Could Different Directions of Infant Stepping Be Controlled by the Same Locomotor Central Pattern Generator?

TANIA LAMB1 AND JAYNIE F. YANG1,2
1Division of Neuroscience and 2Department of Physical Therapy, University of Alberta, Edmonton, Alberta T6G 2G4, Canada

Lamb, Tania and Jaynie F. Yang. Could different directions of infant stepping be controlled by the same locomotor central pattern generator? J. Neurophysiol. 83: 2814–2824, 2000. This study examined the idea of whether the same central pattern generator (CPG) for locomotion can control different directions of walking in humans. Fifty-two infants, aged 2–11 mo, were tested. Infants were supported to walk on a treadmill at a variety of speeds. If forward stepping was elicited, stepping in the other directions (primarily sideways and backward) was attempted. The orientation of the infant on the treadmill belt determined the direction of stepping. In some infants, we also attempted to obtain a smooth transition from one direction to another by gradually changing the orientation of the infant during a stepping sequence. Limb segment motion and surface electromyography from the muscles of the lower limb were recorded. Most infants who showed sustained forward walking could walk in all other directions. Thirty-three of 34 infants tested could step sideways. The success of eliciting backward stepping was 69%. Most of the infants who did not meet our backward stepping criteria did, however, make stepping movements. The different directions of stepping had similar responses to changes in treadmill speed. The relationship between stance and swing phase durations and cycle duration were the same regardless of the direction of stepping across a range of speeds. Some differences were noted in the muscle activation patterns during different directions of walking. For example, the hamstrings were much more active during the swing phase of backward walking compared with forward walking. The quadriceps was more active in the trailing leg during sideways walking. In some infants, we were able to elicit stepping along a continuum of directions. We found no discrete differences in either the electromyographic patterns or the temporal parameters of stepping as the direction of stepping was gradually changed. The results support the idea that the same locomotor CPG controls different directions of stepping in human infants. The fact that most infants were able to step in all directions, the similarity in the response to speed changes, and the absence of any discrete changes as the direction of stepping was changed gradually are all consistent with this hypothesis.

INTRODUCTION

An important concept emerging from the study of neural networks is the idea that different motor patterns can be produced by the same circuitry given the appropriate modulatory mechanism (Marder and Calabrese 1996). These modulatory mechanisms can be a neuromodulator, afferent input, or supraspinal input (Getting 1989). Invertebrate preparations have supplied the most direct evidence for this idea (Marder and Calabrese 1996). The evidence that a single neural network produces several variants of a task is less direct in vertebrate preparations. One example of this was demonstrated during fictive swimming in the lamprey. Varying the concentration of the excitatory amino acid N-methyl-d-aspartate (NMDA) applied to different portions of the lamprey spinal cord produces changes in the intersegmental coordination (Matsushima and Grillner 1992a). If rostral segments of the lamprey spinal cord are perfused with a higher concentration of NMDA compared with the caudal segments, the fictive swimming resembles forward swimming. If the caudal portions are provided with the higher NMDA concentration, this fictive swimming reverses to the backward direction. Other neuromodulators (serotonin and GABA) also can have a role in the modulation of intersegmental coordination and burst frequency (Matsushima and Grillner 1992b; Tegnér et al. 1993).

The scratch reflex in the turtle also has provided evidence for a common neural network mediating the different forms of a task (Mortin et al. 1985; Robertson et al. 1985; reviewed in Stein et al. 1986). The three basic forms of the scratch reflex are differentially elicited by stimulation of different areas of skin (receptive fields). Blends of the forms of the reflex also can be elicited by stimulation of transitional zones that are situated between receptive fields. These blended responses show characteristics of scratch responses elicited from both adjacent receptive fields. In addition, the segments of the turtle spinal cord that are required for the different forms of the scratch response have been identified and shown to be localized within the same region (spanning 4 spinal cord segments) (Mortin and Stein 1989). Moreover, there is compelling evidence that the neural circuitry for one form of the scratch reflex is shared with the circuitry for the other forms of the scratch reflex (Stein et al. 1998). These findings in the turtle are consistent with the idea that there are common neural network components that control the different forms of the scratch response.

