Transient Disturbances to One Limb Produce Coordinated, Bilateral Responses During Infant Stepping

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Yang, Jaynie F., Marilee J. Stephens, and Rosie Vishram. Transient disturbances to one limb produce coordinated, bilateral responses during infant stepping. J. Neurophysiol. 79: 2329–2337, 1998. Transient disturbances were applied to the lower limbs of infants (3–10 mo of age) while they were supported to stepped on a treadmill. The aim was to determine how stepping infants respond to novel disturbances that would disrupt equilibrium during independent walking. Their responses were also compared with those from lower mammals and adult humans. In the first series of experiments, the motion of the limb in the swing phase was transiently stopped by the experimenter grasping the limb for a short time (0.1–1.7 s). During such disturbances, the stance phase was prolonged in the contralateral limb, and the onset of the swing phase was delayed. The degree to which the stepping was modified in the contralateral limb depended on the amount of load experienced by that limb. If the contralateral limb was bearing very little weight at the time of the disturbance, its rhythm did not change appreciably. In the second series of experiments, load was added to the infant by pushing down on the pelvis during the stance phase. This greatly prolonged the stance phase and delayed the swing phase. It did not increase the amplitude of the extensor electromyogram (EMG) of the loaded limb. In conclusion, the neural circuitry controlling stepping in the infants responds to disturbances in an organized fashion that is conducive to maintaining equilibrium and forward progression.

INTRODUCTION

Infant stepping exhibits many of the characteristics of adult walking (Yang et al. 1998). For example, the muscle activation patterns show clear alternation between flexor and extensor muscles of the lower limb. Moreover, the infant is capable of adapting her/his walking to the speed of the treadmill belt in a way very similar to that seen in adults (Grillner et al. 1979), suggesting that sensory input from the periphery is used to modify the stepping rhythm in a rather mature way. Others have shown that coordination of the lower limbs remains unaltered even when each limb is driven by treadmill belts running at different speeds (Thelen et al. 1987), similar to that seen in adults (Dietz et al. 1994).

How mature is the walking pattern in young infants? Our previous work suggests that many aspects of adult walking are already present in the infant. Yet, limited evidence from rats suggest that the modulation of some reflexes during stepping changes dramatically with development in both a quantitative and qualitative way (cf. Iizuka et al. 1997 with Fouad and Pearson 1997). Can infants respond to transient disturbances during stepping in a coordinated manner, with appropriate changes in the muscle activity of both limbs? If so, are the responses conducive to maintaining equilibrium and forward progression?

Studies on the maturation of postural control in humans suggest that rudimentary aspects of the control are present as early as 5 mo of age, well before independent sitting or standing (Hadders-Algra et al. 1996; Hirschfeld and Forssberg 1994; Sveistrup and Woollacott 1996). A fully developed, adultlike pattern of postural control, however, emerges considerably later, in the second decade of life (Forssberg and Nashner 1982; Hirschfeld and Forssberg 1992).

In adults, transient disturbances to one limb during walking, whether mechanical or electrical, result in predictable responses in both limbs. These responses help maintain equilibrium (Dietz et al. 1986; Nashner 1980). Moreover, the responses are especially pronounced in the stance limb, regardless of whether the disturbance is applied to the stance or swing limb (Dietz et al. 1986). Such well-coordinated responses are also seen in intact and reduced quadrupedal animals during walking. For example, electrical stimuli applied to one limb generates responses in both limbs in the cat (Duysens and Loeb 1980; Gauthier and Rossignol 1981). Moreover, mechanical disturbances, such as unexpectedly stepping in a hole, generate coordinated responses from both limbs to prevent the animal from falling (Gorassini et al. 1994; Hiebert et al. 1994).

