Contribution of Feedback and Feedforward Strategies to Locomotor Adaptations

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Lam, Tania, Martin Anderschitz, and Volker Dietz. Contribution of feedback and feedforward strategies to locomotor adaptations. J Neurophysiol 95: 766–773, 2006; doi:10.1152/jn.00473.2005. The aim of this study was to examine the strategies used by human subjects to adapt their walking pattern to a velocity-dependent resistance applied against hip and knee movements. Subjects first walked on a treadmill with their lower limbs strapped to an exoskeletal robotic gait orthosis with no resistance against leg motions (null condition). Afterward, a velocity-dependent resistance was applied against left hip and knee movements (force condition). Catch trials were interspersed throughout the experiment to track the development of adaptive changes in the walking pattern. After 188 steps in the force condition, subjects continued to step in the null condition for another 100 steps (washout period). Leg muscle activity and joint kinematics were recorded and analyzed. The adaptive modifications in the locomotor pattern suggest the involvement of both feedback and feedforward control strategies. Feedback-driven adaptations were reflected in increases in rectus femoris and tibialis anterior activity during swing, which occurred immediately, only in the presence of resistance, and not during the catch trials. Locomotor adaptations involving feedforward strategies were reflected in enhanced pre-swing activity in the biceps femoris and medial hamstrings muscles, which required experience and persisted in the catch trials. During washout subjects showed a gradual deadaptation of locomotor activity to control levels. In summary, adaptive changes in the walking pattern were driven by both feedback and feedforward adjustments in the walking pattern appropriate for overcoming the effects of resistance.

INTRODUCTION

Extensive research in locomotor control over the past decades has elucidated a crucial role of afferent input in shaping the motor output during walking. For example, afferent signals from muscle receptors are important factors for timing the transition between stance and swing, and for regulating the magnitude of muscle activity during the stance phase (Dietz et al. 2002; Nielsen and Sinkjaer 2002; Pearson 2004). Sensory input from the limbs is also thought to drive adaptive modifications in locomotor centers after central or peripheral nerve injury (Pearson 2000).

Lasting modifications in the locomotor pattern are also observed in response to alterations in the walking environment. For example, in animal preparations, aspects of locomotor behavior can be conditioned to overcome an obstacle (Hodgson et al. 1994; Lou and Bloedel 1988). On removal of the obstacle, the animal continued to step with an elevated trajectory. This aftereffect suggests a remodeling of locomotor patterns in anticipation of the perturbation. There is similar evidence from human experiments showing lasting modifications in response to sustained alterations in walking conditions. Human infants (Lam et al. 2003; Pang et al. 2003) and adult subjects (Emken and Reinkensmeyer 2005) adapt to the constant presence of a disturbance to swing phase movements and show aftereffects on removal of the disturbance. There is also evidence for long-lasting modifications in interlimb coordination after a period of walking on a rotating disk (Gordon et al. 1995; Weber et al. 1998) or a split-belt treadmill (Jensen et al. 1998).

The presence of aftereffects after a period of training under new conditions implies the formation or recalibration of the motor output for a given task. Indeed, an influential concept is that the nervous system possesses an internal model of the dynamics of the limb that forms the basis for computing the necessary motor output for a desired movement. When the dynamics of the limb (and/or task) change, errors in movement will result (Shadmehr and Mussa-Ivaldi 1994). These errors, in turn, are instructive to the nervous system for updating the internal model and adjusting the motor output to suit the new demands of the task (Kawato et al. 1987). On return to the original movement condition, the adjusted motor outputs that were formed to compensate for the new condition are no longer suitable, again resulting in a movement error or aftereffect (Shadmehr and Mussa-Ivaldi 1994).

The aim of this study was to examine adaptive modifications in the locomotor pattern of healthy adults to a sustained change in the walking condition. Using an exoskeletal robotic gait device, velocity-dependent resistance was applied against hip and knee movements during treadmill walking. Given the strong contribution of sensory feedback to the locomotor pattern, we hypothesized that feedback strategies would be used to adapt the walking pattern to resistance. We also hypothesized that on removal of resistance, subjects would exhibit aftereffects, consistent with the concept that the nervous system learns the dynamics of the walking environment and adjusts the motor output accordingly.

