Transfer of Motor Performance in an Obstacle Avoidance Task to Different Walking Conditions

Tania Lam and Volker Dietz
Spinal Cord Injury Center, Balgrist University Hospital, 8008 Zurich, Switzerland
Submitted 19 April 2004; accepted in final form 26 May 2004

Lam, Tania and Volker Dietz. Transfer of motor performance in an obstacle avoidance task to different walking conditions. J Neurophysiol 92: 2010–2016, 2004; 10.1152/jn.00397.2004. The aim of this study was to examine whether subjects who have learned a skilled locomotor task can transfer the acquired performance to conditions involving either a change in the external coordinates or in the sensory input from one leg. Subjects were trained to step over an obstacle with minimal foot clearance without visual information about either the obstacle or their legs during treadmill walking. Leg muscle activity and joint kinematics were recorded and analyzed. Acoustic signals provided feedback about foot clearance over the obstacle. After successful training, the transfer of learning between level and downhill walking and to walking with additional weight attached to the leg was examined. It was found that once subjects learned to step over the obstacle at an optimal foot clearance, they could transfer their performance within the first step over the obstacle in the new walking conditions. Closer examination of the transfer between level and downhill walking revealed no consistent kinematic strategy across subjects. To transfer the learned performance to walking with additional weight, subjects consistently and automatically increased biceps femoris muscle activation. The results are discussed in the context of emerging concepts in the neural control of walking and motor learning.

INTRODUCTION

An intriguing question is the extent to which the human motor system can transfer relevant strategies learned in one context to other similar situations. Experimental paradigms using upper limb tasks show the ability of the nervous system to generalize learned motor skills to similar movements, contexts or workspaces, and even the opposite limb (Conditt et al. 1997; Criscimagna-Hemminger et al. 2003; Gandolfo et al. 1996; Morton et al. 2001; Shadmehr and Mussa-Ivaldi 1994). Such studies have yielded valuable insights into how the nervous system codes and generalizes motor skills.

Walking is a motor task that is highly flexible in its adaptation to different situations. Such flexibility is important for effective navigation through different environments and unpredictable circumstances. Extensive work has shown the ability of the locomotor system to adapt to changes in sensory input from the limbs (reviewed in Dietz 2002; Dietz and Duyens 2000; Rossignol 1996). In addition, the walking pattern is easily modified to accommodate different external constraints, for example, navigating over or around obstacles (Patla 1997; Vallis and McFadyen 2003) or different slopes of the walking surface (Leroux et al. 1999, 2002).

Recently, generalizability of learned motor performance during walking has received increased attention. Several studies have focused on whether motor learning in one leg transfers to the opposite leg (Anstis 1995; Earhart et al. 2002a; Prokop et al. 1995; van Hedel et al. 2002). The extent of transfer appears to be dependent on the specific motor skill under investigation. Strategies used to step over an obstacle with minimal foot clearance and under conditions of reduced vision could be transferred to the opposite leg (van Hedel et al. 2002). However, adaptation to walking on a split-belt treadmill (Prokop et al. 1995), on a rotating treadmill (Earhart et al. 2002a), or hopping on a treadmill (Anstis 1995) showed little transfer between the two legs. It has been suggested that the differences in transfer ability might be related to the particular muscle strategies and the level of neuronal control involved in the task (van Hedel et al. 2002). In a series of experiments examining podokinetic after-rotation after walking on a rotating treadmill (Gordon et al. 1995), evidence was found for some transfer of the after-rotation effect when switching from forward to backward walking (Earhart et al. 2001), and to a lesser extent, from stepping to hopping (Earhart et al. 2002b). Recently, the generalization of a postural after-effect, produced by walking onto a stationary surface that was previously moving, was shown to be limited to the original context of adaptation (Reynolds and Bronstein 2004). The differences in the extent of generalizability between different studies might be related to whether a new motor skill was learned (van Hedel et al. 2002) or whether performance involved adaptations to sensory-perceptual manipulations (Anstis 1995; Earhart et al. 2002a; Prokop et al. 1995; Reynolds and Bronstein 2004).

