How Do Infants Adapt to Loading of the Limb During the Swing Phase of Stepping?

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INTRODUCTION

Human infants show a stepping response that is sensitive to transient changes in sensory input (Pang and Yang 2000, 2001; Yang et al. 1998a,b). In this study, we investigated whether infants have the capacity for adapting to sustained changes in sensory input during stepping. Adult humans and other mammals make adaptive modifications after injury or sustained changes in sensory input (Pearson 2000). Changes in the gain of spinal reflex pathways, changes in drive from locomotor generating networks, and input from supraspinal centers have all been shown to be involved in mediating these adaptive responses to the locomotor pattern after peripheral nerve injury (Carrier et al. 1997; Gritsenko et al. 2001; Pearson and Misiaszek 2000; Pearson et al. 1999; Whelan and Pearson 1997).

Some studies have also examined adaptive changes to locomotion that are not induced by nerve injury. In these types of studies, compensations are seen not only in the presence of the perturbation, but long-term adaptive strategies are revealed on the removal of the perturbation from the locomotor environment. For example, decerebrate ferrets adaptively increased the trajectory of their forelimb to avoid a rod placed in the forelimb’s path. When the rod was removed, high stepping continued for up to seven steps before the stepping pattern returned to control trajectories (Lou and Bloedel 1988). Thus in the presence of the obstacle, mechanisms were employed to generate the higher stepping to prevent contact with the obstacle. When the obstacle was removed, the persistent high stepping (after-effect) indicated that these adaptive mechanisms involved feedforward control that anticipated the presence of the obstacle. In humans, analogous experimental results have indicated that feedforward control mechanisms are also employed to adapt to changes in sensory input. Rather than using specific proprioceptive disturbances, the perturbations to locomotion in these cases were more global, involving inter-limb coordination (Gordon et al. 1995; Jensen et al. 1998; Weber et al. 1998) or locomotor speed (Anstis 1995). Nevertheless, the presence of after-effects after removal of the perturbing input indicates the role of feedforward mechanisms to adapt to the initial disturbances.

Is the ability to adapt to sustained changes in the biomechanical properties of the body present in the human locomotor system before independent walking develops? In an attempt to answer this question, this study focused on the swing phase of stepping and examines how infants respond and adapt to a change in the amount of load on their leg. In the present study, two specific questions were addressed. First, can infants adapt to a sustained change in the weight of their leg during treadmill stepping? Second, if they are able to adapt, what is the nature of the strategies used to achieve the adaptation? These data were previously presented in abstract form (Yang and Lam 2001).

METHODS

Subjects and preparation

Twenty-two infants between the ages of 3 and 11 mo and ranging in weight from 5.7 to 11.6 kg were recruited from local public health clinics. Parents/guardians gave voluntary and written consent on behalf of their infant for participation in the study. All procedures were conducted in accordance with the ethical guidelines of the University of Alberta and the local health authority. One month before the
recording session, parents were given verbal instruction on methods to practice the stepping response with their infant as described in Yang et al. (1998a). This helped to ensure that the stepping response could be elicited on the day of the recording session, especially in infants who were <7 mo.

Adhesive joint markers were taped to the skin overlaying the following bony landmarks on the left leg: the superior border of the iliac crest, the greater trochanter of the femur, the knee joint line, the lateral malleolus, and the head of the fifth metatarsal. The lengths of the thigh, lower leg, and foot were measured by hand using a standard tape measure. The mass of the infant was also measured for subsequent anthropometric calculations used in the inverse dynamic calculations (Schneider et al. 1990).

Stepping was elicited by holding the infant under the arms and allowing the feet to touch a slowly moving treadmill belt (0.2–0.3 m/s). The stepping was recorded from the left side with a video camera at 30 frames/s. After a period of undisturbed (control) stepping, a small weight (500–900 g, depending on the infant’s size) made from stretchable cloth (9 cm wide, 21 cm long) and filled with ball bearings was strapped around the left lower leg. The weight was constructed such that the ball bearings were roughly equally distributed around the circumference of the leg. Stepping with the weight on was elicited for a period of 30 s to 2 min, depending on the infant’s tolerance. After this period, the weight was rapidly detached from the limb while the infant was stepping. Care was taken to remove the weight as quickly as possible while minimizing disruption to the ongoing stepping sequence. Stepping was allowed to continue for ≥30 s after the weight was detached. This sequence (control stepping, weight on, weight off) was usually performed once for each infant. In three infants, this sequence was repeated twice and in one infant, the sequence was repeated four times to examine the consistency within subjects of the response to the weight.