METHODS

Twenty healthy subjects (10 males and 10 females) ranging in age from 20 to 33 yr (mean age: 26 yr; SD: 4 yr) were recruited to participate in this study. The weight of the subjects was between 41 and 90 kg (mean: 66.2 kg; SD: 13.8 kg), and the height between 1.57 and 1.87 m (mean: 1.72 m; SD: 8.8 m). Subjects gave written consent...
to participate in the experiments. All procedures were approved by the Ethics Commission of the Canton of Zurich.

Recording procedures

Subjects’ lower limbs were measured to ensure proper fit with the robotic gait device, the Lokomat (Hocoma AG, Volketswil, Switzerland), which was previously described in detail (Colombo et al. 2000). The device, which is mounted over a treadmill by a flexible parallel-guided, permitted flexion/extension at the hip and knee and abduction/adduction at the hip. Subjects were strapped to the exoskeleton device by leg cuffs around the mid-thigh, upper shank, and lower shank, whereas a waist belt provided trunk support. The foot was not attached to the exoskeleton, thus allowing free movement at the ankle.

Surface electrodes (Ag/Ag-Cl) were used to record the activity of the rectus femoris (RF), biceps femoris (BF), medial hamstring (MH), tibialis anterior (TA), and medial gastrocnemius (MG) on the left side. Sagittal-plane joint movements were recorded by twin-axis electrogoniometers (Biometrics, Gwent, UK) taped over the left hip, knee, and ankle joints. The robot’s position sensors at the hip and knee also provided hip and knee joint kinematic data. Signals from force plates located beneath the left side of the treadmill belt allowed for determination of left foot contact and toe-off.

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Subjects were allowed to select their own treadmill speed (1.6–2.2 km/h; mean: 2.1 km/h; SD 0.2 km/h), which remained constant throughout the experimental session. Before the experiments started, subjects familiarized themselves with walking on the treadmill with the robot in the null (control) condition. All subjects reported within 5 to 10 min of practice that they felt comfortable walking with the robot. In the null condition, a model-based impedance-control algorithm to the hip and knee drives, which compensated for the gravitation and friction effects of the robot’s drives, was implemented (Riener et al. 2005). In the force condition, the robot applied resistance against hip and knee movements, defined by

\[
\begin{bmatrix}
\dot{M}_h \\
\dot{M}_k \\
\end{bmatrix}
= -
\begin{bmatrix}
B_h & 0 \\
0 & B_k \\
\end{bmatrix}
\begin{bmatrix}
\dot{\theta}_h \\
\dot{\theta}_k \\
\end{bmatrix}
\]

where \( \dot{M} \) is the instantaneous amount of torque applied, \( B \) is the viscous (or damping) coefficient, and \( \dot{\theta} \) is the instantaneous angular velocity of the hip (H) and knee (K) joints. The values of \( B \) were 5 and 3 N \cdot m \cdot s/ rad for the hip and knee, respectively. The \( B \) values were determined on the basis of pilot experiments, which helped to determine an appropriate amount of resistance that did not fatigue the subjects, while yielding distinct measurable responses in the walking pattern. A comparison of the body mass and the response to resistance indicated that there was no relationship between the subject’s mass and the strength of the response.

Control data were collected from a walking sequence in the null condition. In the force condition, resistance was applied against hip and knee joint movements on the left side only. The sequence of the experiment is illustrated in Fig. 1A. Occasionally, the resistance was removed unexpectedly for a single step cycle. These intermittent steps were called catch trials and they occurred six times during the course of the experiment. At the end of the trial, resistance was turned off and subjects continued to walk for 60 to 100 step cycles in the null condition. This part of the experiment was called the washout period, where deadaptation was examined. Trials were defined by their order of appearance so that the first exposure to resistance was termed ON1 and the first time the resistance was removed was called OFF1, and so forth. The OFF1 through OFF6 trials were the catch trials, consisting of only one step cycle each. The OFF7 trial was the washout period. The ON1 through ON7 trials each consisted of 1, 2, 5, 10, 20, 50, and 100 step cycles, respectively. Thus subjects took a total of 188 steps in the force condition.