The aim of this study was to examine whether the strategies that are learned to execute an obstacle avoidance task with restricted vision (Erni and Dietz 2001; van Hedel et al. 2002) can be transferred between walking conditions: level walking, downhill walking, and walking with additional weight attached to one leg. The difference between level and downhill walking represents a change in the walking environment, and therefore, a change in the external coordinates of motor performance. Walking with additional weight attached to the leg (weighted walking) changes the sensory input from the limb. The aim was to investigate whether the motor system could adapt newly learned strategies to each of these modifications to the locomotor environment. We hypothesized that once subjects learned to step over the obstacle with optimal foot clearance, they would be able to transfer their performance to the other walking conditions.
METHODS

Twelve adult subjects (7 males and 5 females), ranging in age from 18 to 46 yr (mean age, 26 yr), were recruited to participate in this study. The weight of the subjects was between 53 and 98 kg (mean, 69.6 kg), and the height of the subjects was between 1.68 and 1.88 m (mean, 1.77 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

Surface electrodes (Ag/AgCl) were used to record the activity of the medial gastrocnemius (MG), tibialis anterior (TA), rectus femoris (RF), and biceps femoris (BF) on the right side. Sagittal-plane joint movements were recorded by twin-axis electrogoniometers (Biometrics, Gwent, UK) taped over the hip, knee, and ankle joints of the right leg.

The obstacle machine used has been described in detail in previous papers (Erni and Dietz 2001; van Hedel et al. 2002). The machine consists of a short bar that holds a cylindrical foam obstacle 11 cm above the surface of the treadmill. The obstacle itself is 36 cm long and 4.5 cm in diameter. A vertical array of eight light sensors positioned above the obstacle measured foot clearance (height) over the obstacle. Activation of the lowest light sensor without touching the obstacle represented the lowest height over the obstacle. This corresponded to a foot clearance of 2 cm over the obstacle. Activation of the second sensor indicated a foot clearance of 4 cm over the obstacle. Activation of the third to the sixth sensors corresponded to a foot clearance of 6–12 cm, respectively. Activation of the seventh and eighth sensors corresponded to a foot clearance of 15 and 18 cm, respectively, over the obstacle.

Feedback about foot clearance over the obstacle was provided to the subjects by an acoustic signal. The optimal height (activation of the lowest sensor) was signaled to the subject by an acoustic signal consisting of a double beep, 707 Hz, followed by a 1,400-Hz tone. Higher foot clearances were signaled by progressively higher-pitched single-tone beeps (125, 176, 250, 354, 500, 707, and 1,000 Hz, from second highest to the highest, all 400-ms duration), corresponding to activation of the different light sensors.

The obstacle and light sensor array were attached to a track running parallel to the right side of the treadmill. Signals from force plates located underneath the treadmill belt allowed for determination of foot contact. The start of the obstacle was triggered randomly by the force signal due to right foot contact and simultaneously signaled to the subject by an acoustic warning tone (2 kHz, 100-ms duration). The interval between triggers was randomized between 9 and 16 s. All acoustic signals (warning and feedback signals) were played through computer speakers positioned next to the treadmill. Once released, the velocity of the obstacle was the same as that of the treadmill. When it reached the end of its track (the end of the treadmill), it automatically folded up and returned to the front of the treadmill. The distance between the subject and the start position of the obstacle was adjusted in a way to ensure that the arrival of the obstacle occurred during the right swing phase. Thus the right leg was always the leading leg over the obstacle. The time of the swing phase when the foot was over the obstacle was the same for all walking conditions. During level walking, the foot was positioned over the obstacle on average at 60.6 ± 3.4% (SD) of the swing phase. During downhill walking, the foot was over the obstacle at 57.9 ± 3.2% of the swing phase. For a given condition, foot placement before the obstacle was fixed, but the position and timing varied from trial to trial. Before the experiments started, subjects became familiarized with walking on the treadmill. In addition, some practice trials of stepping over the obstacle with full vision were provided prior to the start of the experiment. Subjects were asked to pay particular attention to the timing between the warning signal and the arrival of the obstacle in preparation for the ensuing trials without visual feedback information.

CONTROL TRIALS. Subjects walked on a treadmill at a self-selected velocity (between 2.5 and 4.0 km/h). This speed was used for all subsequent trials of the experiment. Control (unobstructed) trials of level, downhill (15% inclination), and weighted walking were recorded. These control trials were interspersed between the training and transfer trials so subjects always had some exposure to unobstructed walking in each new condition before the obstacle trials.

TRAINING TRIAL. Subjects were fitted with ski goggles that prohibited visual information from the lower half of the visual field and were instructed to look straight ahead. This prevented visual information about the approaching obstacle. Subjects thus had to rely on the acoustic signals to indicate the release of the obstacle and to provide feedback about the foot clearance over the obstacle. Subjects performed at least 50 steps over the obstacle with limited vision. In two subjects, an additional training trial of 50 steps over the obstacle was performed since their performance had not yet stabilized after the first trial. For graphical purposes only, their data from the training trial were normalized in time to 50 steps to allow for comparison with the other subjects. Six subjects underwent training during level treadmill walking (group 1) and six underwent training during downhill walking (group 2).