Data analysis

We focused on our analysis on kinematic and kinetic measures of movement during the swing phase of stepping because the load was applied such that the main effect would be during the swing phase. Furthermore, flexor muscle activity at the knee and hip are difficult to record by surface electromyography in infants given the small size of the legs, the deep location of the muscles (particularly hip flexor muscles), and fatty tissue in these areas. Because our study focused on the swing phase, a measure of flexor activity at these joints is crucial to our analysis and we felt kinetic analysis would provide the best solution.

The data were divided into three sections: control, weight on, and weight off stepping. The selected video data were then digitized from the videotape to the computer at 30 Hz using Adobe Premiere (Adobe Systems, San Jose, CA). The positions of the joint markers were then digitized by hand using custom-written software (D. Garand, Garand International Telecommunications, Edmonton, Canada).

Subsequent analysis was performed using custom software written with MATLAB (MathWorks, Natick, MA). The position data of the trunk, hip, knee, ankle, and toe were filtered using a four-order Butterworth, dual-pass filter. The low-pass cutoff frequency was set to 6 Hz. The velocity and acceleration of the hip, knee, and ankle were then calculated by derivative technique.

Infant treadmill stepping is not as regular or consistent as adult stepping. Often, there is out-of-plane movement due to variable movements, usually external rotation of the leg during swing. To determine the extent of out-of-plane movement, the apparent lengths of the thigh, leg, and foot were measured. If the length varied by >10%, the data set was not used in the analysis. If the apparent length varied within the acceptable range, inverse dynamic analysis was performed to calculate the torques (muscle, gravitational, and interaction) at the hip, knee, and ankle (Hoy and Zernicke 1986). Thigh and leg movements were rarely out of plane. If they were, data from that step were discarded (n = 14 steps discarded). Foot movement was often out of plane. In these situations, two-segment analysis (where the foot and shank were considered as 1 segment) was applied that did not require input from kinematic values from the foot. Of all the infants tested and steps chosen for the complete kinematic and kinetic analysis (462 steps), we used two-segment analysis for 110 steps due to out-of-plane movement at the foot. Two-segment analysis due to out of plane movement at the foot was used in 20 of the infants. Six of 7 infants later categorized in the “after-effect” group and 14 of the 15 infants in the “no after-effect” group had some steps in which two-segment analysis was used. In any case, contribution from forces at the ankle were very small (data not shown), especially considering the relatively small mass of the foot (<1% of body mass and <10% of total leg mass) (Schneider et al. 1990). Furthermore, there was little significant change in ankle torques during the different stepping conditions, probably because the weight was strapped to the lower leg and did not load the foot. Thus separate results from the ankle torque calculations will not be presented in this paper. Due to the range of body weights across individual infants, all torque values from each infant were normalized to the infant’s body mass (Winter 1990). During steps taken with the weight on, the mass of the leg was increased by an amount equal to the added weight (500–900 g). The added weight was thus modeled by increasing the mass of the leg. The center of the mass and moment of inertia of the leg was also adjusted based on the original center of mass and the distance from the knee joint to the middle of the weight (Winter 1990). Because the ball bearings inside the weight were roughly evenly distributed, we felt this would be the best approximation of the added weight to the leg.

Ten control steps were randomly chosen to provide baseline measures of the kinematic and kinetic variables for each infant. Pilot data indicated that a minimum of 10 steps would provide an adequate measure of normal undisturbed infant stepping (data not shown). To measure the effect of adding the extra weight to the leg, the first and last three steps taken with the weight on were chosen for full kinematic and kinetic analysis. The initial steps with the weight on were also of particular importance because an immediate increase in flexor activity due to the extra weight may indicate mechanisms mediated by spinal or brain stem reflex pathways. To gauge whether there was a time-dependent adaptation to the weight, the maximum toe height was measured from all the steps taken (to a maximum of 40) with the weight on.