Subjects were instructed to walk as normally and consistently as possible. They were not warned about the application or removal of resistance and, when questioned afterward, stated that they could not predict or discern the sequence of resistance application and removal. The resistance was always switched on or off during mid-stance (at about 25% of the step cycle). At this time, hip and knee joint angular velocity is quite low. In each subject, the change in hip and knee angles was obtained by taking the difference between the hip or knee angle over a 200-ms window centered on the time of the switch and the corresponding time during the average control steps in each subject. As evident in Fig. 1, B and C, there was no indication of a startle response or any change in the walking pattern at the time the condition was changed. An assessment of the change in leg muscle electromyogram (EMG) also did not indicate any response to the actual switch of the condition (data not shown).

Electromyographic data were amplified, high-pass filtered at 10 Hz, and low-pass filtered at 300 Hz. Goniometer, force plate, EMG, and analog data from the robot were converted on-line to digital form at 1,000 Hz and stored directly to a computer using custom-written software in Soleasy (ALEA Solutions GmbH, Zurich, Switzerland). Off-line processing involved rectifying and low-pass filtering the EMG data at 30 Hz. All other signals were low-pass filtered at 6 Hz using a digital zero-lag fourth-order Butterworth filter.

Data analysis

Force plate signals were used to determine foot contact and toe-off. The step cycle was defined as the period between consecutive foot contacts. The EMG and kinematic data of the last 20 steps of the control trial were averaged together and normalized to 100% of the step cycle to yield an averaged control step for each subject. For intersubject comparison, the EMG amplitude for each muscle was determined on the basis of pilot experiments, which helped to determine an appropriate amount of resistance that did not fatigue the subjects, while yielding distinct measurable responses in the walking pattern. A comparison of the body mass and the response to resistance indicated that there was no relationship between the subject’s mass and the strength of the response.

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The baseline adaptive change in the walking pattern in response to resistance was assessed by examining the locomotor pattern averaged across the last 10 steps of the ON7 trial. Based on this examination, EMG activity related to adaptive strategies was quantified by calcu-
lating the root mean square (rms) value from the rectified and filtered EMG signals over the period lasting from 50 to 60% of the gait cycle (pre-swing) and the period between 70 and 90% of the gait cycle (mid-swing). Adaptations in the kinematic pattern were quantified by measuring the peak flexion angle of the hip, knee, and ankle joints during the swing phase.

The time course of change in kinematic and EMG patterns during adaptation (ON1–ON6 trials) and deadaptation (OFF7 trial) were fitted with the exponential function, $y = a + b \times \exp^{-\frac{x}{\tau}}$, where $a$ represents the offset, $b$ is the gain, and $\tau$ is the time constant of adaptation, representing the number of steps it would take to obtain 63.2% of total adaptation. We defined adaptation or deadaptation to be complete at 95% of steady state. The time at which this occurs was calculated by rounding up the value defined by $-\tau \times \ln(0.05)$.

**Statistical analysis**

A commercially available software package (SPSS 11.0, SPSS, Chicago, IL) was used to conduct all statistical tests. For all statistical evaluations, the level of significance was set at an alpha value of 0.05. To compare changes in the walking pattern during adaptation, a repeated-measures ANOVA was used to compare the control steps, the first step against resistance, and the step at which the adaptation was complete (defined above) for the following parameters: peak hip flexion, peak knee flexion, peak ankle dorsiflexion, pre-swing BF rms, pre-swing MH rms. To describe the changes during deadaptation, a repeated-measures ANOVA was performed for the same parameters comparing control, the first step in the OFF7 trial, and the step at which deadaptation was complete. The Bonferroni adjustment was used to correct $\alpha$ (0.05) for the three possible pairwise comparisons (adjusted $\alpha = 0.017$).

