Interlimb Coordination in Rhythmic Leg Movements: Spontaneous and Training-Induced Manifestations in Human Infants

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Musselman KE, Yang JF. Interlimb coordination in rhythmic leg movements: spontaneous and training-induced manifestations in human infants. J Neurophysiol 100: 2225–2234, 2008. First published July 23, 2008; doi:10.1152/jn.90532.2008. Different rhythmic leg movements in vertebrates can share coordinating neural circuitry. These movements are often similar kinematically, and smooth transitions between the different movements are common. We focused on interlimb coordination of the legs in young infants to determine whether weight bearing and non–weight bearing movements might share coordinating circuitry. If interlimb coordination is controlled by the same circuitry, the same coordination (i.e., either synchronous or alternate) should be seen in different rhythmic movements. Moreover, if we altered the interlimb coordination in one movement through exercise, it should translate to a change in coordination in another rhythmic movement that received no exercise. Video and electrogoniometry were recorded while 46 infants (age, 6.2 ± 1.4 mo) performed non–weight bearing and weight bearing movements. Interlimb coordination was determined from the phase lag between the movement cycles of each leg. Most infants (83%) showed the same coordination in weight bearing and non–weight bearing movements. Ten infants practiced the form of coordination they did not exhibit in the first visit, in weight bearing for 4 wk. Following practice, 8 of 10 infants changed their interlimb coordination in weight bearing to that practiced. Some who practiced synchronous coordination also changed their coordination in non–weight bearing activity. More infants showed both forms of coordination after practice and smooth transitions between the two forms. The results suggest that interlimb coordination is malleable in infants, and there is a partial sharing of the neural substrates for interlimb coordination between different rhythmic leg movements in infants.

INTRODUCTION

Animals exhibit a variety of rhythmic movements that share some underlying neural circuitry. These circuits are reconfigured by sensory input and/or neuromodulators to control different movements (reviewed in Dickinson 2006; Stein 2005). In many cases, the sharing of circuitry is reflected in shared features of the movements, such as similarities in the kinematics and muscle activations (reviewed in Stein 2005). Moreover, movement forms that share circuitry show smooth transitions from one form to another without breaks or discontinuities (Carter and Smith 1986; Earhart and Stein 2000; Mordini et al. 1985; Robertson et al. 1985). The degree of sharing in circuitry has been examined in human adults by inducing an adaptation in one form of movement, such as forward walking on a split-belt treadmill (Reisman et al. 2005) and determining whether the adaptation is expressed in another form of rhythmic movement: backward walking on the split-belt treadmill (Choi and Bastian 2007). Interestingly, there was no transfer of the learning from forward to backward walking, suggesting that there was no sharing of the circuitry involved in the adaptation. Transfer of learning was only found when the direction of the leg movement was the same (i.e., forward walking leg in hybrid walking to regular forward walking). Choi and Bastian (2007) concluded that there may be little sharing of circuitry between forward and backward walking (see their Fig. 6).

Human infants exhibit a variety of rhythmic leg movements including stepping (Andre-Thomas and Autgard 1966), kicking (Thelen et al. 1981), and swimming (McGraw 1939). Few attempts have been made to determine whether the behaviors are similar (Thelen et al. 1981). Coordination between the legs in these movements has been reported to be either mostly alternate or synchronous (Musselman and Yang 2007a,b; Pang and Yang 2001; Piek and Carman 1994; Thelen et al. 1983). Here, alternate and synchronous coordination are relative terms to indicate movements that are closer to being alternate versus synchronous, as has been described for mammalian locomotion (English and Lennard 1982). By using this natural tendency of infants to exhibit predominantly one of the two opposite patterns for interlimb coordination, we determined if weight bearing and non–weight bearing movements might share circuitry for interlimb coordination.