An after-effect (high stepping) that might arise on removal of the weight was gauged by the maximum height in the trajectory of the toe achieved in the first step taken when the weight was removed. A one-tailed z test was used to determine significant increases in toe trajectory height above the mean of control steps (P < 0.05). We thus attempted to group infants according to whether they showed an after-effect or not as measured by these values (Fig. 1).

The swing phase was divided into two equal parts using the following terminology: the first half, or early swing, and the last half, or late swing. For each condition, the average muscle torque during the first half of swing was calculated. This gave an indication of the muscle activity produced to promote clearance of the foot. Muscle torque produced during the last half of swing mainly slows the limb in preparation for ground contact. Because muscle activity produced during early swing would be most affected by the unexpected removal of the weight, we focused on this part of the swing phase although torque profiles for the complete duration of the swing phase are presented.

Additional control experiment

To control for the possibility that the sudden change in cutaneous input due to the sudden removal of the weight contributed to the response observed with removal of the weight, an additional series of experiments was performed in seven additional infants (ages: 7.5–11 mo; weight: 9–12.5 kg) in which the effects of adding the weight were
examined as well as the effects of adding and removing a 6-cm-wide strap of material similarly wrapped around the leg. Analysis of the data from these infants was limited to measuring the height of the toe trajectory during control steps and steps taken after removal of the weight or unweighted band of cloth.

RESULTS

The objectives of this study were to examine whether infants could adapt to an extra load on their leg during stepping and if they could, how this adaptation was achieved. To address the issue of whether learning had occurred, we measured the maximum height of the toe trajectory in the first step with the weight off. In Fig. 1A, each point in the graph represents one infant. For each infant, the difference in maximum toe trajectory height between averaged control steps and the first step with the weight off is expressed as a z score and plotted along the y axis. The infant’s age is plotted along the x axis. The dashed line in the graph delineates a z score value of 1.645, which corresponds with a P value of 0.05 (1-tailed z test). Infants were thus categorized into one of two groups, those that showed an after-effect [corresponding with a significantly higher (P < 0.05) toe trajectory in the 1st step with the weight off; n = 7] and those that did not show an after-effect (n = 15). Note that there was no clear relationship between the presence of an after-effect and the age of the infant. Of the infants who did not show an after-effect, three showed a significantly lower toe trajectory in the first step with the weight off (z score < −1.645). The significance of this finding is unclear but may reflect the inherent variability present in the infant stepping response.

A possible explanation for the lack of an after-effect in the majority of the infants tested might be related to the amount of weight applied or the number of steps taken with the weight. We examined this issue in Fig. 1B, which is a plot describing the characteristics of the sample of infants used in this study. Each data point in the scatterplot represents one infant. The data were plotted as the number of steps taken with the weight against the amount of weight applied (expressed as a percentage of leg mass). This gives an indication of the amount of exposure to the extra weight (number of steps with weight) and the intensity of the exposure (mass of weight). Infants were grouped according to whether they showed an after-effect (●) or not (○). The amount or intensity of the exposure to the extra weight did not seem to have an influence on whether an after-effect was seen. The infants who showed an after-effect had a range of exposure to the weight, from 20 to >100 steps, and a range of weights applied, from 45 to 110% of the mass of the limb.

Kinematics

Figure 2 shows the toe trajectories during the swing phase. The data are shown for two groups of infants, those showing an after-effect and those who did not. In Fig. 2A, the thin solid line surrounded by gray shading represents the average and SE (respectively) of the trajectory of the toe during control steps. Figure 2A shows that the toe trajectory was consistently lower than control when the weight was on throughout the stepping sequence (dashed black lines). The thick solid line represents the response on removal of the weight in the two groups of infants. In seven infants who were categorized in the after-effect group, the high steps taken after the weight was removed is evident in the average toe trajectory of the first step with the weight off (Fig. 2A, left). The high stepping evident in this group of infants is in stark contrast to the return to near control toe trajectory in the other group of infants (Fig. 2A, right).