To describe general changes during the steps against resistance, data were reduced to four parameters by averaging values in sequential sets of 50 steps [steps 1–50 (q1), steps 51–100 (q2), steps 101–150 (q3), and steps 151–188 (q4) against resistance]. Changes in swing phase EMG activity were then evaluated by a repeated-measures ANOVA comparing control values, the first step against resistance, and the four reduced data parameters. A repeated-measures ANOVA was also used to assess differences in activity during the six catch trials compared with control. For these tests, the Bonferroni adjustment corrected $\alpha$ (0.05) for 15 possible contrasts (adjusted $\alpha = 0.003$).

**RESULTS**

**Kinematic and muscle activity patterns during walking**

In Fig. 2, the average EMG and kinematic patterns during walking in the null condition (Fig. 2A) are compared with those of the last 10 steps from the ON7 trial (Fig. 2B). The baseline adaptive changes in the locomotor pattern in response to resistance largely occurred during pre- and mid-swing (i.e., 50–60 and 70–90% of the gait cycle, respectively). RF mid-swing activity as well as BF and MH pre-swing activity were elevated in the steps against resistance. There was no obvious difference in the activity of either the TA or MG. Hip and ankle joint excursions were not appreciably different from control. The knee, however, showed reduced flexion during the swing phase and reduced extension at the beginning of the stance phase.

**Adaptive pattern to resistance during walking**

Figure 3 illustrates the step-by-step changes in the kinematic pattern during the steps against resistance. With the introduction of resistance, some subjects stumbled slightly. Indeed, hip and knee flexion in the swing phase was decreased in the first step against resistance compared with control (Fig. 3, A and D). However, closer examination of the step-by-step change in hip and knee flexion reveals that resumption of normal flexion angles during swing occurred quite rapidly. For hip flexion, fitting an exponential function to all steps against resistance gave a time constant ($\tau$) of 1.1 steps ($R^2 = 0.25$) (Fig. 3B). Thus by the fourth step, adaptation of hip flexion was considered complete. The decrease in hip flexion angle in the first step against the load was significant ($P = 0.000$) but with the fourth step, the difference compared with control was not statistically significant ($P = 0.032$) (Fig. 3C).

Knee flexion in the first step against resistance was reduced by about 12° (Fig. 3D). Adaptation of knee flexion occurred with a time constant ($\tau$) of 2.8 steps ($R^2 = 0.31$) and was complete with the ninth step against resistance (Fig. 3E). However, knee flexion during the swing phase remained reduced through the remainder of the trial ($P = 0.000$ for steps 1 and 9) (Fig. 3F).

At the ankle, there was a significant increase in dorsiflexion during the swing phase in the first step against resistance ($P = 0.000$) (Fig. 3, G and I). Greater ankle dorsiflexion during the

![FIG. 2. Electromyographic (EMG) and kinematic patterns during walking in the null and force conditions. A: average EMG and kinematic patterns during control steps in the null condition. B: EMG and kinematic patterns averaged over the last 10 steps against resistance.](http://jn.physiology.org/)

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swing phase persisted for the first half of the experiment, recovering to control values with a time constant (τ) of 41.3 steps (R² = 0.82) (Fig. 3H). At the ankle, adaptation was thus considered complete by step 124, where ankle dorsiflexion angle was not significantly different from control (P = 0.168) (Fig. 3H).

The step-by-step changes in EMG activity during steps against resistance are illustrated in Figs. 4 and 5. Figure 4A illustrates the average mid swing rms values during steps against resistance. As shown in Fig. 4A, mid-swing RF activity was significantly higher compared with control starting from the first step against resistance (P = 0.003). Elevated RF activity occurred immediately and persisted for the remainder of the experiment, with P = 0.000 for each comparison. An increase in mid-swing TA muscle activity was also evident from the first step against resistance (P = 0.001) and remained elevated over the first part of the experiment (P = 0.000) (Fig. 4D). Thereafter, TA activity returned to control values, corresponding to the change in ankle dorsiflexion (Fig. 3H). Mid-swing EMG activity in the BF (Fig. 4B) was not significantly different from control. In the MH (Fig. 4C), mid-swing activity was reduced over the first part of the experiment (P = 0.000). Thereafter, the change in MH mid-swing activity compared with control was not statistically significant.