If interlimb coordination in weight bearing and non–weight bearing movements share coordinating circuitry, the two activities should show the same interlimb coordination (i.e., either synchronous or alternate). Moreover, if we induce a change in interlimb coordination in one situation (i.e., weight bearing movements) using exercise over a period of a few weeks, there should be a change in interlimb coordination in the other movements that received no practice (i.e., non–weight bearing). Finally, in infants who exhibit both synchronous and alternate movements, the transition between the two forms of coordination should occur smoothly, with steps that assume intermediate values between the two forms of coordination (Earhart and Stein 2000; Stein et al. 1986). These results have been reported in preliminary form (Musselman and Yang 2007b).

METHODS

Subjects

Infants in good health were recruited through community parent/infant groups in Edmonton. Babies ~6 mo of age were
preferentially recruited because infants this age play in supine or prone positions (Piper et al. 1992), which facilitates recording. Moreover, for the training part of the study, infants ~6 mo of age are unlikely to impose other forms of practice (i.e., crawling or cruising) on their own (Piper et al. 1992), which could confound the study. A parent provided written informed consent at the time of testing. Study procedures were approved by the Health Research Ethics Board of the University of Alberta and Capital Health, Edmonton.

Methods

All infants attended a 1-h testing session. Before testing, parents were asked questions concerning their infant's play habits, so that we could determine whether there was a relationship between the play habits and the interlimb coordination expressed in the experiment.

NON-WEIGHT BEARING. Non-weight bearing activity was elicited first, followed by weight bearing activity on a moving treadmill belt. The parents and a researcher played with the infant to induce excitement, and as a result, rhythmic movements of the legs (Thelen 1985). One to two trials of each behavior were attempted. Trials were 0.5–3 min long with 1- to 2-min rests between trials. Kicking occurred in at least one of four ways: 1) lying supine, 2) lying prone, 3) sitting on the edge of a small bench, upper body supported by a researcher and the legs hanging over the edge of the bench, or 4) airstepping. Air-stepping was elicited by holding the infant under the arms in an upright position with the feet suspended.

WEIGHT BEARING. To elicit rhythmic leg movements in weight bearing, the infants were held under the arms by a researcher over a custom-made split-belt treadmill (model INFSBT-FP, R Gramlich and S Graziano, University of Alberta, Edmonton, Alberta, Canada). The researcher's forearms were supported on a platform to minimize imposing movements on the infant. The infants were allowed to support as much of their weight as possible without the legs collapsing into flexion. The two treadmill belts were always set at the same speed, usually possible without the legs collapsing into flexion. The two infants were allowed to support as much of their weight as possible without the legs collapsing into flexion. The two infants were allowed to support as much of their weight as possible without the legs collapsing into flexion.

TRAINING. Nineteen parents agreed to practice one type of interlimb coordination in weight bearing with their infants at home for 4 wk (practice group). An infant was selected for the practice group if he/she showed mostly one type of interlimb coordination at the first testing session. Parents practiced the coordination type that their infant did not show at the first visit. Practice was prescribed for a minimum of 5 min, two times daily, for 1 mo, based on previous experience (Yang et al. 1998). Parents were shown how to induce the desired movement at the first testing session. To induce alternate coordination, the parent supported the infant under the arms and leaned the infant forward. If there was no spontaneous stepping, another adult moved the infants' legs in a stepping motion. This assistance was withdrawn once the infant initiated stepping. To induce synchronous coordination, the parent bounced the infant up and down in standing to generate jumping movements. Jumping was also practiced in the jolly jumper if the parent preferred that method. Parents were asked to avoid play of the opposite coordination type (i.e., not to use the jolly jumper if the infant was practicing alternate coordination). Weekly phone contact with the parents verified the frequency of practice. Following the practice period, infants attended a second testing session. At this session, the parent showed how he/she had been practicing with his/her infant. Practice was deemed successful if the infant actively performed the practiced movement, as seen from EMGs during the parent’s demonstration. Infants who did not actively perform the desired movement were excluded.

CONTROL GROUP. Four additional infants were seen a second time. These infants maintained their usual play patterns between the first and second testing sessions and served as controls. The control group was included to determine whether changes in interlimb coordination occur in a 4-wk period because of growth and maturation. Testing at the second session was identical in procedure to the first session for infants in the practice and control groups.

