Beatrix Vereijken
Faculty of Human Movement Sciences
Free University
Van Der Boechorstrasse 9
1081 BT Amsterdam
The Netherlands

Esther Thelen
Department of Psychology
Indiana University
Bloomington, IN 47405

Training Infant Treadmill Stepping: The Role of Individual Pattern Stability

Received 1 May 1995; accepted 27 February 1996

ABSTRACT: *In this study, we investigated the responsiveness of a developing neuromotor system to training: When is training effective and when are the effects specific to the training condition? Eight infants, six 3-month-olds and two 7-month-olds, received month-long daily training on either a fast-running treadmill, a slow-running treadmill, or a stationary treadmill. Two additional 3-month-old infants served as controls and received no training. Results showed that training led to an increased number of steps. This improvement was inversely related to initial performance: Training had more effect on infants that initially performed unstable stepping patterns. Furthermore, training facilitated the transition from multiple stepping patterns to more alternate stepping. Again, initial pattern preferences influenced these effects of training and often remained visible throughout training. Infant's responses to training at specific speeds were less clear-cut, but some indications were found that this also depended on their initial performances as well as on the characteristics of training. In general, when initial performances corresponded to the training condition, they were strengthened. When they were different from the training condition, training effects generalized to other speeds. These results suggest that the developing neuromotor system is amenable to training whenever performance is unstable, and that training effects interact with the individual's initially preferred patterns. These results are consistent with a dynamic systems view of motor development.* Dev Psychobiol **30:** 89–102, 1997

Keywords: *motor development; infants; dynamic systems; learning*

Only a few decades ago, the predominant view was that early motor skills emerged as infants got older, much like a garden plant unfolds from a seed (e.g., Gesell, 1945). Now, the pendulum has swung the other way, and most researchers agree that experience plays a critical role in the form and timing of new movements (e.g., Adolph, Vereijken, & Denny, 1997; Gottlieb, 1991a, 1991b). The most compelling evidence comes from natural experiments provided by different cultural customs in infant handling. A now classic example is Super's (1976) study of Kenyan Kipsigis children. These babies were advanced compared to American norms in the motor activities of sitting, standing, and walking—all actions which parents specifically encouraged infants to practice. But the infants did not differ in behaviors not specifically

Correspondence to: B. Vereijken
Contract grant sponsor: National Institute of Child Health and Human Development
Contract grant number: HD223800
Contract grant sponsor: National Institute of Mental Health
Contract grant number: K05 MH01102

 CCC 0012-1630/97/020089-14

encouraged by the African mothers such as head lifting, crawling, and turning over. The apparent motor precocity was a function of practice.

Despite the general agreement that experience plays an important role, the processes by which experience influences motor development is poorly understood. Only a few studies have manipulated experience to test its effect on changing skills. Perhaps best known is Zelazo, Zelazo, and Kolb's (1972) demonstration that practice facilitated stepping in 8-week-old infants and prevented the usual disappearance of the newborn stepping response. More recently, Zelazo, Zelazo, Cohen, and Zelazo (1993) showed practice effects on both stepping and sitting in 6-week-old infants. After 7 weeks of daily practice, infants who received exercise of the stepping pattern stepped more, whereas those who practiced sitting sat longer.

Such enrichment studies would seem to be a powerful experimental design because the nature and timing of the added practice can be controlled. The observed effects of practice have nevertheless proven difficult to interpret and the literature reports many accounts of the effects of practice that often seem contradictory. In an attempt to clarify the nature of practice effects, Zelazo et al. (1993) asked the question of whether training-induced changes in early motor patterns are specific to the activity practiced or whether the effects are more general. At one extreme, practice of a pattern such as stepping or crawling may enhance performance of that pattern alone by strengthening the neural pathways involved in that particular activity. They called this a specific effect, as it leads to improvements in the practiced activity only, without affecting other patterns. The Zelazo et al. (1993) study supports this position by showing that practice in sitting did not improve stepping. A second way that training may change a pattern is through increasing muscle strength, an effect that may not be confined to the trained pattern but could be beneficial to other activities as well. With practice, muscles get stronger, and stronger muscles may facilitate the emergence of other patterns within particular contexts as well (Thelen & Fisher, 1983). Finally, practice may produce completely nonspecific effects such as changes in overall muscle tone, levels of arousal, or motivation to move. These training effects should also generalize beyond the trained pattern (Zelazo, 1983).

Support for each of these positions has been reported in the literature, but the question remains of how to untangle specific and nonspecific effects of added practice or training. For example, even at the level of muscle strength effects, there is still debate on the specificity of training: Does practice strengthen muscles used only in that particular activity or is muscle strength a general phenomena? For instance, Zelazo et al.'s (1993) finding that infants trained in sitting were no better in stepping even though both activities used back extensor muscles does not rule out muscle strength changes, as they note, because the muscle strength changes may be relatively specific to the practiced actions. In a similar vein, how specific is practice of a particular pattern of muscle firing? Readers will note that training in one activity such as jogging does not necessarily improve muscle patterns used in swimming, giving rise to the need for cross-training.