Figure 5 illustrates the step-by-step changes in pre-swing rms values. Adaptive changes in response to resistance occurred during pre-swing in the BF and MH muscles (Figs. 2 and 5, A and B, top). The emergence of enhanced BF and MH pre-swing activity was not immediate (not present in the first step against resistance) but was rapid, as shown in more detail in the plots with the higher time resolution (Fig. 5, A and B, middle). The time constants (τ) of adaptation in BF and MH EMG were 1.4 and 2.1 steps, respectively (R² = 0.10 for both). Thus adaptation in pre-swing BF and MH EMG activity was complete after five and seven steps, respectively. The exponential fit to the BF and MH EMG data was consistent with that found for hip and knee flexion (Fig. 3, B and E), although it was not very robust. In any case, the change in BF and MH activity was clearly rapid. The increase in EMG was significant for BF in step 5 (P = 0.009) and MH in step 7 (P = 0.000) (Fig. 5, A and B, bottom).

Aftereffects during the catch trials

Six catch trials, during which the resistance was switched off, were interspersed throughout the experiment (Fig. 1A). In Fig. 6, A and B, the average peak flexion angle in the hip and knee joints during the swing phase from the six catch trials are plotted against control. Although there was no significant change in the first catch trial, there was greater flexion at the hip and knee in subsequent catch trials (P < 0.003).

In Fig. 6, C and D, the rms values of RF and TA during mid-swing are plotted. In the RF and TA, which showed enhanced mid-swing activity during the steps against resistance, there was no difference in mid-swing rms values compared with control during any of the catch trials (P > 0.003). The exception was elevated mid-swing RF activity in the fifth catch trial (P = 0.000, Fig. 6C).

In Fig. 6, E and F, the rms values of BF and MH during pre-swing are plotted. In the BF muscle, pre-swing activity was significantly higher than control in the first four catch trials (P = 0.002 for all, Fig. 6E). Pre-swing BF activity tended to remain enhanced in catch trials 5 and 6, although the increase was not considered to be statistically significant (P values of 0.02, and 0.007, respectively). There was an increase in pre-swing MH activity compared with control in all of the catch trials (P < 0.003, Fig. 6F). These observations are in line with the finding that enhanced pre-swing BF and MH activity occurred very rapidly after the introduction of resistance.
Deadaptation during washout

When the resistance was turned off for the washout period (OFF7), some subjects reported that they felt as if the robot was pushing their legs forward. Subjects continued to step in the null condition for ≤100 steps during washout. At both the hip and knee, there was greater flexion in the first step of OFF7 with \( P = 0.001 \) for both (Fig. 7, A and B, bottom). The peak flexion angles during the swing phase showed a gradual return to control values with time constants (\( \tau \)) of 6.6 steps (\( R^2 = 0.71 \)) and 4.3 steps (\( R^2 = 0.59 \)) at the hip and knee, respectively. Thus deadaptation of hip flexion angle was complete after 20 steps, and in the knee, after 13 steps. In these steps, hip and knee flexion was not different from control (\( P > 0.017 \)).

BF and MH activity during pre-swing was also higher in the first step of the washout period (P values of 0.011 and 0.002, respectively, Fig. 7, C and D). Activity in these muscles returned to control values gradually, with a time constant (\( \tau \)) of 13.5 steps (\( R^2 = 0.87 \)) steps in the BF and 9.9 steps (\( R^2 = 0.77 \)) steps in the MH muscle. Deadaptation of BF and MH pre-swing activity was complete with the 40th and 30th steps, respectively. Thus deadaptation of BF and MH pre-swing activity was complete after experience with stepping against resistance. Changes in BF and MH muscle activity patterns emerged only after experience with stepping against resistance. Catch trials interspersed throughout the experiment and a washout period at the end indicated that some of the changes in motor command were generated in anticipation of resistance.