In mammals, the idea of a common neural network underlying different forms of a behavior has been supported in studies of different forms of cat locomotion. The evidence, however, is far less conclusive than that from invertebrate and simple vertebrate preparations. Intact cats can modify their locomotor pattern to produce speed-related changes (i.e., walk, trot, gallop) (Smith et al. 1993), upslope and downslope walking (Carlson-Kuhta et al. 1998; Smith and Carlson-Kuhta 1995; Smith et al. 1998a), crouched walking (Trank et al. 1996), and backward walking (Buford and Smith 1990). The ability of cats to alter their locomotor patterns in this way could be explained by reconfigurations in the locomotor CPG model originally proposed by Grillner (1981) (Smith et al. 1998b).
These central reconfigurations may be accomplished by supraspinal input (Stein and Smith 1997).

Stein et al. (1986) made the observation that humans also are able to change continuously their direction of stepping in a smooth and automatic manner. Are the different forms of walking controlled by the same circuitry? Thus far forward and backward walking have been studied in adult humans. A consistent result from these studies is the almost perfect reversal in the joint kinematic profile when comparing backward to forward walking (Grasso et al. 1998; Thorstensson 1986; Vilensky et al. 1987; Winter et al. 1989). In contrast, muscle activation patterns are more varied. Results among different laboratories show neither a consistent preservation nor a strict reversal in coupling of muscles between the forward and backward direction (Grasso et al. 1998; Thorstensson 1986; Winter et al. 1989). Grasso et al. (1998) suggested that the preservation of kinematic profiles occurs at the expense of muscle activation patterns, but their results neither support nor refute the possibility that a common neural network is producing the different forms of walking.

Studying adult human walking, however, is not the ideal approach to determine the ability of the human locomotor central pattern generator (CPG) to produce different forms of locomotion. Higher brain centers can intervene at any time, and their contribution cannot be distinguished from that originating from the brain stem/spinal circuitry. Recently, human infants were introduced as an alternative model for studying CPG control of locomotion in humans (Yang et al. 1998b).

Infants exhibit a stepping response that is thought to be mostly under the control of spinal and brain stem circuitry (Forsberg 1985; Peiper 1963). Indirect evidence from a number of sources suggest that the strength of connections from the motor cortex are weak in infants. For example, the threshold for eliciting muscle activity in the upper limbs using transcranial magnetic stimulation over the motor cortex is extremely high in young children <2 yr of age (Eyre et al. 1991; Koh and Eyre 1988; Müller et al. 1991). When it is possible to elicit responses, the conduction velocities are more than an order of magnitude slower than adults in infants under the age of 1 (Koh and Eyre 1988). Histologically, the corticospinal tract is not fully myelinated until the age of 2 (Yakovlev and Lecours 1967). Behaviorally, children do not use the finger tip and thumb in opposition to grasp objects (pincer grip) until 6 mo of age at the earliest (Halverson 1943). Development of the pincer grip in monkeys was shown to be correlated with the maturation of the corticospinal tract to the cervical enlargement; this occurs around the age of 7 mo (Flament et al. 1992b; Hall et al. 1992). Maturation of connections to the lumbar enlargement occurs shortly thereafter (Flament et al. 1992a). Thus with the current information, it is reasonable to suggest that infant stepping is not likely under strong cortical control. We cannot rule out the possibility that indirect pathways from the cortex are mature in the infant. Nevertheless, although it is important that we continue to seek evidence for the state of maturation of motor tracts in infants, we believe infants provide a unique opportunity to study the neural control of walking before extensive influence from the cerebrum is present.

The goal of this study was to determine whether different directions of stepping in human infants might be produced by one CPG system. We reasoned that if the same circuitry can produce all directions of stepping, then infants who can step in one direction will be able to step in all other directions, infants will respond in the same way to speed changes regardless of the direction of stepping, and changes in direction of walking can be achieved in a continuous manner without any discontinuity in the stepping rhythm. The incidence of stepping across different age groups, temporal parameters of gait, and the continuous manner in which infants altered their stepping direction provided evidence supporting the idea that different directions of locomotion can indeed be mediated by a common neural network. Preliminary results have been published in abstract form (Yang et al. 1998a).

METH O DS

Fifty-two infants (male and female) ranging in age from 2 to 11 mo were studied. Infants were recruited from the maternity ward of a local hospital and from some local community health clinics. Parents were required to give voluntary and written consent on behalf of their infant for participation in the study. Ethical approval was obtained from the University of Alberta and the local health authority.