Instrumentation

Knee movements were measured with twin-axis electrogoniometers bilaterally (Penny and Giles, Biometrics, Blackwood Gwent, UK). The goniometer arms were aligned with the long axes of the femur and tibia. Two infants were observed to kick mainly from the hips, so the goniometers were instead placed over their hip joints bilaterally (goniometer arms aligned with the midline of the trunk and long axis of the femur).

Surface EMGs were recorded from the quadriceps and hamstrings bilaterally. Recordings from the gastrocnemius-soleus and tibialis anterior were obtained from a few infants only, because preliminary data showed that these muscles were not consistently involved in kicking. Disposable, silver-silver chloride electrodes, 1-cm recording diameter (Kendall, Chicopee, MA) were placed 1 cm apart (center-to-center) on the above-mentioned muscles. The signals were amplified and band-pass filtered at 10–1,000 Hz (AMT-8, Bortec Biomedical, Calgary, Canada).

Movements were videotaped in the sagittal plane, either from the left or right side of the infant (30 frames/s, Canon Elura 50). The leg facing the camera was the reference leg. White adhesive markers were placed on the reference leg at the midline of the trunk above the iliac crest, greater trochanter, lateral knee joint line, lateral malleolus, and head of the fifth metatarsal. Markers were also applied to the contralateral leg over the medial knee joint line, medial malleolus, and medial aspect of the great toe. The infants wore black leotards to enhance the contrast with the markers.

The video and analog signals were synchronized by a timer that advanced an LED counter visible to the camera, and a TTL pulse was recorded with the analog signals, at a rate of 1 Hz. The goniometer signals and the full-wave rectified EMGs were amplified, low-pass filtered at 30 Hz, and converted from analog to digital form at 250 Hz (Axoscope, Axon Instruments, Foster City, CA). All raw signals were also recorded on video tape with a pulse code–modulated encoder (A.R. Vetter, Redersburg, PA) for back-up.

Analysis

The video footage was reviewed off-line. Sequences of at least two sequential cycles in both legs were identified. A cycle was defined as the onset of knee or hip flexion to the subsequent onset of knee or hip flexion based on the goniometer...
signals (change in joint angle $\approx 20^\circ$ and no pauses $\approx 1$ s). The fully extended knee and neutral position of the hip were defined as $0^\circ$. Positive angles represent flexion. An infant’s data were included if he/she performed $\geq 15$ non–weight bearing cycles and $\geq 15$ weight bearing cycles. A customized software program (Matlab, MathWorks, Natick, MA) was used to quantify the phase lag between the movements of the two legs. Phase lag was defined as the delay in time from the onset of the cycle in the reference leg to the onset of the cycle in the contralateral leg, expressed as a percentage of the cycle in the reference leg.

Some infants showed transitions between alternate and synchronous coordination in weight bearing and non–weight bearing. A transition was defined as a change in phase lag of $\geq 20\%$, in which the phase lag changed from synchronous (phase lag 75–25%) to alternate (phase lag of 25–75%) coordination or vice versa. A smooth transition was defined as one without pauses in limb movement $\geq 0.03$ s.

**Statistics**

The distribution of phase lags for all the cycles was first plotted as a histogram. Using circular statistics (Batschelet 1981), the phase lag was represented as an angle in a circle. For simplicity, the angles were also represented from 0–100% as is commonly done for rhythmic movements (Gosgnach et al. 2006). The mean vector angle (henceforth referred to as mean phase lag) and mean vector length were calculated for each type of rhythmic movement for each infant. The mean vector length ($0 \leq r \leq 1$) is a measure of dispersion, with $r = 0$ indicating a random distribution (Batschelet 1981). Whether the phase lag distribution differed significantly from random was determined with Rayleigh’s test (Batschelet 1981). A nonrandom distribution indicates that one type of interlimb coordination was more frequently performed. Distributions that appeared bimodal from inspection of the phase lag histogram were further analyzed to determine whether they were bimodal, using the Dip Intensity test (Giacomelli et al. 1971).