**Discussion**

This study examined the strategies used by human subjects to adapt to a velocity-dependent resistance against hip and knee movements during walking. Adaptation was characterized by both immediate and gradual changes in muscle activation patterns during the swing phase. Immediate adaptations consisted of increased RF and TA activation during swing. Changes in BF and MH muscle activity patterns emerged only after experience with stepping against resistance. Catch trials interspersed throughout the experiment and a washout period at

**Fig. 5. Adaptive changes in pre-swing EMG activity during the force condition.** Pre-swing rms values of the BF (A) and MH (B) were calculated for each step against resistance. Top and middle: thick dashed lines surrounded by a thin dotted line represent the mean and 95% confidence interval of the mean of the control steps. Middle: time base is expanded to show in more detail the step-by-step change in EMG activity over the first 10 steps against resistance. Exponential function describing the change in BF and MH activity is illustrated by the thick solid line. Bottom: average pre-swing rms values of each muscle during the control steps (ctrl), the first step against resistance (s1), and the fourth step against resistance (s4) are plotted. Asterisks indicate a statistically significant difference of \( P < 0.05 \) from control.

It is thought that the nervous system is capable of predicting the forces that will be experienced during upcoming movement to produce the appropriate motor commands (Shadmehr and Mussa-Ivaldi 1994). This prediction is based on an internal representation, or model, of the dynamic properties of the limb in the environment. Thus when the properties change, such as with the application of an external force, errors in movement kinematics result. Through experience, the internal model is updated and the motor commands are modified to account for alterations in movement condition (Shadmehr and Mussa-Ivaldi 1994; Thoroughman and Shadmehr 1999). On return to the original movement condition, the modified motor commands will no longer be valid, again resulting in movement errors called aftereffects (Shadmehr and Mussa-Ivaldi 1994). The presence of aftereffects after removal of the perturbation can be accounted for by the notion that the nervous system uses internal models to control and adapt movements (Kawato 1999).

There is growing evidence that an internal model is used in the control of gait. Aftereffects after repeated exposure to a disturbance during stepping have been reported in decerebrate ferrets (Lou and Bloedel 1988), spinalized cats (Hodgson et al. 1994), spinalized rats (Timoszyk et al. 2002), and human infants (Lam et al. 2003; Pang et al. 2003). More recently, the use of an internal model for the legs was confirmed in adult humans who adapted their walking pattern to a robotic device that applied an upward-pushing force at the ankle (Emken and Reinkensmeyer 2005). In that study, it was further demonstrated that the rate of adaptation to a novel force perturbation during gait could be altered by manipulating movement errors.
Results from the present study provide insight into the neural strategies associated with an internal model that is used to adapt to sustained changes in sensory input during walking. Furthermore, a comparison of muscle activity patterns between steps against resistance with those in the catch trials distinguishes adaptations mediated by feedback mechanisms from those mediated through predictive strategies in response to the resistance.

In the current study, the observations made during the catch trials at specific time points indicate the rapid formation of motor commands in anticipation of the resistance. Aftereffects (increased hip and knee flexion during swing) were already present in the second catch trial, which was introduced after the third step against resistance. Thus it appears that predictive strategies were already formed after only a few steps in the new condition. Such rapid adaptation during walking is in contrast to the number of movements typically required before feedforward adaptations were evident in motor commands for reaching in a novel force condition. For example, strong aftereffects were not observed until more than 250 reaching movements were made in a velocity-dependent force field (Shadmehr and Mussa-Ivaldi 1994). In a later study, Thoroughman and Shadmehr (1999) demonstrated that adaptive changes in arm muscle EMG activity occurred over the first 100 trials. The difference in time course between adaptations during walking and reaching could be related to the task. During walking, numerous intra- and interlimb reflex mechanisms are involved to ensure stability and safety of the body in the event of any sudden disturbances (Dietz and Duysens 2000; Pearson 2004; Zehr and Stein 1999). Thus rapid and appropriate adaptations to ensure maintenance of body equilibrium may also be prepared for the possibility of a sustained perturbation during locomotion.

During the washout period, aftereffects persisted for several steps before the walking pattern returned to control levels. It is unclear why deadaptation in the current study was relatively slow. In the study by Emken and Reinkensmeyer (2005), a return to control foot trajectory during washout appeared rapid, in fewer than five steps. One factor that could account for the different deadaptation times is that our subjects took more than 150 steps against resistance, whereas Emken and Reinkensmeyer (2005) applied perturbations in sets of only 25 steps at a time. Another possibility is that the functional demands of the movement condition may drive the urgency with which the system adapts to new task dynamics. In the study by Emken and Reinkensmeyer (2005), the aftereffects consisted of a decrease in foot trajectory height, whereas the opposite was true in the current study. With a decrease in foot height, a greater risk of stumbling is posed. Thus the relative risk to locomotor stability arising from the change in swing trajectory may mediate the speed of return to the control walking pattern.