The maximum toe trajectory height during the swing phase was measured for each step taken with the weight on and off and plotted in Fig. 2, B and C, as a change from control steps of all infants. Each point in the plots represents the average change in maximum toe trajectory height across the infants in each group (after-effect and no after-effect). If repeated trials were obtained from an infant, only the first trial with the weight on was included in these ensemble plots. Both groups of infants tended to attain lower toe trajectory heights throughout the stepping period with the weight on (Fig. 2B). However, the group of infants who did not show an after-effect tended to show lower toe trajectory heights throughout compared with the group who did show after-effects (for quantification, see Fig. 4). In addition, there was no discernable pattern of adaptation in toe trajectory height during the period with the weight on in either group of infants. There was similarly no apparent time-dependent pattern of adaptation seen in hip or knee flexion during the period with the weight on (data not shown).

When the weight was removed, the maximum toe trajectory height returned to control values in the infants who did not
show an after-effect (Fig. 2C, right). In the other group of infants, maximum toe trajectory height was significantly elevated in the first step after the weight was removed ($t$-test, $P < 0.05$). In subsequent steps, the maximum toe trajectory height tended to remain slightly elevated compared with control levels (Fig. 2C, left).

In four infants, we tested the consistency of the response to sudden removal of the weight by repeating trials of stepping with the weight on at least two times. In three of these infants, we observed high stepping after removal of the weight that was consistent across repeated trials. In one infant, high stepping was not observed after removal of the weight and this was also consistent across repeated trials. Figure 3A shows the average response across three infants of successive steps after the weight was removed following the first trial with the weight on (○) and following the second trial with the weight on (△). In both cases, high stepping was seen in the first step after the weight was removed. After the first trial with the weight on, the height of the toe trajectory was significantly higher than control values in the first step after the weight was removed ($P < 0.05$) in all three infants. After the second trial with the weight on, the height of the toe trajectory also tended to be higher than control values although this difference was only significant in one of the three infants in this group. The other two infants had $z$ scores of 1.29 and 1.58, which correspond to $P$ values of 0.09 and 0.06, respectively. Figure 3B illustrates data from a single infant where repeated trials with the weight on were obtained four times (the 1st 2 trials from this infant were also included in Fig. 3A). After the first trial with the weight on (○), the height of the toe trajectory was significantly higher than control levels in the first step after the weight was removed (△). This pattern was observed after each of the subsequent three trials with the weight on (Fig. 3B). Figure 3C illustrates data from a single infant where two repeated trials with the weight were recorded. After each trial with the weight on, this infant did not show high stepping in the steps immediately following removal of the weight. This infant was one of the three infants who showed a significantly lower toe height after removal of the weight (see Fig. 1A). To summarize, in the four infants tested in this way, there was a consistent trend in the response to removal of the weight across repeated trials.

For each infant, the maximum toe trajectory, maximum hip flexion, and maximum knee flexion was measured for the steps when the weight was on and when the weight was removed and compared with control steps. The group of infants who did show an after-effect appeared to adapt their stepping well to the extra weight on the leg. When the weight was on, there was no overall statistical difference in the average height of the toe trajectory or maximum hip or knee flexion achieved compared with control steps ($P > 0.05$) (Fig. 4, A, C, and E, weight-on...
steps). When the weight was removed, the height of the toe trajectory, maximum hip flexion, and maximum knee flexion angle in the first step was significantly higher than control ($P < 0.05$; Fig. 4, A, C, and E, weight off, 1st step). The group of infants who did not show an after-effect tended to have a statistically lower toe trajectory and less hip and knee flexion when the weight was on ($P < 0.01$; Fig. 4, B, D, and F, weight-on steps). When the weight was removed, the maximum toe trajectory height and maximum hip or knee flexion achieved in the first step was not different from control ($P > 0.05$).

**Hip torques**

Figure 5 illustrates averaged hip torques during the swing phase from infants who showed an after-effect (left) and those who did not show an after-effect (right). Muscle, interaction, and gravitational torques acting about the hip are illustrated. The solid line surrounded by the gray shading represents the mean and SE of muscle torque, respectively. The hip muscle torques generated during control steps are comparable between the two groups of infants (Fig. 5, A and B). Hip muscle torques were flexor at the beginning of swing, coinciding with knee flexor muscle torques (Fig. 6) as the leg moves up and forward to clear the ground. Toward the end of swing, hip muscle torques became very low or switched to the extensor direction (Fig. 5A). This corresponds with knee flexor muscle torque during late swing (see Figs. 6, A and B) and may reflect activity in the hip extensor/knee flexor hamstrings muscle group to slow the leg down and prepare for the support phase. The effect of gravity is greatest in the latter part of the swing phase and tends to pull the hip toward extension. This appears to be the main torque acting about the hip to help in braking the leg to prepare for foot contact. This would also account for the low muscle torque generated at this point given that the torque due to gravity is sufficient to slow the leg down at the end of swing.

