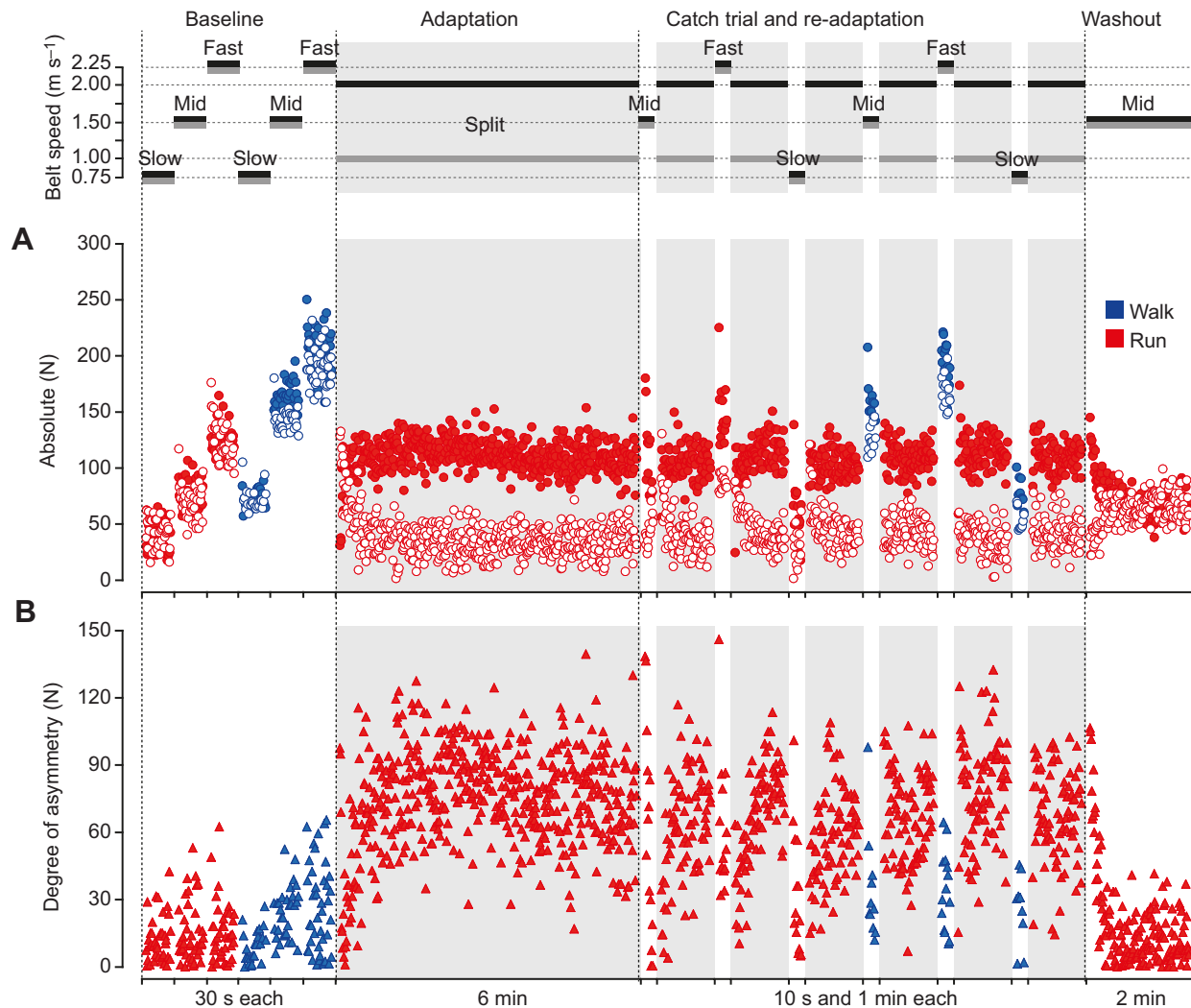
**Fig. 3. Experimental protocol and a representative example of the time series change in the peak anterior braking force in a single subject after adaptation to walk.** Experiment 1 started with both walking and running on a 'tied' treadmill with different velocities (30 s each). After adaptation period to either walk or run on 'split' belt (driven asymmetrically at 2.0 and 1.0 m s$^{-1}$ in the velocities) for 6 min, 10 s catch trials ('tied') and 1 min re-adaptations ('split') were repeated six times [to account for two gaits (walk and run) and three velocities (slow, 0.75 m s$^{-1}$; mid, 1.50 m s$^{-1}$; fast, 2.25 m s$^{-1}$). Finally, there were 2 min washout periods to either walk or run in 'tied' for 2 min. The order of exposure to different gaits during the baselines and for the catch trials were flipped in half ($N$=8) of the subjects. (A) Absolute values on a stride-to-stride basis, bilaterally. Filled circles and open circles represent the faster side (right) and the slower side (left) under the 'split' condition during the adaptation period, respectively. (B) Side-to-side differences in the peak anterior braking force for each stride cycle.