Neuromuscular responses

The major adaptive changes in activity were related to swing, with little effect during the stance phase. The slow
speed of walking chosen by the subjects may have been a contributing factor to this effect. However, hip and knee joint velocities are generally higher during the swing phase compared with the stance phase, except for higher knee velocity with higher speeds during late swing/early stance (Winter 1991). Thus at any given speed, the velocity-dependent resistance used here will likely have a greater effect during swing, although greater disturbances at phase transitions may occur with higher walking speeds.

In the present study, responses in the RF and TA muscle were observed with the first step against resistance. Although the response in RF persisted through all of the steps against resistance, the increase in mid-swing TA activity, corresponding to the change in ankle dorsiflexion angle, returned to control values over the course of the experiment. Nevertheless, the RF and TA response to resistance is compatible with responses observed after transient swing phase obstructions during human walking (Dietz et al. 1986, 2004; Ghori and Luckwill 1989). The response latencies to such obstructions, ranging from 50 to 150 ms, were interpreted to involve polysynaptic spinal (Dietz et al. 1986) or supraspinal pathways (Ghori and Luckwill 1989). The contribution of reflex-mediated responses to walking is well established (Pearson 2004) and thus not a surprising finding. Further, the fact that responses in these muscles were generally absent during the catch trials is consistent with the suggestion that they were feedback-mediated responses. However, we also cannot discount an influence of cortical descending pathways on these muscles during walking in adult human subjects (Bonnard et al. 2002; Capaday et al. 1999; Petersen et al. 2001; Schubert et al. 1997).

After a few steps against resistance, there was an additional change in the locomotor pattern consisting of the appearance of enhanced pre-swing BF and MH activity. The observation that enhanced BF and MH activity corresponded with the aftereffects (persisting during the catch trials and early stages of the washout period) indicates that these adjustments represent a modification in the motor commands for walking in anticipation of the resistance. In addition, the emergence of enhanced BF and MH activity was associated with improvements in hip and knee flexion during the steps against resistance. Indeed, pre-swing activation of the knee flexors would be an appropriate strategy to prepare the swing limb for moving against resistance. This strategy, reminiscent of adaptive strategies for stepping over obstacles in cats (McFadyen et al. 1999) and adult humans (McFadyen and Winter 1991; Patla and Rietdyk 2002), could assist knee flexion as well as hip and ankle flexion through intersegmental interactions (Patla and Prentice 1995).

A curious observation was that peak hip flexion and ankle dorsiflexion recovered to control levels, whereas peak knee flexion improved but remained at a reduced level in the steps against resistance. The significance of hip position in regulating the transition from swing to stance phase was recently demonstrated in cats (McVea et al. 2005). Thus one possibility is that recovery of hip flexion ensured a stable transition from the swing to stance phase while walking against the resistance. Intersegmental interactions from enhanced knee flexor muscle activity in combination with direct enhancement of hip flexor activity through the RF muscle could account for the recovery of hip flexion during swing. At the same time, the knee extensor action of the RF muscle may have restricted the recovery of peak knee flexion angle (Piazza and Delp 1996). Further investigations incorporating dynamic analysis of limb movement with analysis of muscle activity patterns will help to elucidate the mechanical and neuromuscular strategies contributing to locomotor adaptations to resistance.

In conclusion, the results of this study demonstrate the use of both feedback and feedforward control strategies to adapt the walking pattern to a velocity-dependent resistance against hip and knee movements. Feedback strategies are assumed to be involved in adaptations that occurred with the first step against resistance and that were not present during the catch trials. Feedforward adaptive strategies are assumed to be reflected in adaptations that required experience to develop and continued to be present during the catch trials. The observations made during unexpected catch trials during the experiment indicate that modifications in motor commands occurred rapidly to ensure the stability of ongoing locomotion.

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REFERENCES