TRANSFER TRIALS. The first transfer trial consisted of 30 steps over the obstacle during either downhill (for group 1 subjects) or level walking (for group 2 subjects). The second transfer trial consisted of 30 steps over the obstacle with additional weight on the right (leading) leg during level walking. Standard weight cuffs weighing either 2.5 or 3 kg (depending on the subject’s mass) were secured around the leg, just above the ankle, with Velcro straps and tensor wraps. Using normative data provided by Winter (1990), the amount of additional weight was estimated between 20 and 30% of the mass of the subject’s leg. The relationship between the added weight and the percent increase in leg flexor EMG during the swing phase was calculated using the Pearson correlation coefficient. There was no significant relationship between the amount of added weight and the increase in flexor EMG during the swing phase ($r_{\text{MG}} = 0.34$, $r_{\text{BF}} = -0.02$, $r_{\text{TA}} = -0.14$, $r_{\text{MG}} = -0.1$, $P > 0.05$). Thus the range of extra weight added to the leg between subjects was sufficiently narrow to allow the data to be collapsed across subjects.

EMG 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 obstacle machine (foot clearance over obstacle, obstacle hits) were converted on-line to digital form at 1,000 Hz and stored directly to a disk using a 266-Hz PC and custom-written software in Soleysee (ALEA Solutions, Zurich, Switzerland). Goniometer and force plate signals were subsequently low-pass filtered at 30 Hz (with a 4th-order Butterworth filter), and EMG signals were full-wave rectified using Soleysee routines.

Data analysis

For each subject, the EMG and joint angle data were averaged across 20 control (unobstructed) steps during level, downhill, and weighted walking. Force plate signals were used to determine foot contact and toe off. The step cycle was defined as the period between consecutive foot contacts. All EMG and kinematic data were normalized in time for the duration of stance and swing phases (60 and 40% of the step cycle, respectively).

For each step over the obstacle, performance was first assessed by determining whether the foot hit the obstacle. If not, foot clearance over the obstacle was determined by the lowest activated light-sensor. For intersubject comparison, the EMG amplitude for each muscle was normalized to the peak rectified EMG value of that muscle during level walking in each subject. EMG activity related to obstacle
avoidance was quantified by calculating the average rectified EMG value from the beginning of the swing phase until the foot was over the obstacle. For unobstructed steps, the average rectified EMG value over the first 60% of the swing phase was calculated to provide corresponding control values. Changes in the kinematics of walking were quantified by measuring the peak flexion angle of the hip, knee, and ankle joints during the swing phase.

The transfer of learning was assessed by comparing the performance of subjects at the end of the training trial (average of the last 5 steps) with that during the first step of each of the transfer trials. We considered that full transfer occurred if there was no significant difference between the performance at the end of the training trial and the beginning of the transfer trial. Performance was primarily assessed by foot clearance over the obstacle. Foot clearance data were assigned into four categories [<2 cm (optimum), <4 cm, 4–18 cm over the obstacle, or hits]. The four categories were chosen based on the functional aspects of the task.

Statistical analysis

To analyze changes in foot clearance, nonparametric statistical methods were applied to the categorized data defined above. To assess whether transfer occurred between the walking conditions, Friedman’s repeated measures ANOVA was performed. Adaptive strategies over a single trial were described by fitting the averaged data from the EMG signals during the training and transfer trials with the function \( Y = aX^b \), where the parameter \( Y \) is the average EMG amplitude and \( X \) is the step number. The coefficient, \( b \), describes the slope of the data in log-log coordinates. Repeated measures ANOVA was used to evaluate group differences in EMG amplitude between the end of the training and the first five steps of each transfer trial. All statistical tests were evaluated at the 0.05 level of significance. Multiple comparisons were evaluated with an adjusted \( \alpha \) level using the Dunn (Bonferroni) method.