Kuiper’s test was used to identify significantly different phase lag distributions between the two types of leg movements for individual infants and for group data (Batschelet 1981). Kuiper’s test compares the cumulative distributions of two samples. It is adapted for circular statistics from Kolmogorov and Smirnov’s test (Batschelet 1981). The sign test (Moore and McCabe 1999) was used to assess the statistical significance of the total number of infants with similar distributions of phase lag. An independent $t$-test was used to compare the mean ages of the infants with similar and different distributions. For those infants who engaged in practice, we also compared the phase lag distribution between the first and second sessions for each form of movement. Significance was set at $P < 0.01$ for all statistical tests. Mean values are reported with $\pm SD$.

To examine the group data for all movements, the distribution of phase lags from each infant was first normalized to the total number of cycles recorded from the infant and expressed as a percentage (i.e., histograms in Fig. 1). Average histograms were calculated across subjects.

**RESULTS**

**Subjects**

Forty-six of the 68 infants tested met the inclusion criteria for analysis (age range, 3.2–9.7 mo; mean $\pm SD = 6.2 \pm 1.4$ mo; 23 boys and 23 girls). Ten of 19 infants (mean age, 5.9 $\pm$ 0.5 mo; 6 boys and 4 girls) practiced successfully and completed a second testing session. Three infants participated successfully as controls (mean age, 5.6 $\pm$ 1.0 mo; 2 boys and 1 girl).

Most infants showed one type of interlimb coordination

Of the 92 individual phase lag distributions (2 per infant), 69 (75%) were nonrandom, and the vast majority of distributions (98%) for individual subjects were unimodal. Examples of alternate and synchronous coordination for individual infants are shown in Fig. 1, A and B, respectively. Of those infants who

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**FIG. 1.** Phase lag distributions for single infants showing the beginning of a cycle in 1 leg as a function of the cycle in the other leg (cycle from 0 to 100%). Each distribution is presented as a histogram and a polar plot. The black arrow in the polar plot represents the mean vector (maximum length = 1, represented by the outer circle). Each filled dot on the perimeter represents 1 cycle. A: example of an infant who showed alternate coordination in both weight bearing and non–weight bearing. B: another infant who expressed synchronous coordination in both activities. Bin size in the histograms is 2.5%.
showed nonrandom distributions for both weight bearing and non-weight bearing movements, 41% showed the alternate form (similar to Fig. 1A) and 51% showed the synchronous form (similar to Fig. 1B). Although there is a visible difference in the spread of the distribution between the subjects shown in Fig. 1, A (alternate) versus B (synchronous), this was not a consistent finding between the two forms of coordination.

To determine whether kicking position affected the interlimb coordination expressed, we studied nine infants who kicked in different positions (i.e., supine, prone, sitting, or air-stepping). The distributions of interlimb coordination were similar between kicking in different positions ($P > 0.01$).

Group data are shown in Fig. 2. Distributions of phase lag for all the cycles recorded are shown for non–weight bearing and weight bearing (Fig. 2A). Although there was a continuum across all phase lags, greater proportions of cycles are clustered around 50 and 0 or 100%. The distribution of the mean phase lag (i.e., vector angle) for all the infants, during weight bearing and non–weight bearing movements (Fig. 2B), showed the same pattern ($P > 0.01$).

Younger infants (<5 mo old) tended to show alternate coordination, whereas older infants showed both alternate and synchronous, as reflected by the mean phase lag for non–weight bearing (Fig. 3A, vertical dashed line separates infants <5 and >5 mo old). Moreover, the vector length increased moderately with age (Fig. 3B). Weight bearing activity also showed similar trends, but vector length showed no strong relation with age (data not shown).

Comparison of interlimb coordination in weight bearing and non–weight bearing movements

Most infants (38/46 or 83%) showed the same interlimb coordination when weight bearing on the treadmill and when kicking ($P > 0.01$, Kuiper’s test comparing weight bearing and non–weight bearing distributions of phase lag for each infant). The sign test indicated that the proportion of infants showing similar distributions could not be caused by chance. Interestingly, the average age of the infants who had different distributions was significantly greater than the infants found to have similar distributions ($7.6 \pm 1.6$ and $5.9 \pm 1.2$ mo, respectively, independent $t$-test comparing group means, $P < 0.01$).