In this paper, the response to transient disturbances during stepping is examined. The infants were all between 3 and 10 mo of age. At this age, the cortical influence on the lumbar spinal cord is small. Myelination of the spinal tracts is incomplete (Yakovlev and Lecours 1967), and an extensor plantar response remains (Peiper 1961). In the first series of experiments, the right limb was suddenly halted during the swing phase, and the response in the contralateral limb was examined. During the disturbance, the stance phase of the contralateral limb was prolonged. The magnitude of the prolongation, however, was dependent on the amount of weight bearing at the time of the disturbance. Thus, in another series of experiments, transient loads were applied during stepping, to determine how adding more load affected the overall step cycle. The results indicated that increased load during the stance phase prolonged the stance phase and delayed the swing phase. This pattern is similar to that seen in decerebrate or spinal cats (Duysens and Pearson 1980; Pearson et al. 1992). Such responses could assist the maintenance of equilibrium during walking. They are present before the infant can stand or walk independently.

METHODS

Subjects

Twenty-one infants were studied. None could walk independently. Twelve were studied during disturbances applied in the
swing phase and 12 during loading of the stance phase. Three were studied during both types of disturbances. The infants ranged in age from 3 to 10 mo (7.2 ± 1.9 mo, mean ± SD). Infants were recruited through the maternity wards of hospitals, and the public health division of Capital Health in Edmonton. Ethical approval was obtained from the appropriate facilities. A parent provided informed, written consent for the infant to participate in the study. Only healthy babies, born at or after 32-wk gestation were included.

Seven infants had systematic practice in stepping while the remainder did not. The parents were instructed either on the phone or in person on how to elicit stepping in infants (Andre-Thomas and Aughtarden 1966). They were asked to have the infant practice stepping for 1 or 2 min, twice a day (see Yang et al. 1998).

**Recording procedures**

All subjects were weighed on an infant scale or on the force platform, depending on where the experiment was performed (i.e., laboratory with or without Gaitway treadmill system). Beckman type surface electromyographic (EMG) electrodes were placed over four muscle groups in the lower limbs in either of the following combinations: quadriceps (quads) and tibialis anterior (TA) of both limbs, gastrocnemius-soleus and TA of both limbs, or quads, hamstrings, gastrocnemius-soleus, and TA of the left limb. Generally, miniature electrodes (2 mm recording diameter) were used for the lower leg, and regular electrodes (7 mm recording diameter) were used for the thigh muscles, except for the very young infants, in which miniature electrodes were used on all muscles. The skin was cleaned with rubbing alcohol before application of electrodes. The electrode pairs were separated by ~1 cm.

Adhesive skin markers were placed over the superior border of the iliac spine, the greater trochanter, the knee line, the lateral malleolus, and the head of the fifth metatarsal of the left lower limb. Force-sensitive resistors (FSRs) (Interlink Electronics, Camarillo, CA) 2.5-cm diam were used to indicate foot contact during stepping in experiments performed on a regular treadmill. One or two FSRs were taped to the sole of the foot or shoe, depending on the size of the infant’s foot, and the footwear they normally preferred. FSRs were not needed in experiments performed on a treadmill with a force platform imbedded under the belt (see STANCE PHASE DISTURBANCES). A twin-axis electrogoniometer (Penny and Giles, Blackwood Gwent, UK) was placed over the right hip joint, because the motion of the right hip was obscured on video.

When the infants were fully instrumented, they were held over a slowly moving treadmill belt with their feet making contact with the belt. The treadmill belt speed was adjusted to a level that seemed optimal for eliciting stepping movements. A video camera recorded the motion of the left side of the body. EMG, force sensitive resistors or force platform, and electrogoniometer signals were recorded on VHS tape with a pulse code modulation encoder (A. R. Vetter, Bakersburg, PA). The video and analog signals were synchronized by a digital counter that incremented light-emitting diode numbers visible to the video, and by a pulse on analog tape at a rate of 1 Hz.