RESULTS

Performance: foot clearance over obstacle

Most subjects were able to learn to step over the obstacle without vision and with optimal foot clearance over the obstacle within 50 steps. The overall performance of all subjects is summarized in Fig. 1. Data were divided according to whether subjects were trained in the level condition (Fig. 1A) or the downhill condition (Fig. 1B). The plots show the average performance, indicated by foot clearance over the obstacle (as detected by the light sensors), with each step over the obstacle. Obstacle hits are not included in these plots. As shown by the graphs in the left panel (training), performance was variable across subjects in the first 20 steps over the obstacle. Thereafter, performance became more consistent. There was a difference in performance during the training trial between the two groups of subjects. Subjects who were trained to step over the obstacle in the downhill condition performed worse at the beginning of training than those who were trained in the level condition \((P < 0.05)\). However, all subjects learned the task by the end of the training trial.

Subjects maintained similar levels of performance when they switched to the other walking conditions. Subjects who were trained to step over the obstacle during level walking could transfer this learning to both the downhill walking condition, and subsequently, walking with additional weight attached to the leg (Fig. 1A). Similarly, subjects who were trained to step over the obstacle during downhill walking were able to transfer the performance to the level and weighted walking conditions (Fig. 1B). No further learning was evident, as shown by the relatively flat plots in the middle and right panels of Fig. 1, A and B. However, there was some variability during the transfer trials due to fluctuations in performance in single subjects.

Individual data of all subjects are summarized in Fig. 1C. In these plots, steps with obstacle hits were included, and data from both groups of subjects were pooled together. The data were categorized into four groups (see METHODS), and the performance of each subject was plotted for the first five steps of training, the last five steps of training, the first step of the first transfer trial, and the first step of the second transfer trial. Due to technical problems that resulted in missed foot clearance measurements, some of the bars do not sum up to the total number of subjects. At the beginning of training, the majority of subjects either stepped too high over the obstacle or hit the obstacle. By the end of training, performance was much improved, and most subjects were able to step over the obstacle with optimal foot clearance. Improvement in performance is shown by the fact that the average foot clearance during the

FIG. 1. Performance: foot clearance over the obstacle. Average performance of all subjects in (A) group 1 and (B) group 2 during the training (left), 1st transfer (middle), and 2nd transfer trial (right). Average foot clearance over the obstacle is plotted as a function of the step number in the trial. Error bars represent SE. Gray shaded region represents the optimal foot clearance (<2 cm over the obstacle). Steps with obstacle hits are omitted. C: performance of all subjects were categorized into 4 categories [<2 cm (optimal clearance), <4 cm, 4–18 cm over the obstacle, and hits] for the 1st 5 steps of the training trial, the last 5 steps of the training trial, the 1st step of the 1st transfer trial, and the 1st step of the 2nd transfer trial. In this plot, data from subjects of both groups were pooled together. Some of the bars do not equal the total number of subjects because foot clearance could not always be measured due to technical problems.

J Neurophysiol • VOL 92 • OCTOBER 2004 • www.jn.org
first five steps of training was significantly higher than that of the last five steps of the training trial \((P < 0.05)\).

When subjects switched to the new walking condition, there was no significant difference in performance in the first step of transfer trial 1 with that at the end of training \((P > 0.05)\). However, when subjects switched to transfer trial 2 (weighted walking), performance worsened in one-half of the subjects, either in the form of obstacle hits or by elevated foot clearance (>4 cm) over the obstacle. Nevertheless, the average performance at this time was not significantly different from that at the end of the training trial \((P > 0.05)\).

**Learning and transfer: EMG and kinematic patterns**

Basic differences exist between level, downhill, and weighted walking. In line with previous reports (Kuster et al. 1995; Leroux et al. 2002), characteristic changes in limb kinematics occurred during downhill walking. There was significantly less flexion at the hip during the swing phase \((P < 0.05)\), slightly more flexion in the knee throughout the step cycle, and less plantar flexion of the ankle at the beginning of the swing phase. While the major changes in EMG activity occurred during the stance phase, only minor changes were seen during swing (Fig. 2A). During weighted walking, there was a greater activation of the BF, TA, and MG muscles during the swing phase. However, there was no difference in the kinematic patterns between control and weighted walking (Fig. 2B). Data from the ankle goniometer during weighted steps were not included because the added weight attached to the lower leg interfered with the goniometer position.