Recording electrodes (silver-silver chloride surface electrodes, Beckman type) were placed on the skin overlying the tibialis anterior (TA), gastrocnemius/soleus (GS), quadriceps, and hamstrings muscles after cleaning the skin with rubbing alcohol. In most infants, electromyographic (EMG) recordings were taken from one side. In the other infants, EMG recordings were taken from only the GS and TA muscles from both legs. Regular-sized electrodes (7 mm recording diameter) were used unless the infant was very young or very small, in which case miniature electrodes (2 mm recording diameter) were used. The electrode pairs were separated by 1–2 cm. Force-sensitive resistors (FSRs; Interlink Electronics, Camarillo, CA) were taped to the soles of the feet to record the time of contact each foot makes with the treadmill surface. Adhesive joint markers were placed over 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 on both legs. In some infants, joint markers also were placed over the anterior aspect of the ankle joint, over the superior border of the patella, directly under the anterior superior iliac spine (ASIS) and on the abdomen directly above the ASIS to obtain limb segment motion data from a coronal view for sideways walking. Skin markers, of course, will move with the skin, so they cannot indicate the precise position of a segment. We are interested in the gross movements of the limbs during walking for which these markers are adequate. The analogue data from the electrodes and FSRs were recorded on VHS tape with a pulse-code modulated encoder (A. R. Vetter, Rebersburg, PA). A video camera was used to record the motion from one side. A digital timer synchronized the analogue and video data by generating a light signal on video and a pulse on analogue tape at a rate of 1 Hz.

To elicit stepping, infants were held under their arms with their feet touching a slowly moving treadmill belt (0.1–0.6 m/s). The infant was allowed to bear as much of his or her own weight as possible, the rest being supported by the investigator holding the infant. Short trials (0.5–2 min, depending on the infant’s endurance) were recorded with rest breaks in between.

If an infant could step forward, he or she then was tested in the other directions of stepping. Infants who did not show forward stepping were excluded from the study. Backward stepping was defined as those steps in which the infant’s leg actively moved backward so that the lateral malleolus reached a point posterior to the greater trochanter. Sideways stepping was defined as those steps in which the leading leg was observed to be abducting and the trailing leg adducting past neutral. The infant was held facing different directions with respect to the motion of the treadmill belt to achieve stepping in these directions. Additionally, attempts were made in some infants to gradually turn them along a 180° path during stepping to achieve a continuous
sequence of stepping in all directions. For some infants, different directions of stepping were elicited at a range of speeds. Stepping sequences must have comprised at least 4 consecutive steps to be accepted for further analysis.

Data analysis

Video data were examined for sequences of sustained, alternating stepping. The EMG data were high-pass filtered at 10 Hz, full-wave rectified, and low-pass filtered at 30 Hz. All the analogue data from the EMGs, the FSRs, and synchronization light were converted to digital form at 200 Hz using a computer software program (Axoscope, Axon Instruments, Foster City, CA). EMG and FSR data were averaged over single cycles with alignment to the beginning of foot contact as indicated by the FSRs or video image. Data were analyzed separately according to the direction of stepping. All stepping sequences occurring in a particular direction at a given speed were averaged together. Only noise-free EMG data were included in the averages. The averaged EMG recordings from backward and sideways stepping were normalized to the peak EMG for each muscle obtained from the forward stepping trials at the same speed. These averaged EMG traces over a step cycle were then normalized in time by distributing the trace into a series of 100 time sections using a custom-written computer program (MATLAB, MathWorks, Natick, MA).

Cocontraction was calculated in a similar manner as reported in a previous paper (Yang et al. 1998b). The area under averaged and normalized noise-free EMG data from the TA and GS muscle groups was calculated after removing a bias using a custom-written computer program (MATLAB, MathWorks). The bias was defined as a 50- to 100-ms period of quiescent muscle activity within the averaged and normalized data. The area under the averaged EMG from a muscle was defined as 100%, and the amplitude at each point in time expressed as a percentage of this total. The index of cocontraction was defined as the overlap in area between the TA and GS muscles. For example, if at a given point in time in the step cycle both EMGs were not zero, then the overlap at that time was given as the EMG with the lower amplitude. The total index of cocontraction in the step cycle is the sum of these individual overlap points with the maximum possible overlap being 100%. Indices were calculated for forward, backward, and sideways stepping. The cocontraction indices were compared with data obtained from a previous study (Yang et al. 1998b) using Student’s t-test. The co-contraction indices also were compared between forward, sideways, and backward stepping using ANOVA.