The mean phase lags expressed when kicking and when weight bearing on the treadmill are plotted against each other for all infants except the six who showed random distributions of phase lag in weight bearing and non–weight bearing (Fig. 4). The majority of infants showed similar mean phase lags in non–weight bearing and weight bearing movements (i.e., fall near the unity line).

Play habits

Sixteen of the 18 infants who showed synchronous coordination in weight bearing and non–weight bearing activities used the jolly jumper ≥5–7 times/wk. In contrast, only 1 of the 17 infants who showed alternate coordination jumped in a jolly jumper 5–7 times/wk.

Practice of an interlimb coordination pattern

Five infants practiced alternate coordination and five practiced synchronous coordination. Eight of the 10 infants showed a significant change in coordination of the weight bearing task at the second visit ($P < 0.01$, Kuiper’s test). This finding indicated that the practice successfully altered their interlimb coordination during weight bearing. Of the two infants who did not show a change, one practiced alternate coordination and the other synchronous coordination. One of these infants showed the trained pattern in weight bearing (just below statistical
significance), and a significant change in the non–weight bearing distribution. Hence, only one baby failed to show any change in interlimb coordination as a result of practice.

Data from the nine infants that altered their interlimb coordination are shown in Fig. 5. Figure 5A shows the interlimb coordination during weight bearing and non–weight bearing activities for the infants that practiced synchronous coordination. Before training, they expressed predominantly alternate coordination. After 4 wk of practice, all five showed synchronous coordination in weight bearing. Three of the five also showed a change in the non–weight bearing activity (2 statistically significant, 1 showed a trend, Kuiper’s test comparing 1st and 2nd testing sessions for each infant separately). Figure 5B shows the coordination for the infants that practiced alternate coordination. Before training, these babies showed synchronous coordination. After training, all babies switched to alternate coordination during weight bearing, although some infants showed cycles of synchronous coordination as well. Interestingly, none of these babies changed their interlimb coordination in non–weight bearing. The three infants in the control group showed no significant change in interlimb coordination of weight bearing and non–weight bearing tasks over a 4-wk period ($P > 0.01$, Kuiper’s test, each infant tested separately). Infants who participated in the practice part of the study also showed more bimodal distributions of phase lag at the second visit. Before training, 1 of 16 distributions was significantly bimodal, whereas after practice, 4 of 16 were significantly bimodal ($P < 0.01$, Dip Intensity test).

Infants made smooth transitions between alternate and synchronous coordination

Seven of the 10 infants in the practice group showed transitions between the two types of coordination, whereas only 26% (12/46) of infants showed such transitions at the first testing session. Transitions were observed during weight bearing and non–weight bearing activities, but they were more commonly seen during weight bearing movements. Figure 6 shows data from two infants during transitions on the treadmill (1 infant showed an alternate to synchronous transition and the other infant a synchronous to alternate transition). Not only did the phase lag change with the transition, but the cycle and extension durations often changed as well. Typically, cycle and extension durations were shorter during synchronous compared with alternate movement (Musselman and Yang 2007a).

Figure 7 shows the interlimb coordination and the cycle and extension durations of the reference leg for six infants who performed an alternate to synchronous transition (8 sequences) and four infants who showed the synchronous to alternate transition (7 sequences). Three infants showed both types of transition and therefore were counted in both groups of infants. In some cases, the interlimb coordination changed instantaneously (i.e., 1 cycle), whereas other transitions were more gradual. Similarly, the cycle duration of the reference leg changed over one to three cycles. Changes in extension duration mirrored changes in cycle length. In contrast, changes in flexion duration of the reference leg were independent of cycle duration and showed no consistent pattern across the transition. If the reference limb showed an instantaneous change in cycle

![Figure 3](http://jn.physiology.org/)

**FIG. 3.** The effect of age on interlimb coordination. A: the mean phase lag for kicking is shown as a function of age. Infants <5 mo of age (left of vertical dashed line) tended to show alternate coordination (i.e., ~50%), whereas older infants showed either alternate or synchronous coordination. Divisions between our definitions of alternate and synchronous forms of coordination are shown in the horizontal, dashed lines. B: the length of the mean vector increased moderately with age.