The main difference between level and downhill walking patterns during the swing phase was seen in the joint kinematics (Fig. 2). Thus in examining the strategies used to transfer the learned performance between level and downhill walking, the analysis focused on the change in peak flexion at the hip, knee, and ankle joints (Fig. 3). This value is the difference between obstructed and averaged control (unobstructed) steps (Fig. 3, *inset*) for each walking condition. Each symbol in Fig. 3 represents the average change in peak flexion over the last five steps of training and the first step of the transfer trial in an individual subject. In group 1, subjects switched from level to downhill walking. In this case, a larger change in hip flexion might be expected, since during downhill walking the hip does not flex as much as during level walking (Fig. 2A). The opposite would be expected for subjects in group 2. On the other hand, little difference may be expected in the change in knee or ankle flexion since the changes in peak flexion at these joints between level and downhill walking are relatively minor (Fig. 2A). However, we found no systematic difference and no specific strategy adopted by subjects transferring from level to downhill walking (Fig. 3A) or by subjects transferring from downhill to level walking (Fig. 3B). Only steps with optimal foot clearance over the obstacle were included. Thus even with performance level controlled, there was intersubject variability in the kinematic changes involved in the transfer between walking conditions.

When unobstructed level and weighted walking were compared, a difference in the amplitude of flexor muscle EMG occurred but with little difference in joint kinematics (Fig. 2B). Thus the change in flexor muscle EMG amplitude was examined more closely. In Fig. 4, the amplitude of BF EMG amplitude is plotted as a function of step number for each of the obstacle trials. During training, a decrease in BF amplitude during the swing phase occurred over the course of the training trial (Fig. 4, A and B, left). BF EMG amplitude during the first transfer trial was maintained at the level recorded at the end of the training trial \((P > 0.05)\). However, with the change to the weighted walking condition, an immediate increase in BF EMG amplitude occurred (Fig. 4, A and B, right). This increase was significant with respect to the values at the end of training \((P < 0.05)\). Moreover, this greater BF EMG amplitude was maintained throughout the weighted walking trial \((b = -0.007 \text{ and } 0.03)\), which indicates that no further adaptation in BF activity occurred during this new walking condition.

Figure 5 shows TA EMG amplitude plotted as a function of step number for each of the obstacle trials. Similar to the BF EMG amplitude, there was a gradual decrease in the amplitude of the TA EMG during the training trial (Fig. 5, A and B, left). The \(b\) coefficient from the power function fit was \(-0.11\) for group 1 and \(-0.16\) for group 2. When the walking condition
was changed to either level or downhill walking, TA EMG amplitude was maintained at the level recorded at the end of the training trial ($P < 0.05$; Fig. 5, A and B, middle). When subjects switched to weighted walking, TA EMG amplitude was maintained at the same level as in the previous trial ($P < 0.05$; Fig. 5, A and B, right), unlike the pattern observed in the BF muscle (Fig. 4).

**DISCUSSION**

The aim of this study was to investigate whether subjects can transfer a newly learned motor task to different walking conditions. The results indicate that adaptive strategies used for stepping over an obstacle can be transferred to other walking conditions, even without visual control. Subjects who learned to step over an obstacle with an optimal foot clearance during level walking could transfer this skill to downhill walking and vice versa (a change in the external environment). Subjects could also transfer their learned performance to the weighted walking condition (a change in sensory input from the limb).

Learning optimal foot clearance

Without visual input of either the limb or the obstacle, subjects had to rely mainly on the acoustic feedback signals and proprioceptive input from the legs to control foot clearance over the obstacle. Normally, visual information has a dominant role in the control of limb trajectory and foot placement during complex walking tasks (Beloozerova and Sirota 2003; Drew et al. 1996; Patla 1997). In the absence of vision, proprioceptive information is of crucial importance for the control of movement trajectories, as shown for upper limb movements in individuals without proprioception due to large-fiber sensory neuropathy (Ghez et al. 1995). During walking, the assumption that the nervous system utilizes proprioceptive input to control the kinematic pattern is partly supported by studies using anesthetized cat preparations (reviewed in Bosco and Poppele 2001). Dorsal spinocerebellar tract neurons receive input from a variety of sensory receptors, including muscle afferents, and respond to changes in the endpoint position of the limb (Bosco et al. 2000). It has been proposed that such mechanisms could provide a basis for the kinematic control of locomotion (Lacquaniti et al. 1999). Support for this assumption comes from studies showing that kinematic patterns of the lower limb are conserved across different forms of walking, despite changes in limb kinetics (Grasso et al. 1998, 2000; Ivanenko et al. 2002). Whether subjects walk backward or forward (Grasso et al. 1998), crouched or upright (Grasso et al. 2000), or with full or minimal body weight support (Ivanenko et al. 2002), toe trajectories are strikingly well conserved, whereas muscle activity patterns can vary. In the context of these results, the concept of kinematic control of walking (Lacquaniti et al. 1999) is likely to be applicable.
Transfer of performance to different walking conditions

Rossetti et al. (1994) could provide a basis for learning limb movement trajectories to step over the obstacle, with mainly proprioceptive input in conjunction with acoustic feedback about foot position.