**SWING PHASE DISTURBANCES.** Once good sustained stepping was obtained, disturbances were randomly applied by hand to the right lower extremity. The right limb was stopped momentarily during its flight, either in the first or second half of the swing phase. The duration of this disturbance was varied between 0.1 and 1.7 s. The duration was estimated from the video record, with an accuracy of 33 ms.

The initial results indicated that the response of the contralateral limb was dependent on the amount of weight support on that limb at the time of the disturbance. Thus, in some infants the disturbance was applied while the infant was bearing different amounts of weight. The amount of weight borne was controlled by the experimenter who was holding the infant. For example, at the time of the disturbance, or shortly before, the experimenter holding the infant would lift the infant to decrease the amount of load on the feet. In some trials, this resulted in a stepping. In a few trials, the disturbance duration was prolonged to (>

**STANCE PHASE DISTURBANCES.** Trials were also performed in which the limb was not disturbed during the swing phase, but additional load was applied instead during the stance phase, to examine the effect of load alone. Sudden loading was applied by having the infant bear more of her/his own weight, as controlled by the experimenter supporting the infant, or by another experimenter pushing down transiently on the pelvis. Loads were always applied transiently during the stance phase of one step. The amount of load added could not be controlled exactly. Because the FSRs only provided qualitative information about loading, five subjects were studied in another laboratory, where a Gaitway treadmill system (Kistler Instruments, Amherst, NY) with a force platform embedded under the treadmill belt, was available (courtesy of Dr. Brian Andrews). In these experiments, the exact amount of force could be estimated. FSRs were not used in these experiments, because the force platform provided information on foot contact.

**Data analysis**

A hard copy of the raw data were printed on a chart recorder, and the sequences of good data corresponding to the video record were identified. The EMG data were full-wave rectified and low-pass filtered at 30 Hz, then A/D converted together with the FSR (or force platform), goniometer, and synchronization pulse data at 250 Hz (Axotape, Axon Instruments, Foster City, CA).

**LOADING DISTURBANCES.** Trials in which the infant was transiently loaded were analyzed in a similar way. The duration of the load was estimated from video. Response to loading was quantified by comparing the duration of the disturbed step cycle to that preceding and following it. In some trials, the stepping rhythm stopped after load was applied. These trials were analyzed separately. For the experiments carried out on the Gaitway treadmill, the force platform was calibrated with known weights. Four force-sensitive cells, one at each corner of the force platform, measured vertical force. The total force was the sum of the four signals. The amount of load added in each loading disturbance was estimated as follows. The average force over the stance phase was estimated for the disturbed step and the preceding undisturbed step. The difference in force between these two stance phases represented the amount of load added during the disturbance. The amplitude of the extensor EMG (either gastroc-soleus or quads) and their burst duration during loading was compared with that in undisturbed walking. Only subjects who showed extensor EMGs free of artifact and clear FSR signals were used. The average EMG amplitude during...
the stance phase was calculated by dividing the area under the rectified and smoothed EMG signal during the stance phase by the duration of the stance phase. The stance phase was defined by the FSR or force platform signal indicating foot contact with the ground. The burst duration of the extensor EMGs was estimated visually. Both the amplitude and duration estimates from the EMG signal were analyzed using custom-written programs (MATLAB, MathWorks, Natick, MA).

**Statistical analysis**

A repeated measures analysis of variance (ANOVA) was used to compare the durations of the pre-, during, and postdisturbance steps at a significance level of 0.05. Bonferroni t-test was used to compare the data post hoc. The level of significance for the post hoc tests were adjusted to 0.017 to guard against an increase in type I errors with multiple comparisons (Myers 1979). Student’s t-test was used to compare stepping in 1) practiced versus unpracticed subjects and 2) early versus late disturbances in the swing phase. Differences in the EMG amplitude and burst duration during the stance phase were compared for loaded versus normal steps using a paired t-test. All t-tests were performed at a level of 0.05.