![Figure 4](http://jn.physiology.org/)

**FIG. 4.** Mean phase lag in non–weight bearing is plotted as a function of the mean phase lag in weight bearing for each infant. With a few exceptions, most data points fall near the unity line. Each circle is from 1 infant. Phase lags >75% were reflected about 0 (i.e., subtracting the phase lag by 100%).
DISCUSSION

The primary new findings are that the majority of infants expressed the same interlimb coordination in weight bearing and non–weight bearing activities. Moreover, practice of one type of coordination in weight bearing over 4 wk induced a change in the coordination expressed during weight bearing, and in addition, translated to a change in non–weight bearing activity in some infants who practiced synchronous coordination. Finally, infants with both synchronous and alternate coordination in their repertoire showed smooth transitions between the two forms of coordination. Together, these findings suggest that there is partial sharing of circuitry for interlimb coordination of rhythmic leg movements in weight bearing and non–weight bearing in young infants. Furthermore, there must be close interaction between the circuitry for synchronous and alternate coordination to allow the seamless transition of movement between the two modes.

Expression of interlimb coordination

As a group, infants showed a full range of phase lags for interlimb coordination in both weight bearing and non–weight bearing movements (Fig. 2A), indicating that the phase relationship between the legs can assume any value from completely synchronous to completely alternate. Two phase lags were more commonly adopted, however; phase lags around 0 or 100% (synchronous) and around 50% (alternate) (Fig. 2). The same pattern is seen in rhythmic limbed movements of other neonatal and adult vertebrates under a variety of movement conditions (e.g., intact turtles walking and swimming: Walker 1979; intact cats stepping: English 1979; neonatal rats swimming: Bekoff and Trainer 1979; Cazalets et al. 1990;
chicks hatching and stepping: Bekoff et al. 1987). Because the two types of interlimb coordination are seen in spinal preparations (Bradley and Smith 1988b; Faytein and Viala 1976; Field and Stein 1997; Grillner and Rossignol 1978; Guiliani and Smith 1985; Stelzner et al. 1975), and at least alternate coordination has been reported in human adults with clinically complete spinal cord injuries (Dimitrijevic et al. 1998; Gerasimenko et al. 2002), the coordination likely reflects the two primary forms of left-right commissural circuitry in the spinal cord, mutually excitatory or inhibitory (reviewed in Kiehn 2006).

Age-related trends in expression of interlimb coordination

The younger infants (<5 mo old) in our group showed alternate coordination, in agreement with other reports (Thelen et al. 1983; Touwen 1976). They occasionally, however, exhibited synchronous coordination also, just as has been shown in other young mammals (Bekoff and Trainer 1979; Bradley and Smith 1988a; Faytein and Viala 1976; Howland et al. 1995). Hence, while synchronous coordination is not as commonly expressed in the very young human, the neural substrates for the activity are operational.

After 5 mo of age, alternate and synchronous forms of coordination were equally likely in our subjects, although individual infants tended to show only one type. These results are somewhat different from those of Thelen et al. (1983), who suggested that infants show a decline in alternate kicking between 4 and 8 wk of age and an increase in synchronous kicks over the first 6 mo of age. The difference in results could be attributed to the small number of subjects examined in the earlier study (8 infants).

Lack of experience may be the main reason why infants younger than 5 mo did not show much synchronous coordination. Both alternate and synchronous forms of coordination were seen in a small number of infants (3/46) in the initial portion of this study (i.e., phase lag distribution was bimodal). In contrast, a much higher proportion of infants exhibited a bimodal distribution of phase lag after they practiced the opposite form of coordination. Because the practice was only for 4 wk, age is unlikely to be the major reason for the change. This is further supported by the fact that none of the infants in the control group changed their interlimb coordination. Hence, exposure to different forms of interlimb coordination likely caused this greater diversity in the movement form and may be the main reason why older infants more commonly showed both forms of coordination.