Statistical analysis

The success in eliciting backward and sideways stepping was compared across age groups. The incidence of backward and sideways stepping was expressed as a percentage of infants who could step forward.

A repeated-measures analysis of covariance (ANCOVA), with speed as the covariate, was used to determine differences in stepping frequency between forward, backward, and sideways stepping (leading leg and trailing leg). Stepping frequency was defined as the reciprocal value of cycle duration. All stepping sequences occurring in a particular direction at a given speed were averaged together. Only noise-free EMG data were included for further analysis. The Welch t-test was used to compare the slope (regression coefficient, b) values between each direction, using data from forward stepping as the reference (Glass and Hopkins 1996; Pedhazur 1982). Significance was evaluated at a level of 0.05 for all of the preceding statistical tests.

To quantify differences in muscle activity patterns between the different directions of stepping, ANCOVA was used to compare average EMG amplitude. Data from an individual infant was included only if the infant contributed data to forward stepping and at least one other direction (i.e., backward or sideways). Of the total 52 infants tested, 34 were tested for both backward and sideways stepping. Each cycle of normalized and averaged EMG recording for each muscle was divided into 10 equal bins (i.e., representing one-tenth of the step cycle) and the average EMG amplitude within each of these bins was calculated. The division of the step cycle into 10 bins is arbitrary. It was chosen to allow estimates of the stance and swing phases (bins 1–6 roughly correspond to the stance phase and bins 7 and 10 correspond to the swing phase). We felt this was the most appropriate way to divide the step cycle without making the statistical tests too cumbersome. The following comparisons on EMG amplitude were conducted: forward versus backward, forward versus the leading leg of sideways, and forward versus the trailing leg of sideways. The Dunn (Bonferroni) method of multiple comparisons was used to compare the data post hoc. Thus the level of significance was adjusted to 0.005 to account for the 10 post hoc comparisons to minimize the increase in type I errors associated with multiple comparisons (Glass and Hopkins 1996).

A Incidence of Backward Stepping

<table>
<thead>
<tr>
<th>Number of Infants</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
</tr>
</thead>
<tbody>
<tr>
<td>Failed</td>
<td></td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>4</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Successful</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>5</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>3</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

B Incidence of Sideways Stepping

<table>
<thead>
<tr>
<th>Number of Infants</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
</tr>
</thead>
<tbody>
<tr>
<td>Failed</td>
<td></td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Successful</td>
<td>5</td>
<td>1</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>3</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

FIG. 1. Incidence of stepping in backward (A) and sideways (B) directions in infants who could step forward. Numbers inside the bars represent the number of infants in each group.
RESULTS

Incidence of stepping in different directions

Backward stepping was attempted in 48 of the 52 infants. Thirty-three infants successfully demonstrated sustained, alternating stepping in a backward direction (69% success rate). Backward stepping could be elicited in an infant as young as 2 mo old. By 9 mo old, all infants tested could step backward consistently (Fig. 1). Sideways stepping was attempted in 34 infants. All except one were successful in demonstrating sustained, alternating sideways stepping (97% success rate). Interestingly, sideways stepping appears to be more easily elicited than backward stepping, especially when comparing infants in the younger age groups (2–5 mo; Fig. 1). However, it is important to note that of the infants who “failed” the backward stepping criteria (n = 15), only three (aged 2–3 mo) showed no response at all. In the remaining 12 infants, alternating stepping movements were elicited, but the stepping did not meet our criteria for backward stepping. In most of these infants, the stepping movements resembled in-place stepping, rather than backward stepping. In 3 of the 12 infants (all in the 8-mo age group), backward stepping by a single limb was...
observed. In these cases, the recording limb was held stiff while the other limb made backward stepping movements. Other than the fact that these steps were not alternating, these infants met our backward stepping criteria. We presume that the presence of the electrodes and joint markers on the recording limb produced peculiar sensory inputs that might have interfered with the infants’ stepping patterns.