for each stride cycle (Fig. 3B and Fig. 4B) in a single subject for Experiment 1 (adaptation to walk) and Experiment 2 (adaptation to run), respectively. Generally, in the adaptation and the re-adaptation periods, the GRF component undergoes modifications distinguished in two phases: an initial rapid phase (abrupt changes in the early stages) and a subsequent slow phase (later gradual changes) and eventually a plateau. One-way analysis of variance (ANOVA) comparisons for the degree of asymmetry during the last 10 s of the adaptation and re-adaptation periods revealed no significant differences for either Experiment 1 (adaptation to walk) or Experiment 2 (adaptation to run). This indicates a stability of adaptation through the experiment.

As a consequence of the adaptation, subsequent exposure to the tied-belt condition resulted in an evident aftereffect in which the GRF was significantly asymmetric. It did, however, depend on the combination of gaits between the adaptation and the aftereffect phases. It is clear that the aftereffect size is larger under the same gaits as in the adaptation periods, as it can be found in both the

absolute value of each leg (Fig. 3A and Fig. 4A) and in the difference between the legs (Fig. 3B and Fig. 4B). A paired Student's $t$-test to evaluate the stability in the emergence of an aftereffect revealed significant differences in the degree of asymmetry between the first catch trial and the first 10 s of the washout period in Experiment 1 (adaptation to walk) ($P$<0.01) and a similar, although insignificant, tendency ($P$=0.066) in Experiment 2 (adaptation to run). The emergence of the aftereffects was therefore not stable; rather it decayed over the course of the experiments.

In Table 1, the group mean of the cadence for both walking and running during each of the catch trials is shown for both experiments. For all the velocities tested, running always showed a higher cadence compared with walking. For both Experiments 1 and 2, the statistical analysis revealed significant main effects for gait [Experiment 1 (adaptation to walk): $F$=373.788, d.f.=1, $P$<0.001; Experiment 2 (adaptation to run): $F$=758.543, d.f.=1, $P$<0.001] and velocity [Experiment 1 (adaptation to walk): $F$=370.928, d.f.=2, $P$<0.001; Experiment 2 (adaptation to run):

**Fig. 4. A representative example of the time series change in the peak anterior braking force in a single subject after adaptation to run.** (A) Absolute values on a stride-to-stride basis, bilaterally. Filled circles and open circles represent the faster side (right) and the slower side (left) under the 'split' condition during the adaptation period, respectively. (B) Side-to-side differences in the peak anterior braking force for each stride cycle.

$F$=189.319, d.f.=2, $P$<0.001]. There were also significant interactions in both experiments [Experiment 1 (adaptation to walk): $F$=151.880, d.f.=2, $P$<0.001; Experiment 2 (adaptation to run): $F$=139.373, d.f.=2, $P$<0.001].

Fig. 5A,B describe to what extent the acquired movement patterns transferred across gaits with different velocities. In Fig. 5A, where the degree of asymmetry is compared across different gaits and velocities after adapting to walk, a two-way ANOVA revealed significant main effects for gait ($F$=22.322, d.f.=1, $P$<0.001) and velocity ($F$=4.957, d.f.=2, $P$<0.05). The emergence of an aftereffect was always greater in walking than in running. In running, the mean

values were maintained near the baseline level (normalized to 1). There was also a significant interaction ($F$=7.682, d.f.=2, $P$<0.01) and *post hoc* comparisons revealed a significant difference between the mid and fast conditions (Fig. 5A). A paired Student's *t*-test comparing the aftereffect sizes between fast and mid 2 (first 10 s of the washout period) demonstrated a significant difference ($P$<0.05).