When the weight is on the leg, there is an overall increase in hip muscle torque in both groups of infants (Fig. 5, C and D). The effect of the additional weight on the leg is also reflected in the interaction and gravity torques throughout the swing phase. At the beginning of swing, there was greater gravity torque produced in the flexor direction as the hip is facilitated into flexion by the extra weight. There was also higher hip flexor muscle torque during the first half of swing compared with control. During the second half of swing phase, greater hip extensor muscle torque was generated, coinciding with the larger increase in knee flexor muscle torque (see Figs. 5D and 6D). This may reflect greater recruitment of the hamstrings muscles to compensate for the large flexor interaction torque, thus decelerating the limb in preparation for support phase. Toward the end of swing, there is also a larger hip extensor torque due to gravity as a result of the extra weight on the leg, which would also help to decelerate the limb in preparation for support.

There was little qualitative difference between the torques produced in the step after the weight was removed and control steps in the infants who did not show an after-effect (Fig. 5F). In the infants who showed an after-effect, there was greater hip flexor muscle torque at the beginning of the swing phase of the first step with the weight off, compared with control steps. This corresponds with the higher toe trajectory and greater hip flexion in the first step after the weight was removed (see Figs. 2 and 4).

**Knee torques**

Figure 6 illustrates the averaged knee torques during the swing phase from infants who showed an after-effect (left) and those who did not show an after-effect (right). Muscle, interaction, and gravitational torques acting about the knee are illustrated as for the hip torque figures. Knee torques generated during control steps are comparable between the two groups of infants (Fig. 6, A and B). At the beginning of swing, knee flexor muscle torques are lowest while gravitational torques are extensor and at their largest. This reflects the influence of gravity assisting the forward movement (knee extension) of the leg as flexion is initiated. During the first half of swing, knee flexor muscle torque gradually increases as the leg is lifted up and forward to clear the ground while gravitational torques gradually decrease. Knee flexor muscle torques continue to increase through to late swing as the leg is moved forward through swing to counteract the extensor interaction torques. Knee flexor muscle torques reached highest values toward the end of swing, serving to slow the leg in preparation for foot contact.

When the weight was on the leg, all of the torque components tended to increase in both groups of infants (Fig. 6, C and
The effect of the extra weight on the leg is reflected in the greater torque due to gravity especially at the beginning of swing. Knee muscle torques show greater flexor activity, likely to counteract some of the extensor effect of gravity at this point while at the same time helping to clear the ground. Toward the end of swing, gravity torques approach zero while knee muscle torque reaches peak flexor activity.

When the weight was removed, the torque profiles at the knee in the infants who did not show an after-effect returned immediately to normal (Fig. 6F). In the second group of infants who showed an after-effect, the torque profiles returned to normal but did so more slowly (Fig. 6E). This suggests that the infants were adapting to the loading conditions during the swing phase.
infants, the observed after-effect was only slightly reflected in the torque profiles (Fig. 6E). During the beginning of swing, knee muscle torque in the first step with the weight off did not appear to be greatly different from control steps. Near the end of swing, flexor muscle torque was higher than control, probably to help counteract the extensor interaction torque at the knee at this time.