Figure 2A shows stick figures of forward and backward stepping from a 9-mo-old infant. In contrast to forward and backward walking in adults (Grasso et al. 1998; Thorstensson 1986; Vilensky et al. 1987; Winter et al. 1989), the kinematic profiles do not show a symmetrical reversal in time. This infant’s averaged EMG traces are shown later (Fig. 6). Figure 2B shows stick figures taken from a 5-mo-old infant stepping forward, sideways, and backward. This infant was also one who did not meet our backward stepping criteria (note that the ankle joint is never positioned posterior to the hip joint). However, stepping movements did occur. When comparing the infants in Fig. 2A and B, it is clear that the younger infant was more flexed during forward walking. During backward walking, the younger infant was not able to extend the hip beyond neutral. This is typical of many of the infants who failed our backward stepping criteria. This flexed posture may account for the inability of many of the younger infants to meet our backward stepping criteria because the legs are at a biomechanical disadvantage to extend backward.

**Temporal parameters of stepping in different directions**

Figure 3A demonstrates the strong linear correlation between stepping frequency and treadmill speed ($P < 0.01$ for each direction of stepping). The ANCOVA ($n = 26$) yielded no significant difference in stepping frequency between the different directions of stepping. However, it does appear that there was a general trend of increasing stepping frequency (i.e., decreasing cycle duration) from forward to sideways to backward stepping (Fig. 3B).

Much of the change in cycle duration with speed was due to the change in stance duration for forward ($r^2 = 0.92$), backward ($r^2 = 0.94$), and sideways (leading leg) stepping ($r^2 = 0.89$; Fig. 4). Swing duration was more weakly related to cycle duration for these same directions of stepping ($r^2$ values range from 0.33 to 0.64). In the trailing leg of sideways stepping, there was a different relationship between phase and cycle duration. In this case, both the stance and swing durations varied with cycle duration ($r^2$ values of 0.49 and 0.70, respectively). For the relationship between phase (stance and swing) and cycle duration, there was no significant difference in the $b$ values between forward and backward and forward and the leading leg of sideways stepping. In contrast, the trailing leg in sideways stepping differed significantly from forward stepping ($P = 0.0016$ for stance; $P = 0.0008$ for swing).
EMG patterns

Figure 5 illustrates the index of cocontraction averaged across all subjects who showed good EMG recordings from the TA and GS muscles. Yang et al. (1998b) previously showed that the cocontraction index for the TA-GS pair was significantly higher in infants compared with adults. In the present set of data, we found no significant difference in the cocontraction index for any direction of stepping with that reported previously for infants (Yang et al. 1998b). In addition, there was no significant difference between cocontraction indices between the different directions of stepping.

An example of TA-GS cocontraction is seen in Fig. 6. This figure illustrates the averaged EMG pattern of step cycles from a single representative subject stepping in three different directions at the same speed. Note the activity in the TA muscle, corresponding to activity in the GS muscles during stance phase. Indeed, the cocontraction indices from the TA-GS muscle pair calculated from this infant were higher than average (82% during forward stepping, 72% during sideways stepping, and 64% during backward stepping).

Overall the EMG bursts from a particular muscle generally occurred at the same time in the step cycle regardless of the direction of stepping. The only exception was the hamstring muscle group in which activity started earlier in the swing phase during backward stepping. Similar trends were seen when the data were averaged across subjects (Fig. 7). Two of the 12 ANOVAs (for each of the muscles and walking directions) were statistically significant. Subsequent post hoc test revealed nine comparisons to be significantly different (P < 0.005; see figure legend to Fig. 7). The statistical tests may have been too restrictive, however, and thus were unable to detect some of the obvious differences seen in Fig. 7. However, some interesting trends were noted and will be discussed in the following text. The number of infants who contributed data to the EMG averages is shown in Table 1.

The EMG waveforms for forward stepping were most similar to those of the leading leg of sideways stepping. Even in this comparison, however, some differences were noted. For example, the flexor muscles (TA and Hams) were in general more active during sideways stepping than forward stepping (Fig. 7B). The differences between the extensor muscles were most obvious for the trailing leg in sideways walking (Fig. 7C). Presumably, the propulsive action of extensors is not as important for the trailing leg.

The EMG was most different for the hamstring muscle between forward and backward walking. The strong activity of the hamstrings during backward walking was probably important for generating the hip extension and knee flexion needed during the swing phase (see Fig. 7A). The extensor muscles also showed some differences. The GS does not show the propulsive activity in late stance during backward walking. This trend also is seen in adult walking where the quadriceps take over more of the propulsive role normally assumed by the plantarflexors (Winter et al. 1989).