Fig. 5B compares the aftereffect sizes after adapting to run. There was a significant main effect for gait ($F$=27.343, d.f.=1, $P$<0.001) but not for velocity ($F$=3.203, d.f.=2, $P$=0.055), despite the differences in the mean values. There was also a significant interaction ($F$=8.505, d.f.=2, $P$<0.01). The results clearly show that the degree of asymmetry was always greater for running than for walking.

## DISCUSSION

The present study investigated whether adaptation acquired through walking or running on a split-belt treadmill (driven asymmetrically in velocities of two belts) transfers across the gait modes with different velocities. As found in the degree of asymmetry in the anterior braking component of the GRF, prominent aftereffects (asymmetry in the magnitude of the GRF) were evident in the adapted modes (walking after adaptation to walk and running
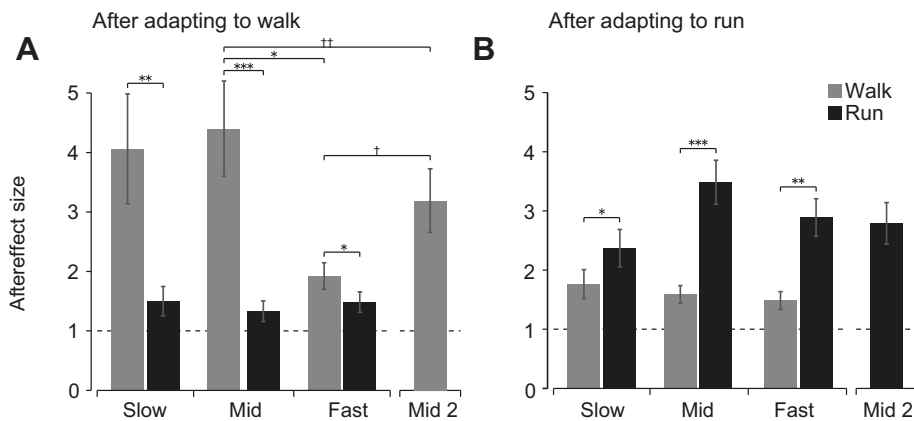
**Table 1. Group mean of the cadence (steps min$^{-1}$) during each trial period for walking and running at each velocity**

|  | Slow | | Mid | | Fast | |
|---|---|---|---|---|---|---|
|  | Walk | Run | Walk | Run | Walk | Run |
| Experiment 1 | 100.9 (3.3) | 153.0 (1.8) | 130.3 (2.0) | 161.1 (1.8) | 159.9 (2.7) | 165.3 (2.1) |
| Experiment 2 | 98.8 (3.0) | 159.3 (2.3) | 124.6 (1.8) | 164.3 (2.4) | 158.4 (3.6) | 170.6 (3.3) |

Numbers in parentheses represent s.e.m.

**Fig. 5. Group mean of the aftereffect size after adaptation to walk or run.** Aftereffect size normalized to baseline is shown for Experiment 1 (A, adaptation to walk) and Experiment 2 (B, adaptation to run). Error bars represent the s.e.m. Statistically significant differences: *$P<0.05$, **$P<0.01$, ***$P<0.001$, $^{\dagger}P<0.05$ (*t*-test), $^{\dagger\dagger}P<0.01$ (*t*-test).

after adaptation to run) at all velocities tested (slow at 0.75 m s$^{-1}$, mid at 1.50 m s$^{-1}$, fast at 2.25 m s$^{-1}$). In contrast, such aftereffects were far less evident in adjacent modes (running after adaptation to walk and walking after adaptation to run) irrespective of the velocity.

We had hypothesized that mode-dependent control would be supported if there were larger aftereffects in the adapted mode irrespective of the velocity. Support for velocity-dependent control, however, would be realized if the two gait modes exhibited a similar aftereffect size under each velocity setting. Since there was almost always a greater aftereffect size in the adapted mode irrespective of the velocities, the results of the present study indicate a largely mode-dependent control by the CNS between human walking and running. An aspect of velocity dependence was also evident, as noted in a previous study (Vasudevan and Bastian, 2010), but only for walking.