**RESULTS**

**Disturbing the motion of the swing limb**

When the right limb was suddenly stopped during the middle of the swing phase, the rhythm in the contralateral limb was altered. Figure 1 shows stick figures of the contralateral (left) limb during the step preceding the disturbance, and the disturbed step. The most extended position achieved in each step is also shown. The right limb was held fixed for 500 ms during the swing phase in this disturbance. Note that the left limb reaches a much more extended position during the disturbed step. Extension occurs mostly at the metatarsophalangeal joint, but also at the hip and ankle (9 and 16°, respectively, in this case). EMG activity from the same trial is shown in Fig. 2. There was a prolongation of extensor activity (L Quad), and a delay in the onset of the flexor activity (L TA).

Another example from a different subject is shown in Fig. 3. The FSR signals are shown for both limbs. The goniometer signal from the right hip and EMG from the left TA are also shown. The goniometer signal shows that the disturbance disrupted the motion of the swing limb. The FSRs show a prolongation of the right swing and left stance phases as a result of the disturbance.

Similar results were seen whether the infants had practice stepping or not. The average prolongation of the disturbed step compared with the undisturbed step immediately preceding it was 0.475 ± 0.251 (SD) s for subjects with practice versus 0.527 ± 0.135 s for subjects with no practice (difference was not significant, t-test, P > 0.05). Disturbances applied either early or late in the swing phase were also not significantly different. The average prolongation of the disturbed step was 0.500 ± 0.189 s for disturbances applied in the first half versus 0.541 ± 0.363 s for disturbances applied in the second half of the swing phase. Thus the data were pooled (a total of 58 disturbances from 12 subjects).

The average cycle time of the left limb (contralateral to disturbance) for the disturbed step and those preceding and following it are shown in Fig. 4. These were significantly different (repeated-measures ANOVA, P < 0.05). Post hoc tests on the individual means showed that the disturbed step was different from both the step preceding and following it, but the pre- and postdisturbance steps were not different from each other (Bonferroni t-test).

The degree of prolongation of the stance phase in the left limb was related to the amount of weight bearing on that limb at the time of the disturbance. In some trials, the weight
FIG. 2. Muscle activity and foot contact pattern from the same subject as that shown in Fig. 1, during the same disturbance of the swing limb. The rectified and smoothed electromyogram (EMG) from a knee flexor and an ankle extensor muscle of each limb are shown for the step preceding, during, and after a disturbance to the right limb. The force-sensitive resistor (FSR) data (in arbitrary units) for each limb is shown below the corresponding EMG traces. The motion of the right limb was halted for 500 ms during the swing phase (solid line at the top of the graph). The EMG activity of the right limb is considerably altered by the disturbance. Note that the contralateral limb (left) prolonged its extensor activity, and delayed the onset of flexor activity. Note that the FSRs do not indicate the step off (△) has been added. The timing was derived from the video record.

on the left limb either started low or decreased during the disturbance, as the treadmill belt pulled the left limb progressively into greater extension. In such trials, left swing occurred even if the disturbance continued. An example is shown in Fig. 5A. Of the 58 trials recorded, 4 were considered to have low weight support (i.e., weight support low at or within 200 ms of onset of the disturbance). These trials produced significantly less prolongation of the contralateral step cycle than the others (0.194 ± 0.269 s vs. 0.496 ± 0.208 s, P < 0.05 in t-test).

In some trials, the subject bore little or no weight (i.e., aistep). In these, stepping in the contralateral limb continued, despite the fact that the disturbance was halting stepping in the disturbed limb (Fig. 5B). This was also observed in infants who showed good weight bearing, but were lifted up during the application of the disturbance (not shown). Note that when weight support is low, the EMGs are not as regular, and the alternation between extensor and flexor activity is less clear (Yang et al. 1998).

Transient loading of the stance limb

Transient loading during the stance phase also resulted in a prolongation of the stance phase and a delay in the onset of the swing phase (Fig. 6). Note the prolongation of the gastrocnemius-soleus (GS) EMG, and the delay in onset of the TA EMG (Fig. 6A). The FSR signals from both feet show that while the left stance phase was prolonged, the right swing phase was also prolonged, so that the two limbs remained 50% out-of-phase with each other.