Transitions

In some trials, attempts were made to gradually turn the infant continuously from a forward to sideways to backward orientation during a sequence of stepping (stepping through a
180° path). This was attempted in 14 infants ranging in age from 2 to 11 mo old. Of the infants tested, eight were able to step from the forward through sideways to the backward direction. Of these eight infants, however, only two were able to make the transition through 180° in a smooth and continuous manner. The six other infants did show stepping in the transition directions but were not considered to have made smooth transitions. Typically their legs collided with each other during the transition directions, causing a disruption in their stepping.

The forward to sideways transition appears to be more easily elicited than the transition into backward stepping as 11 of the 14 infants were able to step continuously from forward to sideways. In 2 of the 14 infants, smooth transitions were not made into any direction. In these infants, stepping to criteria was not elicited during the transition from one direction to another. In four other infants, only the forward to sideways transition was attempted. All four of these infants were successful in this attempt. Transitions always were attempted in the forward-sideways-backward order except in one infant where the order was reversed. Figure 8 shows the progressive decrease in stance phase duration in an infant who was able to make a smooth transition from forward to sideways to backward stepping. Figure 9 illustrates some examples of rectified and filtered EMG signals of single steps in the different directions. Generally, there was a gradual decrease in cycle duration as stepping proceeds from the forward to sideways and finally to the backward direction. Both the TA and GS muscles showed a striking conservation of motor patterns across all directions of stepping (Fig. 9). Note that in this example, TA

![Table 1](http://example.com/table1.png)

**Table 1. Number of infants who contributed EMG data**

<table>
<thead>
<tr>
<th>Direction</th>
<th>TA</th>
<th>GS</th>
<th>Quad</th>
<th>Hams</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forward</td>
<td>24</td>
<td>26</td>
<td>22</td>
<td>21</td>
</tr>
<tr>
<td>Backward</td>
<td>17</td>
<td>18</td>
<td>14</td>
<td>13</td>
</tr>
<tr>
<td>SL</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>ST</td>
<td>12</td>
<td>12</td>
<td>10</td>
<td>9</td>
</tr>
</tbody>
</table>

Number of infants who contributed electromyographic (EMG) data for each muscle in each direction of stepping. Age range: 2–11 mo. TA, tibialis anterior; GS, gastrocnemius-soleus; Quad, quadriceps; Hams, hamstrings; SL, leading leg of sideways stepping; ST, trailing leg of sideways stepping.
activity in this particular infant during forward stepping tended to be higher than other directions of stepping (cf. Fig. 7). Hamstrings and quadriceps EMG records are not illustrated because their EMG signals tended to be smaller and therefore less clear without averaging.

**DISCUSSION**

The data show that infants are able to step in different directions at all ages tested and adapt their stepping to changes in speed in the same way regardless of the direction of stepping. Furthermore infants can make transitions between the different directions of stepping in a continuous way. We argue that these findings are consistent with the idea that the same pattern generators for locomotion can produce different directions of walking.

**Methodological considerations**

There were a number (15) of young infants (≤4 mo) that were classified as “failures” for backward stepping. Nine of 15 of these infants demonstrated alternating stepping movements when presented with a treadmill belt moving backward under their feet but failed our criteria because of inadequate hip extension. Three other infants stepped backward very well with one leg while holding the other leg stiff, again failing our definition of stepping. In the final three infants, who were the youngest of the infants tested (aged 2–3 mo), no backward stepping response was elicited at all. Our criteria for backward stepping were set arbitrarily, however, and may have been too stringent for young infants. The fact that 80% (12 of 15) of these failures produced some form of stepping suggests that stepping can be produced by backward movement of the treadmill belt in the majority of infants.

EMG recordings from infants are always more likely to contain cross-talk between muscles because of the small stature of infants. This issue is discussed at length in an earlier paper (Yang et al. 1998b), and a method was reported to estimate the degree of overlap in activity between flexors and extensors. Using the same methods, we established that the overlap between antagonistic muscles in this study was approximately the same. However, the presence of reciprocal activation of antagonist muscles demonstrates that the cross-talk, although present, is present only in a limited way (see Fig. 7, TA vs. GS, Quad vs. Hams). Furthermore the comparison of patterns between muscle groups is not integral to our central thesis. Our focus is on how a particular muscle performs in different tasks. Thus the effect of a small amount of cross-talk between muscles should not greatly compromise this comparison.
Response to speed is similar for the different directions of stepping