### Possible factors underlying mode dependency for walking and running

In the context of previous results on animal studies, a possible explanation for the mode-dependent control for walking and running probably arise as dissimilarities in cadence (or movement frequencies) of the respective gait modes. Here, running showed higher cadences than walking at all velocities tested (Table 1), and thus a reasonable explanation can be made based on a series of studies focusing on the swimming behavior of larval zebrafish (Budick and O'Malley, 2000; McLean et al., 2008). The swimming behavior of larval zebrafish largely occurs in two different modes (referred to as 'slow swim' and 'burst swim', respectively) depending on the movement characteristics including the movement frequency (on average, 33.8 Hz for slow swim and 56.6 Hz for burst swim) (Budick and O'Malley, 2000). In the different swimming modes of the larval zebrafish, McLean et al. (2008) demonstrated that different groups of spinal interneurons were recruited while motoneurons were recruited only incrementally or decrementally in accord with changing movement frequencies.

In addition, a recent study of the stepping movements of mice revealed aspects similar to those identified in zebrafish regarding the relationship between mode specificity and the neural mechanisms of the spinal interneurons: in mice that underwent experimental lesions in specific groups of locomotion-related spinal interneurons, the emergence of normal alternate stepping was mode-specific (as categorized in two types: slow stepping and fast stepping) and dependent on the subtypes of the spinal interneurons that underwent lesion (Talpalar et al., 2013). From the results of these basic studies, we speculate that the gait-mode-dependent control of human

walking and running observed in the present study may reflect the difference in movement frequencies found in the respective gait modes.

However, it is possible that cadence alone may not be a dominant factor distinguishing walking and running. For example, subjects walked 'fast' and ran 'slow' at an almost equal cadence in Experiment 2 (adaptation to run) (Table 1). Despite the similar cadence, the emergence of an aftereffect after adapting to run was still far less when walking 'fast' than when running 'slow' and a similar tendency was observed when the subjects walked 'fast' and ran 'slow' in Experiment 1 (adaptation to walk). Given the results, then, what factors aside from cadence were responsible for the only partial transfer of adaptation across the gait modes with different velocities?

In a series of studies addressing the association between walking and running under changing velocities, it was clearly shown that there are certain characteristic features that depend on gait rather than velocity (Cappellini et al., 2006; Ivanenko et al., 2007, 2008). For example, Cappellini et al. (2006), on the basis of recordings of activities in 32 locomotor-related muscles in humans, demonstrated that the activation timing of the basic motor patterns could be simplified into five synergistic components. These components showed different distributions in the respective gait cycles of walking and running. In that study, when walking and running were compared at the same velocities (5, 7, 9 km h$^{-1}$, and additionally 3 km h$^{-1}$ and 12 km h$^{-1}$ for walking and running), gait-dependent features were evident irrespective of, or less dependent on, the velocity of locomotion. Although speculative, and any direct association with the present results is unclear, these differences between walking and running may partially explain the present results in which the transfer of adaptation between the two gaits was limited and minimally influenced by the moving velocities. Given the differences in kinematics between walking and running (Ivanenko et al., 2007), it is also possible that more specific neural mechanisms underlying each limb movement play a significant role in the present results.

In contrast, from a perspective of the dynamic systems approach, a preference for different velocities between walking and running are the reflection of the velocity at which each gait mode is more stable and the energy expenditure is less than at other velocities (Diedrich and Warren, 1995). Thus, gait transitions to the other mode take place when less stable and the energetic cost is reduced (Diedrich and Warren, 1995). The emergence of an aftereffect in the present results, however, was not necessarily dependent on the different preference for the velocities; rather, it was dependent on the gaits.

## Velocity dependence of the aftereffects within walking and running

In the present study, in addition to the mode-dependent trends (always greater aftereffects in the adapted modes), the aftereffect sizes within each mode (aftereffects among walking after adapting to walk and running after adapting to run) varied to some extent depending on the velocities during the catch trials (Fig. 5A,B). With the greatest size of aftereffect observed under 'mid' conditions in both experiments, it was less evident in other conditions. For example, walking 'fast' after adapting to walk exhibited the least aftereffect (Fig. 5A), whereas for running after adapting to run, the aftereffect size tended to be the smallest when running 'slow' (Fig. 5B). Particularly for walking after adapting to walk, the results could be explained by the previously demonstrated velocity dependence of adaptation transfer (Vasudevan and Bastian, 2010). That is, the emergence of aftereffects was strongly linked to velocities nearest the slower side of the two belts during split-belt adaptation (Vasudevan and Bastian, 2010). This is in accord with the present results, which showed an equally great aftereffect under 'slow' ($0.75 \text{ m s}^{-1}$) and 'mid' ($1.50 \text{ m s}^{-1}$) as opposed to 'fast' ($2.25 \text{ m s}^{-1}$) velocities, relative to the velocities used for the split-belt adaptation (2.0 and $1.0 \text{ m s}^{-1}$) (Fig. 5A).