Possibility of shared circuitry for interlimb coordination of rhythmic movements

Recent findings in the rodent have identified many classes of commissural interneurons in the spinal cord that control interlimb coordination of the legs in locomotor movements (Butt and Kiehn 2003; Kremer and Lev-Tov 1997; reviewed in Kiehn and Butt 2003). The considerable complexity in classes of commissural interneurons identified in the rodent spinal cord suggests the possibility that different types of rhythmic leg movements in mammals use different crossing fibers. Furthermore, recent results in human adults suggest that the circuitry involved in forward and backward walking, including that associated with interlimb coordination, may be quite different because there was no transfer or interference between the adaptation to forward and backward walking on a split-belt treadmill (Choi and Bastian 2007).

Our evidence, however, is consistent with partial sharing of circuitry for interlimb coordination in the movements for two reasons. First, the vast majority of our infants showed the same type of interlimb coordination in weight bearing and non–weight bearing movements. Second, and more importantly, when an infant practiced the coordination pat-
tern that was not performed at the first visit, this resulted in the expression of the same coordination pattern in the unpracticed movement (i.e., non–weight bearing) in some cases. Surprisingly, this transfer of learning was only seen in infants who practiced synchronous coordination. One possible explanation for this difference between the groups is a discrepancy in practice time. Although the practice duration we specified was the same for both groups, anecdotal evidence (comments from parents) suggested the infants who practiced synchronous coordination practiced more than the prescribed time (an average of 20 min/d rather than the prescribed 10 min/d) because they spent extended periods of time in the jolly jumper. It is impossible to restrict patterns of coordination in our case, as has been done in other animals (Viala et al. 1986). Hence, the effective duration of practice may have been different between our groups, and in retrospect should have been documented.

A plausible explanation for our results is as follows. Circuitry coordinating the movements of each leg interacts with mutually excitatory or inhibitory interconnections. With repeated practice of alternate coordination, the mutually inhibitory circuits were presumably activated by descending and/or peripheral input. Hence, in the second visit, this alternate coordination was expressed when the descending and/or peripheral input were present (i.e., during weight bearing), but not when they were absent (i.e., non–weight bearing). In contrast, perhaps because of the greater amount of time spent in practice by the group that trained in synchronous coordination, the mutually excitatory neural circuits between the legs may have been sufficiently reinforced that they could be expressed even when the descending and/or peripheral input was not present (i.e., non–weight bearing). The conclusions arrived at by Choi and Bastian (2007) are very different from ours. Of course, there are many differences between the studies, including the time course of learning and the similarities of the two tasks compared. We suggest, however, that the adaptation induced by short-term exposure to the split-belt environment could also have been upstream from the circuits in the spinal cord (i.e., descending and/or peripheral input). These circuits are clearly different for forward and backward walking and may indeed reside in the cerebellum (Morton and Bastian 2006). Changes to upstream circuits would allow the spinal circuits used to remain the same. These ideas may be testable with animal models in the future.

FIG. 7. Changes in cycle parameters during transitions from alternate to synchronous (left, subplot i) and synchronous to alternate (right, subplot ii). Coordination between the left and right legs (A), cycle duration of the reference leg (B), and extension duration of the reference leg (C) are plotted for 8 and 7 transitions on the left and right, respectively. Each line type refers to a single transition. For the plots in A, phase lags >75% were reflected about 0% by subtracting the phase by 100%. Cycle and extension durations are expressed as a percentage of the duration of the 1st cycle.
Coordination is clearly malleable through experience. Weight bearing, and the transfer of learning in the practice interlimb coordination during weight bearing and non-weight bearing, because a small proportion of infants exhibited different young infants. The sharing is unlikely to be complete, about the transition and perhaps are both operative during the transition period.

Conclusions

The results are consistent with the idea that there is some sharing of circuitry for interlimb coordination between weight bearing and non-weight bearing leg movements in young infants. The sharing is unlikely to be complete, because a small proportion of infants exhibited different interlimb coordination during weight bearing and non-weight bearing, and the transfer of learning in the practice group was not complete. Finally, the expression of interlimb coordination is clearly malleable through experience.

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