The response to speed change was similar for all directions of stepping tested. The similarity in the response to this type of external perturbation argues for the presence of a common locomotor network mediating stepping in different directions. Changes in cycle duration in response to speed changes were accomplished primarily by changing the stance duration, regardless of the direction of stepping. In a number of infants, we attempted to elicit continuous stepping through 180°, and we observed changes of a continuous nature as stepping proceeded through the different directions. For instance, there was a progressive decrease in cycle duration as stepping proceeded from forward to sideways to backward at a given speed. Concomitant with this was the steady decrease in the proportion of cycle duration devoted to the stance duration.

In addition, the slopes of the regression lines describing the relationship between the phases of the cycle (stance and swing) and cycle duration were not statistically different between the different directions. The only difference seen was in the trailing leg of sideways stepping. However, this difference may be due to the style of sideways stepping. Most infants stepped sideways without crossing one leg over the other. This non-crossing pattern of stepping resulted in the trailing leg frequently colliding with the leading leg at the end of swing (e.g., Fig. 2B). The collision artificially prolonged the swing phase, producing the relationship seen. If we discount the results from the trailing leg because of the mechanical artifact, the remaining relationships (Fig. 4, A–C) are remarkably similar.

Muscle activation patterns in different directions of walking

The similarity in EMG patterns between different directions of walking was not predicted by early hypotheses on how a locomotor CPG could mediate different forms of walking. Grillner (1981) originally theorized that the locomotor CPG was organized such that the switch from forward to backward walking would be achieved by a switch in coupling between the hip and knee joint muscles. However, subsequent findings in intact cats and adult humans have not been consistent with this theory (Buford and Smith 1990; Grasso et al. 1998; Thorstensson 1986; Winter et al. 1989). In intact cats, basic muscle synergies are similar for forward and backward walking (Buford and Smith 1990). Generally, single-joint flexors were active during swing and single-joint extensors were active during stance. Although the motor patterns of single-joint muscles were well conserved, the changes in the pattern of bifunctional muscles with different forms of cat locomotion are more complex. Similarly in infants, we found that the flexor muscles are generally active during swing and the extensor muscles are generally active during stance for all directions of stepping along a 180° path. The exception was the switch in the activity pattern of the hamstrings muscles in backward stepping compared with the other directions of stepping. This type of switch has been reported in detail in many other bifunctional muscles in the cat (Pratt et al. 1996). Pratt et al. (1996) suggested that the differences seen between forward and backward walking in bifunctional muscle patterns are due to the greater complexity of their function and presumably the greater complexity in their inputs from central and peripheral sources. They propose that the greater number of output options available to multijoint muscles allow for a better ability to meet the mechanical demands of the task. Unfortunately, we cannot differentiate the specific functions of bifunctional muscles using surface EMG recordings from human infants because of the small dimensions of the infants’ legs.

The EMG patterns were statistically different for a small number of comparisons. Many trends were noted, however, that could be physiologically important. For example, the extensors from the trailing leg were consistently lower than forward walking, whereas the flexors from the leading leg were consistently higher. This suggests that the role played by the leading and trailing legs were asymmetric compared with forward walking. In forward and backward walking, the hamstring muscle clearly plays a different role (as discussed in the preceding text), but the ankle plantarflexors and knee extensors also might have slightly different roles to play. For example, the push-off burst in the plantarflexors is absent, and the quadriceps activity is more prolonged in the stance phase during backward walking.

Whatever the differences in the EMG patterns, they do not affect our main conclusion that the different directions of walking are likely produced by similar circuitry. There is ample evidence that the same circuitry can produce radically different movement patterns in other animals (e.g., Marder and Calabrese 1996; Stein et al. 1998). It is curious that the EMG patterns from infants walking in different directions are so similar. This is in contrast to some of the results from adults and from other animals (e.g., Buford and Smith 1990; Grasso et al. 1998; Thorstensson 1986; Trank et al. 1996). It is possible that many of the differences seen in other animals and adult humans are related to the change in the role of the muscles to produce propulsion and postural adjustments for the different directions of walking. These infants are held over a treadmill so that the need for propulsion and postural control are much reduced. These mechanical factors could account in part for the differences observed between infants compared with adult humans and cats.