In running after adapting to run, however, the velocity dependence was not evident (as revealed by the lack of a significant main effect for the velocity after adaptation in running). This could be attributed to the difference in motor strategies between walking and running in accord with the changing gait velocities and the neural mechanisms underlying them. For example, Grillner et al. (1979) demonstrated that the cycle duration (and therefore the movement frequencies as well) of walking varied to a great extent with changing velocities, whereas that of running was far less variable. The recruitment of locomotion-related neural mechanisms is closely related to movement frequency (McLean et al., 2008; Talpalar et al., 2013). It is thus possible that the less velocity-dependent variation in the movement frequencies of running may allow for a larger inter-velocity transfer of the adaptation compared with walking, as seen in the present results.

## Methodological considerations

The gait velocities tested in the present study (0.75, 1.50 or $2.25 \text{ m s}^{-1}$) were selected to differentiate the relative preferences for velocity in walking and running. On the basis of the preferred walk-to-run transition velocities of each subject ($1.681\pm0.183 \text{ m s}^{-1}$, 0.75 and $2.25 \text{ m s}^{-1}$) were outside the mean±3 s.d., and $1.50 \text{ m s}^{-1}$ was within the 1 s.d. ranges, respectively. In addition, the velocities used for adaptation and re-adaptation (1.0 and $2.0 \text{ m s}^{-1}$ each) were chosen on the basis of our preceding study (Ogawa et al., 2012), in which the subjects could both walk and run comfortably. Despite the known limitations in the inter-velocity transfer of adaptation in walking (Vasudevan and Bastian, 2010), the use of the present velocity settings resulted in a significant aftereffect at all of the velocities in the adapted modes and therefore was appropriate for the purpose of the study.

The emergence of the aftereffect was not stable; rather, it decayed throughout the course of the experiment. Indeed, the comparisons of the first catch trials with those of the initial part of the washout periods revealed a significant difference (Experiment 1, adaptation to walk) or a similar tendency (Experiment 2, adaptation to run, $P$=0.066). However, we suspect that the influence on the present results has been minimal because the orders of exposure to the 'fast' and 'slow' catch trials were flipped between walking and running in

one half of the subjects (8 of 16). We have also confirmed that there were no changes in the overall results, even when the results of the first catch trials (mid) were replaced with those obtained in the initial 10 s of the washout periods (mid 2 in Fig. 5A,B). The overall results are therefore expected to remain unchanged even with different order of velocities in the catch trials.

## Summary

In the present study, we observed that in human walking and running, adaptations acquired in one mode transferred to the other mode in only a limited manner. This limitation was evident at different velocities, each reflecting a relative preference to execute either walking or running. Our results thus demonstrate a largely mode-dependent control by the CNS between human walking and running and a limited velocity dependency. Therefore, walking and running are not simply dependent on velocity, but are controlled by the CNS as two completely distinct forms of locomotion in humans.

## MATERIALS AND METHODS
### Subjects

Sixteen male volunteers (ranging in age from 20 to 34 years old) with no known history of neurological or orthopedic disorders participated in the study. Prior to participation, they gave written informed consent for participation in the study. The experimental procedures were approved by the local ethics committee of the National Rehabilitation Center of Persons with Disabilities, Japan. All procedures were conducted according to the Declaration of Helsinki.

### Experiments

In the experiments, subjects walked and ran on a split-belt treadmill (Bertec, Columbus, OH, USA) in which two belts (one underneath each foot) could be driven independently in velocity. In the present experiment, the treadmill was operated in either a 'tied' mode (two belts moving at the same velocity) or a 'split' mode (at different velocities) (Reisman et al., 2005) as dictated by the protocol.

To assess the preference to either walk or run in relation to velocity, preferred walk-to-run transition velocities were determined for each subject. Prior to taking measurements, the subjects warmed up by walking and running at a comfortable velocity for approximately 5 min. To determine the transition velocity, we used a protocol similar to that used by Hreljac (1993) and Kram et al. (1997). At a constant velocity, in the 'tied' mode, the subjects walked and ran alternately for approximately 30 s. They were then asked whether they preferred to walk or run at that velocity. The treadmill velocity was initially $1.2 \text{ m s}^{-1}$, a velocity at which all subjects reported a preference for walking. The velocity was then increased by $0.1 \text{ m s}^{-1}$ and the subject again underwent the above process and reported their preference. This was repeated until the subject reported a preference for running for three consecutive velocities. The lowest of the three consecutive velocities was recorded as the preferred walk-to-run transition velocity for the subject.