We suggest that the observed variability in foot clearance may represent a normal variability in the motor system (van Beers et al. 2002) as perfect performance across subjects was never observed. Sensitivity analysis showed that small changes in individual lower limb angles could account for variability in toe clearance during the swing phase (Winter 1992). The lack of visual control could also contribute to the variability of steps over the obstacle (Patla 1997). In addition, studies of upper arm pointing tasks show that a lack of visual information about either the target or the hand contributes to variability of performance (Desmurget et al. 1997; McIntyre et al. 1998; Rossetti et al. 1994).

Transfer of performance to different walking conditions

Despite a change in the geometric configuration of the legs between level and downhill walking, subjects could transfer their learned performance. However, no common specific strategy could be identified. Subjects showed a variety of changes in hip, knee, and ankle joint kinematics. This is in line with the observation that subjects have variable changes in the shoulder, elbow, or wrist angle during learning and transfer of a catching task (Morton et al. 2001). These findings, along with the present results, are consistent with the assumption that, during functional movement, position of the limb is coded and controlled with respect to the endpoint, rather than at the level of individual joints (Bosco and Poppele 2001; Bosco et al. 2000; Shadmehr and Moussavi 2000).

The locomotor pattern is sensitive to immediate and longer-term changes in the sensory input from the limbs (for reviews, see Dietz 2002; Dietz and Duysens 2000; Pearson 2000; Rossignol 1996). Here, sensory input was modified by adding extra weight to the lower leg leading to an enhanced leg flexor muscle activation during the swing phase. Length- and load-sensitive muscle afferents from the flexor muscles, as identified in reduced cat preparations, might be involved in this effect (reviewed in McCrea 2001). Stimulation of group I flexor muscle afferents has been shown to increase flexor EMG amplitude during the swing phase of locomotion in decerebrate cats (Lam and Pearson 2002; Quevedo et al. 2000). Such proprioceptive feedback pathways might have influenced the walking pattern in a feedback manner, presumably in conjunction with subjects’ conscious knowledge of the extra weight.

During the first step over the obstacle with weight, there was an immediate increase in BF EMG amplitude, and no further adaptive changes took place over the rest of the trial. It remains open whether the immediate increase in BF EMG was due to feedback signals (e.g., from load-sensitive flexor muscle afferents), or alternatively, whether subjects adopted a predictive feedforward strategy. Subjects had some practice in weighted walking prior to the obstacle trial, but in any event, the stereotyped pattern of muscle activity during locomotion precludes the ability to discriminate between feedback- and feedforward-control strategies. In the early stages of learning a reaching task under perturbing conditions, it is thought that changes in EMG patterns are largely influenced by feedback control (Thoroughman and Shadmehr 1999). As learning progresses, EMG patterns are gradually refined to better accommodate the perturbation. It was suggested that the improvement was based on the formation of predictive commands developed from the motor performance during the earlier, feedback-controlled movements (Thoroughman and Shadmehr 1999). We show that subjects could appropriately and quickly adjust their motor commands to the additional weight on the leg and achieve an optimal foot clearance. This might have been attained by combining a strategy to program the desired foot trajectory in space and an adaptive strategy to the additional weight. Such a combination of strategies would be in line with experiments on a reaching task showing that, after subjects learned a kinematic and dynamic transformation separately, they performed better in a condition where the two transformations were combined (Flanagan et al. 1999).

In conclusion, the data from this study show that newly learned motor skills can be transferred to changes in either the geometry or dynamics of the leg during walking. During
walking, countless external and internal changes in conditions can be encountered. The ability to generalize walking strategies to different conditions would thus be an efficient approach through which the nervous system can deal with novel situations. Studies of the nervous system’s ability to generalize motor skills could be important for designing efficient rehabilitation strategies that optimize the flexibility and adaptability of recovered movement control after a neurological lesion.

ACKNOWLEDGMENTS

We thank H. van Hedel and L. Linenburger for valuable support and fruitful discussions during this study.

GRANTS

This study was supported by an operating grant from the Swiss National Science Foundation (31–64792.01). T. Lam was supported by a postdoctoral fellowship from the Canadian Institutes of Health Research.

REFERENCES

Earhart GM, Jones GM, Horak FB, Block EW, Weber KD, and Fletcher WA. Podokinetic after-rotation following unilateral and bilateral podokineti