**Quantification of muscle torques**

For each infant, the average muscle torque over the first half of swing phase was calculated. These averaged torque values were then averaged across infants in each group (after-effect and no after-effect group) to quantify the changes in hip and knee muscle torques between the different walking conditions (control, weight on, weight off 1st step; Fig. 7). In the first step taken with the weight on, there was an immediate increase in hip and knee muscle torques during the first half of the swing phase (Fig. 7, A and B, weight on, 1st step). Hip and knee muscle torques remained elevated throughout walking sequences with the weight on (see Figs. 5, C and D, and 6, C and D). Despite the increased hip and knee muscle torques, it appears that the infants, especially those that did not show an after-effect, still had difficulty with maintaining the same level of ground clearance with the weight on because toe trajectory profiles remained slightly lower compared with control steps (see Fig. 2). When the weight was removed, hip and knee muscle torques during the beginning of swing returned immediately to normal values in the infants who did not show an after-effect (Fig. 7, A and B, right, weight off, 1st step). In contrast, the group of infants who did show an after-effect continued to produce elevated hip muscle torques, reflecting the existence of an after-effect in these infants (P < 0.01, Fig. 7A, left, weight off, 1st step). Knee muscle torques during the beginning of swing in the first step with the weight off were not significantly different from control (Fig. 7B, right, weight off, 1st step).

**Additional control experiment**

To control for the possibility that a sudden change in cutaneous input as a result of the sudden removal of the weight caused a change in the first step after removal of the weight, an additional series of experiments was performed in seven infants. In these experiments, the effects of adding and removing the weight was examined as in the other infants. In addition, trials during which an unweighted band of cloth was strapped to the leg and did so by recruiting greater flexor muscle torque at the knee and hip. This was exemplified by the
increase in hip and knee flexor muscle torque, which occurred within the first step with the weight on (Fig. 5–7). Of further interest was whether infants showed an after-effect after the weight was removed, which would indicate that learning had occurred. The criteria we used (see METHODS) resulted in a separation of the infants into two groups—those who showed a high stepping response after removal of the weight (n = 7) and those who did not (n = 15). However, the scatterplot in Fig. 1 demonstrates a continuum of responses after removal of the weight rather than a clear separation of infants into two groups.

A limitation in the criteria we used to assess the presence of an after-effect was the fact that infant stepping is variable, and thus differences in the kinematic variables after removal of the weight could be difficult to identify. If long-term adaptive strategies were involved, one would predict that there would be a gradual improvement in limb trajectory over time with the weight on. Generally, however, any time-dependent pattern of adaptation could not be discerned by a step-by-step analysis of the change in kinematic parameters (Fig. 2A). It is also possible that the timeline for such an adaptation is much longer than we were able to study (T. Lam and K. G. Pearson, unpublished results from intact cats). Infants lose interest in stepping on the treadmill after a few minutes, so we are restricted to studying short-term changes only. Another possible restriction is the amount of added weight to the limb. Whether this influenced the adaptation is unclear. The average additional weight experienced by the infants was 76% of the total weight of the limb. It is possible that this was too heavy and prevented proper adaptation of the stepping pattern to the extra weight. Indeed, most infants showed difficulty with stepping with the weight on because the amount of hip and knee flexion generated when the weight was on was significantly lower than control in most of the infants (Fig. 4, right). A previous investigation on the effects of adding weight to infants' legs during stepping elicited on a stationary surface also found slight decreases in both the number of steps taken and the amount of hip or knee flexion generated (Thelen et al. 1984). A complete assessment of the relationship between the amount of added weight and the incidence of stepping would require specific testing of the effect of different weights in the same infant by recording repeated trials.

We also examined the possibility that any change in the stepping pattern after removal of the weight was due to a sudden change in cutaneous input on removal of the weight and not reflective of an adaptive process. This issue was addressed in a series of experiments using additional infants not initially involved in the original study. With this data, we were able to rule out the possibility that the change in sensory input with removal of the sandbag weight contributed to the appearance of a high step. High-stepping never resulted after removal of the unweighted band of cloth whether the infant showed an after-effect after removal of the weight or not (Fig. 8).