In the main procedure, which focused on the transfer of adaptation across gaits, each subject participated in two experiments: one involving an adaptation to walk (Experiment 1) and another to run (Experiment 2) (Figs 3 and 4). These experiments were assigned in random order. All the experiments started with baseline measurements, where the subjects walked and ran on tied belts with velocities of 0.75, 1.50 and $2.25 \text{ m s}^{-1}$ (30 s each). These velocities were selected on the basis of the preferred walk-to-run transition velocity as obtained in our pilot experiments in order to differentiate the relative ease (or difficulty) for executing each gait. Following the baseline, subjects underwent split-belt adaptation to walk (Experiment 1) or to run (Experiment 2) for 6 min, a series of six 10 s catch trials (walk or run at three different velocities in tied modes) and 1 min re-adaptation periods alternately and 2 min washout periods. For eight of the subjects, the order of exposure to the catch trials was flipped between walking and running compared with those in the other eight, except for those under a velocity of $1.5 \text{ m s}^{-1}$, which were delivered first and fourth in the series (see Figs 3 and 4). During the adaptation and re-adaptation periods,

the treadmill was driven in the split mode and the velocities were set at 1.0 m s$^{-1}$ (left) and 2.0 m s$^{-1}$ (right). These velocities were chosen on the basis of our previous study in which subjects were able to both walk and run comfortably (Ogawa et al., 2012). During the change in belt velocity, the subjects stood with their feet on either side of the treadmill belt. They were then told to step on the belts after proper belt velocities were reached. They were instructed to step on the belts with their left foot first and always to start their gait by either walking or running from their first step depending on the task. Between each period of changing the belt velocities, there were 7 s intervals to step off and again to step on the belts. During the experiments, one experimenter stood adjacent to the treadmill for safety. The subjects were told to hold on to handrails if they felt they were in danger of falling. All of them, however, were able to walk and run adequately without using the handrails.

## Recordings

The three orthogonal components ($\mathbf{F}_x$, mediolateral; $\mathbf{F}_y$, anteroposterior; $\mathbf{F}_z$, vertical) of the GRF were measured using two force plates mounted underneath each treadmill belt. The obtained force data was low-pass filtered at 8 Hz and was recorded at a sampling rate of 1 kHz (Power Lab, AD Instruments, Sydney, Australia). Stride cycles for both walking and running were detected using custom-written software (VEE pro 9.0, Agilent Technologies, Santa Clara, CA, United States). Based on the vertical $\mathbf{F}_z$ component of the GRF, timing of foot contact and toe-off for each stride was determined for both left and right sides.

To address the degree of adaptation and transfer while walking and running, the peak anterior braking force was calculated for each stride cycle. This GRF component has been found to exhibit a prominent difference between the limbs (thus, asymmetry) after split-belt adaptation both in walking and running (Ogawa et al., 2012). To evaluate the degree of asymmetry as an indication of adaptation and transfer, inter-limb differences in the GRF component for each stride during the 10 s catch trials and first 10 s of the washout periods were calculated. The obtained values were then normalized to the mean value of the respective gait and velocity during the baseline. This was done to take into account any asymmetry in the natural movement pattern of each subject.

## Statistical analyses

First, to determine the stability of adaptation throughout the experiment, a one-way ANOVA with repeated measures was used to compare the degree of asymmetry during the last 10 s of the adaptation and the re-adaptation periods. A paired Student's $t$-test was used to compare the degree of asymmetry between the first catch trial and the first 10 s in the washout period to assess stability in the aftereffect size over the course of the experiment. A two-way ANOVA with repeated measures was used to test for statistically significant differences in the degree of asymmetry and cadence between gait mode (walking or running) and velocity (0.75, 1.50 or 2.25 m s$^{-1}$). When the ANOVA revealed significant main effects or interactions, Bonferroni's *post hoc* comparison was used to identify significant differences among the variables. Data are basically presented as means±s.e.m. Data for the preferred walk-to-run transition velocity are presented as means±s.d. Significance was accepted when $P<0.05$.

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