FIG. 3. Muscle activity, foot-contact patterns, and goniometer signal from the right hip for one subject during disturbance of the swing limb (right) in stepping. Steps preceding, during, and after the disturbance are shown. The signal from the force-sensitive resistor (FSR) indicates foot contact with the ground when the signal is high (arbitrary units). The goniometer signal is represented in degrees, with zero degrees representing the neutral position (i.e., trunk and thigh aligned), and positive values representing flexion. Note that the hip angle never achieves the neutral position during stepping in this subject, reflecting the more flexed posture of infants. Note that during the disturbance to the right limb (duration shown by solid line at the top of the graph), the goniometer signal on the right hip shows a prolongation of the flexed position as a result of the disturbance. As in Fig. 2, the stance phase is prolonged on the contralateral (left) side while the flexor activity is delayed. Note also that when the right limb resumes stepping, it does so in coordination with the left side.

FIG. 4. Duration of the step cycles on the left side preceding, during, and after a disturbance to the right limb. The disturbances were applied during the swing phase on the right side. Averages across 12 subjects are shown with SE. The disturbed step was significantly different from the pre- and postdisturbance steps. The pre- and postdisturbance steps were not significantly different from each other.
DISCUSSION

The data show that infant stepping is highly responsive to sensory input from the periphery. Transient disturbances applied to one limb in the swing phase affect the rhythm in the contralateral limb. Load added during the stance phase prolongs the duration of the step cycle. The responses to these external disturbances appear organized in a way that would facilitate equilibrium and forward progression during walking.

Characteristics of the response to disturbances

Halting the motion of the swing limb causes the contralateral leg to prolong ground contact. In bipedal walking, this could prevent falling. Similar disturbances in adults produce comparable responses (Dietz et al. 1986). An intriguing aspect of our results is the importance of afferent input from the ipsilateral limb in controlling that limb during walking. For example, when the movement of the swing limb was temporarily halted, the response in the contralateral stance limb was very dependent on the conditions in the stance limb. If the weight support was high, the response was clear. If the weight support was low, the effects were muted.

The duration of the step cycle and the stance phase are shown for 11 of the 12 subjects in Fig. 7, A and B. In the remaining subject, loading always stopped the stepping rhythm, so that the duration of the step with added load was very long, and there were no post disturbance steps. Both the stance phase and the cycle duration of the disturbed step were significantly prolonged compared with both the pre- and postdisturbance steps. The pre- and postdisturbance steps were not significantly different from each other (Bonferroni t-test, post hoc).

The exact amount of load added during the disturbance was estimated in 5 of the 12 infants who stepped on a treadmill instrumented with a force platform. Figure 8 shows the data from one of the subjects during one of the disturbances. The FSR signal is in arbitrary units. The EMG from the gastrocnemius-soleus (GS) is not as clear when weight support is low.

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The EMG amplitude and duration from the extensor muscles (GS or quads) was estimated in a smaller number of subjects, in whom the extensor EMGs were free of artifact. The trend was for longer burst durations during loading, and no increase in amplitude, but the differences were not significant (Fig. 7, C and D).
FIG. 7. Effect of load on the duration of the step cycle (A), the duration of the stance phase (B), the amplitude (C), and the duration (D) of the extensor EMG burst. A: the duration of the step cycle is shown for steps preceding, during, and after the application of additional load, averaged across 11 subjects (mean ± SE). The step with the added load is significantly longer (28%) than the steps preceding and after it. The pre- and postloading steps are not significantly different from each other. B: most of the change in the duration of the step cycle resulted from a prolongation of the stance phase. C: the EMG amplitude for steps with and without extra load were averaged separately across the stance phase for each subject. Pooled data across subjects are shown here (n = 4 for quadriceps and n = 6 for gastrocnemius-soleus). EMGs were not significantly different between normal steps and steps with added load. D: there was a trend for the EMG burst durations to be longer during loaded steps, but the difference was not significant.