Backward and forward walking are different between infants and adults

The existing literature on forward and backward walking in higher vertebrates has been focused on intact preparations (i.e., adult humans and cats) (Grasso et al. 1998; Thorstensson 1986; Winter et al. 1989). The changes in EMG pattern that occur with change in direction in adult human walking are quite irregular (Grasso et al. 1998). Indeed findings are also variable between the laboratories that have examined motor patterns in adult forward and backward walking (cf. Grasso et al. 1998; Thorstensson 1986; Winter et al. 1989). However, there are other factors likely influencing locomotor output that need to be taken into account when considering backward and forward walking in adult humans and intact cats. Buford et al. (1990) and Buford and Smith (1990) emphasize the postural adaptations that are required for backward walking in cats. The key role of posture in regulating motor patterns during cat locomotion also is highlighted in studies of crouched walking and slope walking (Carlson-Kuhta et al. 1998; Smith et al. 1998a; Trank et al. 1996). In adult humans, Grasso et al. (1998) argue that rather than having a strict regulation of EMG patterns,
locomotion is more highly controlled via limb segment motion. If the movement trajectory of backward walking is reversed in time, it is very similar to that of forward walking (Grasso et al. 1998; Thorstensson 1986; Winter et al. 1989). In their scheme, Grasso et al. (1998) propose that the control of muscle activity is secondary to the attainment of the behavioral goals of the nervous system. Thus in intact cats and adult humans, it appears that the regulation of backward walking is governed by other factors such as postural control or limb joint motion, whereas the regulation of muscle activity patterns occurs secondarily to the execution of these functions.

The infants we studied, all 12 mo of age, likely have minimal cerebral influence directing their motor output (Koh and Eyre 1988; Müller et al. 1991). In addition, the infants were supported while stepping on the treadmill, and presumably factors such as equilibrium did not influence their stepping. Compared with adults, the EMG in infant stepping is less variable between subjects and between different directions (Fig. 7). This is quite different from the intersubject (Grasso et al. 1998) and interlaboratory variability in EMG patterns between backward and forward walking in adults (cf. Grasso et al. 1998; Thorstensson 1986; Winter et al. 1989). On the other hand, limb joint motion in adult humans is very similar between backward and forward walking, whereas it is quite different in infants. Why were the kinematics different (between forward and backward walking) although the EMGs were similar? The kinematic differences were seen mostly at the hip and knee. First, there are some apparent differences in the EMGs of the GS and Quad, even though statistically, they were not different. Second, we were recording the gross activity of four large muscle groups only. The differences seen in the hamstrings likely produced some of the large differences seen at the knee. We have not recorded from any of the single joint hip muscles (because of technical difficulties), which are likely to have a very important role in the limb movement particularly during swing phase. Together, we feel these factors could account for the kinematic differences seen. Because motor cortical function is immature in infants, the precise regulation of limb joint motion in adults in contrast to that in infant stepping suggests that the control of kinematic variables seen in adults originate from higher brain centers.

Conclusions

We feel that the present data are consistent with the idea that a common locomotor CPG controls walking in all different directions in infants. We cannot exclude the possibility that a separate CPG exists for each direction of stepping. Although a separate CPG may exist for forward and backward walking and conceivably even a third CPG for sideways walking, it seems quite unlikely that separate locomotor CPGs exist for all possible directions of walking (theoretically an infinite number of directions). There was little that made one direction of walking stand out from the others. There was a similarity in the response to changes in treadmill speed, regardless of the direction of walking. Furthermore there were no discrete changes in either EMG phasing patterns or the temporal parameters of stepping as the direction of stepping was changed gradually. Although the data presented here cannot directly reveal the nature of the neural circuits involved, they are compatible with the idea that a common central pattern generator could govern locomotion in different directions.

We thank Drs. A. Prochazka and R. B. Stein for helpful comments on earlier versions of this manuscript and R. Vishram and C. Mason for technical assistance.

This study was supported by operating grants from the Medical Research Council and the Natural Sciences and Engineering Research Council of Canada. T. Lamb was supported by a studentship from the Alberta Heritage Foundation for Medical Research and a graduate scholarship from the province of Alberta.

Address for reprint requests: J. F. Yang, Dept. of Physical Therapy, 2-50 Corbett Hall, University of Alberta, Edmonton, Alberta T6G 2G4, Canada.

Received 10 August 1999; accepted in final form 25 January 2000.

REFERENCES