All infants showed an ability to adapt to the stepping pattern to the extra weight on the leg. This was characterized by an increase in hip and knee flexor muscle torque within the first three steps taken with the weight on. The rapid and appropriate response to the extra weight suggests a mechanism that could be mediated by reflex pathways. Candidate pathways could include those characterized in reduced cat preparations. Stimulation of hip flexor group I muscle afferents during the swing phase prolongs flexor burst duration and increases flexor burst magnitude in the fictive (McCrea et al. 2000; Perreault et al. 1995; Quevedo et al. 2000) and decerebrate walking cats (Lam and Pearson 2001b). Furthermore, these pathways may have a functional role in mediating flexor activity in response to proprioceptive feedback during the swing phase (Lam and Pearson 2001a). Whether similar flexor muscle afferent pathways to flexor motoneurons also exist in humans remains to be determined. If they do exist in humans, it is possible that increases in the production of hip and knee flexor activity in response to the extra weight on the leg were mediated by these reflex pathways. In addition, we cannot rule out the possibility that the intrinsic properties of muscles played a role in mediating the increase in muscle torque when the weight was on. Indeed, the angular velocities of the lower limb joints tended to be lower with the added weight compared with control stepping (data not shown), and thus the muscles could have generated more force. Muscles are able to generate more force as the velocity of contraction is slowed and do so to compensate for inertial loads (Partridge 1966). However, there was no difference in the velocity of limb movement between the two groups of infants, thus we do not believe that this factor would have contributed to the different responses seen in these two groups.

Motor learning of discrete tasks is often discussed within the context of an "inverse internal model," which is defined as an internal representation of the system and as such has the ability to issue a set of motor commands given a desired sensory outcome or movement trajectory (Kawato 1999). As a theory, it provides a compelling framework within which motor learning can be investigated. One prediction of the internal model concept for motor control is that any recalibration of the motor command for a given task in response to a change to the mechanics of the body will be revealed on unexpected removal of the mechanical disturbance. Whether recalibration of the motor command occurs at the level of the motor or sensory pathways is not known. Nevertheless, the recalibration allowed for the resumption of normal trajectories and the reduction in endpoint errors in the presence of the perturbing input. Unexpected removal of the disturbance reveals this recalibration in the form of a temporary distortion in movement. Whether adaptive strategies during locomotor tasks employ an inverse internal model is not clear. However, there is some evidence supporting this concept. For example, decerebrate walking ferrets adapted to repeated presentation of an obstacle in the path of the forelimb's trajectory by increasing the height of the paw trajectory. When the obstacle was removed, there was a persistence of the conditioned behavior for several steps before returning to control levels (Lou and Bloedel 1988). A similar after-effect (high-stepping) response was also observed in treadmill-trained spinal cats after exposure to a bar placed in the swinging limb's trajectory, suggesting the existence of a short-term motor learning response at the level of the spinal cord (Hodgson et al. 1994). Similarly in humans, there are some reports of after-effects occurring in locomotor tasks after a period of adaptation to a novel environment (Anstis 1995; Gordon et al. 1995; Jensen et al. 1998; Weber et al. 1998). For example, Weber et al. (1998) showed that there is a reconfiguration of the sensorimotor mechanisms that guide the trajectory (direction) of locomotion. Subjects who stepped on a circular treadmill for as little as 7.5 min continued to produce a curved
trajectory of walking when they were subsequently asked to step blindfolded over ground in a straight line (Weber et al. 1998). Thus there are some indications that feedforward control, which may or may not involve recalibration of a hypothetical inverse internal model for walking, is available to adapt locomotor output to sustained changes in sensory input. Whether human infants also use feedforward control during adaptations of their stepping pattern could not be determined with certainty using the present paradigm. However, recent results from this laboratory using a different paradigm (Pang and Yang 2002) suggest that some infants did have an anticipatory response during obstructed treadmill stepping, thus lending support for the idea that there is some capability for feedforward control during human infant stepping.

Our results show that human infants can adjust their stepping pattern in response to sustained changes to the mechanical properties (weight) of the leg. Variability inherent in the infants’ stepping pattern may have limited our ability to draw definitive conclusions about whether any long-term adaptive strategies were developed in response to stepping with the additional load on the leg. If there were after-effects in some infants, this indicates the possibility that there was a recalibration of the motor commands used to generate stepping. Furthermore, we show that all infants could compensate to the extra load on their leg and did so by recruiting greater flexor torque at the hip and knee joints. This is well before the development of mature and independent walking and suggests that some of these adaptive mechanisms may reside in subcortical structures.

Thanks to L. Burkholder for assisting with the data analysis. We also thank Drs. T. E. Milner, K.G. Pearson, and R.B. Stein and the anonymous reviewers for valuable comments on earlier versions of the manuscript.

This research was supported by a grant from the Natural Sciences and Engineering Research Council of Canada to J. F. Yang. T. Lam was supported for valuable comments on earlier versions of the manuscript.

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