The effect of load on the infant step cycle was clear. Adding load during the stance phase, whether by disturbing the contralateral limb or by pushing down on the pelvis, prolonged the duration of the stance phase and the step cycle. Removing load, whether by the treadmill pulling the leg back or by the experimenter lifting the baby, both resulted in initiation of the flexor burst and swing phase. Moreover, previous data on airstepping in the infant showed cycle durations that were much shorter than those seen in treadmill walking (Yang et al. 1998). Together, these results are consistent with those reported for spinal and decerebrate cats (e.g., Conway et al. 1987; Duysens and Pearson 1980; Gossard et al. 1994; Giuliani and Smith 1985; Pearson and Collins 1993; Whelan et al. 1995). In some of these studies, loading was simulated by electrical stimulation of the muscle nerve (Conway et al. 1987; Gossard et al. 1994; Guertin et al. 1995; McCrea et al. 1995; Pearson and Collins 1993; Pearson et al. 1992; Whelan et al. 1995) or the ventral root (Duysens and Pearson 1980; Pearson et al. 1992). In other studies, muscle force was increased by direct stretch of the extensor muscles (Duysens and Pearson 1980) or transient unweighting or weighting of the hindlimbs (Hiebert 1997). In all cases, increase in load prolonged the stance phase, whereas decrease in load shortened the stance phase.

FIG. 8. Data from a single subject during a loading disturbance applied to the right limb during the stance phase. These data were collected on the treadmill with a force platform. The EMG data are shown together with the data from the force platform. Foot-contact (▼) and lift-off (▲) times are shown for the right foot at the bottom of the graph. Note the prolongation of extensor activity, and the delay of the onset of flexor activity. This was a trial with a particularly high loading force (48% of the subject's body weight). Note the increase in force during a disturbed step, and the clear demarkation of foot-contact in the force signal for all steps.
The powerful effect of loading during walking in infants is in contrast to earlier reports in adults (Stephens and Yang 1996a,b). The results suggest that the circuitry in the spinal cord/brain stem for controlling how to respond to loads during walking is more potent in the infant. With maturation, changes occur that modify how adult humans respond to load. More modest effects from activating load-sensitive afferents were also reported for the intact cat (Whelan and Pearson 1997). Presumably, the influence of the cerebrum modifies the behavior of the spinal/brain stem circuitry. Indeed, recordings from cells in the motor cortex in intact cats suggest that a large proportion of these cells fire at the transition from the stance to swing phase, and may play a role in this transition (Armstrong and Drew 1984; Drew 1991).

Adding load to the limb in the stance phase may have inadvertently placed the hip in a more flexed position while under load. A more flexed position of the hip may itself inhibit the initiation of swing, as suggested by work on spinal cats (Grillner and Rossignol 1978). Detailed examination of the data suggests that the effect of hip position may have been quite weak, however. As seen in Fig. 1, under load, the hip was extended beyond the extension angle achieved in undisturbed steps, yet the flexor burst was still inhibited. Distinguishing the importance of hip position versus load on the limb will require further experiments.

Lower centers in the central nervous system contain details for how to respond to disturbances

Bernstein (1967) suggested that the details of movement are organized at lower levels of the nervous system, to free the higher centers of such laborious tasks. With respect to walking, considerable evidence from animal work supports his idea (e.g., reviewed in Grillner 1981; Rossignol 1996). Some data from humans also suggest that the human spinal cord may be capable of generating the rhythmic movements of walking, although the evidence is less direct (e.g., Bussel et al. 1989; Calancie et al. 1994; Dietz et al. 1996; Holmes 1915; Kuhn and Macht 1948). The present study provides further evidence that the circuitry for stepping is operational in infants. It is probably controlled by the lower centers in the CNS (Forssberg 1985). Not only do these lower centers control the details for generating the rhythmic movements, but they also contain the circuitry for responding to unexpected disturbances in an organized, useful way, like that seen in spinal cats (Forssberg et al. 1975, 1977).

Are these well-coordinated responses innate or learned? It is unlikely that these young infants would have had experience with disturbances of this nature. Thus these responses are most likely innate. The seven infants that had practiced stepping might have encountered disturbances of this nature, yet no differences were observed. These results are another example of well-developed, innate behavior being present well before the behavior is needed for functional activities (Forssberg and Nashner 1982; Hadders-Algra et al. 1996; Hirschfeld and Forssberg 1994; Sveistrup and Woollacott 1996). Presumably, the circuitry for such behavior is later modified and refined by experience, as shown by others for other motor tasks such as postural control (Hadders-Algra et al. 1996; Sveistrup and Woollacott 1997) and precision grip (Eliasson et al. 1995; Forssberg et al. 1991).

Comparison between the responses in adults and infants

The maturity and sophistication of the response in these infants can be estimated by comparing them to adults faced with similar disturbances. When the right limb was unexpectedly stopped during its swing phase and prevented from progressing into stance in these infants, the contralateral limb remained in the stance phase. For bipedal walking, this is an important strategy to maintain balance. Dietz et al. (1986) provided a similar but much shorter disturbance (20–160 ms) to adults by holding the swing limb momentarily at different points during the swing phase with a cord attached to the lower leg. When the disturbance was applied early in the swing phase, the contralateral stance phase was prolonged, just as in infants.

Transient loading in the infants, in contrast, produced quantitatively different responses than those seen in adults. Our earlier work suggested that activation of load-sensitive receptors in the lower limb during walking, whether by electrical stimuli to peripheral nerves (Stephens and Yang 1996a) or weights applied to the body (Stephens and Yang 1996b), has little effect on the duration of the step cycle. Transiently adding loads equivalent to 30% of the adult’s body weight causes an increase in the amplitude of the extensor EMGs, but prolongs the duration of the stance phase only slightly (3%). The same load has an even smaller effect on the cycle duration (0.5%) (Stephens and Yang 1996b). In contrast, load experienced by the lower limbs during the stance phase of infant stepping has a very powerful effect on the duration of the step cycle (28%, see Fig. 7), but no effect on the EMG amplitude. Based on the results obtained from the treadmill instrumented with a force platform, the loads applied to the infant were in the same range as those applied in the adult (22% of body weight for the infants and 30% body weight for the adults).

Why were the response of adults and infants similar for the disturbances applied during the swing phase, and different for loads applied during the stance phase? We think it may be explained by the participation of higher centers in the nervous system in the adult, but not in infants. When load is applied to the infant during the stance phase, the spinal/brain stem system might respond by the rule that load means the limb is not ready for the swing phase. Therefore the stance phase is prolonged and the swing phase is delayed, just as in the decerebrate cat (e.g., Duyens and Pearson 1980). In contrast, when load was applied during the stance phase in the adult in a very controlled and consistent way, there was no real danger to the individual or to their forward progression. Thus higher centers in the nervous system could diminish the influence of the spinal/brain stem system, increasing extensor EMG amplitude to avoid disruption of the stepping rhythm. In contrast, halting the swing limb threatens equilibrium and continued forward progression. In this case, it is functionally important that the adult also modify its stepping, to ensure stability. We do not know whether the response in the adult represents the behavior of similar spinal/brain stem circuits as in the infants, or whether supraspinal systems take over the control, and happen to generate a similar response.

Summary

In summary, infants respond to unexpected disturbances during stepping in an organized fashion that appears to be...
suited for maintaining equilibrium and forward progression. All this occurs well before independent walking is possible. Some of the responses are similar to those seen in reduced cat preparations, whereas others show some similarity with those seen in adults.

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