If we accept the view that motor development is influenced by experience, then it is critically important to understand what happens with practice. In this article, we go beyond the debate as phrased by Zelazo et al. (1993) and pose the issue in a new light, using principles of dynamic systems. Existing literature shows us that developing systems—as dynamic systems—have the property to change in both general and specific ways. Our question thus becomes: What determines when training has an effect and what determines the nature of the effect? The present article is a first attempt to tackle these issues.

A DYNAMIC SYSTEMS FRAMEWORK FOR UNDERSTANDING PRACTICE EFFECTS

The last decades have seen the rapid advancement of dynamic systems' applications to human behavior. Although many of the ideas have been around for a longer time and have been emphasized before by several researchers (e.g., Bernstein, 1967; Fentress, 1981; von Holst, 1939/1973), this approach is the first to integrate current insights and empirical facts into one general theory, and to provide the methodology and analytical tools to operationalize the relevant issues (e.g., Kelso, Holt, Kugler, & Turvey, 1980; Kugler, Kelso, & Turvey, 1980).

The basic assumption in a dynamic systems approach to development is that patterns of behavior are dynamically assembled from multiple, heterogeneous components within a task context. The issue is not the maturational status of the brain or the experiential history of the child alone, but how these components interact to produce patterns of varying stability. Thus, the primary concern is relative stability of movement patterns, where stable performance is operationally defined as the system's preference for a pattern under particular circumstances, the relative lack of variability of that pattern, and the ability of that pattern to resist perturbations (Kelso, 1990; Kelso & Schoner, 1988; Thelen & Ulrich, 1991; von Holst, 1939/1973).

From dynamic systems principles, pattern stability has two important consequences when considering the effects of practice. First, for patterns to change, they cannot be rigidly stable (e.g., Kelso, 1990). Behavior that is too stable cannot evolve new forms or readily adapt to new environmental conditions, such as those imposed by practice regimes. Second, the pattern imposed by training (the to-be-learned pattern) may coincide with one of the existing patterns in the movement repertoire. In this case, practice leads to a strengthening of that pattern (e.g., Schoner & Kelso, 1988). By contrast, if the to-be-learned pattern is different from existing patterns, there is competition between the patterns, leading to a reduction in stability. These ideas were experimentally supported and modeled in a recent adult learning study (Schoner, Zanone, & Kelso, 1992; Zanone & Kelso, 1992). In this study, participants had to learn a new timing relationship between two fingers wiggled back and forth. The authors provided a convincing qualitative demonstration that the initial pattern stability influenced what participants learned. In other words, there was possible competition between what the subject already preferred to do, and what the task demanded that he or she learn.

To take this pioneering work on learning dynamics a step further, we hypothesize that training patterns in infancy may also depend on the interaction between current pattern stability and new tasks: Cooperation versus competition between required and preferred patterns might determine the training effect. In the case of cooperation between the patterns, the training enhances and thus strengthens the already existing pattern. Practice can be expected to lead to specific effects, that is, an increase of patterns explicitly trained. When there is competition, however, training may be ineffective, having little effect or destabilizing the current pattern. Or when no preferred pattern emerges, training may lead to generalized training effects like increased muscle strength, increased motivation, and so on. In short, we propose the following hyotheses: When patterns are unstable there can be change, and when there is cooperation between the pattern to-be-learned and existing movement patterns, the change will be specific to the training condition.

Under this scheme, specific as well as nonspecific practice effects can be understood as being a function of both the stability of the individual infant's existing motor patterns and the conditions of training. This implies that individual training regimes must be evaluated in relation to the infants' initial pattern stability (Muchisky, Gershkoff-Stowe, Cole, & Thelen, 1996). To this end, we need to move away from the traditional practice of collapsing individual data into group means as this obscures relations that reside at the individual level. Instead, it is crucial to compare individual performance before practice with individual improvement as a result of training (Zanone & Kelso, 1992).

TRAINING TREADMILL STEPPING

In this article, we report the effects of training of an infant motor pattern as a function of the condition of training and the stability of already existing patterns. We chose treadmill stepping in prelocomotor infants as the task, as this skill is ideally suited for experimental manipulation. When held supported on a small, motorized treadmill, infants as young as 1 month of age perform coordinated stepping movements. Treadmill stepping is similar to phenomena in other vertebrates where patterned behavior is elicited precocially when young animals are placed in facilitative environmental contexts, which presumably provide for components of the behavior that are not yet mature (see, for instance, Fentress, 1981; Stehouwer & Farel, 1984).

Although treadmill stepping can be elicited in infants as young as 1 month, early stepping is unstable. Infants take few steps and they step in several bilateral patterns: with one leg only or with both legs simultaneously, as well as in an alternating fashion. Starting around 3 to 4 months of age, infants step increasingly in an alternating mode. At that time, however, performance is still quite variable. By 7 months, alternation has become a stable, preferred pattern, especially when the treadmill is moving relatively fast (Thelen, 1986; Thelen & Ulrich, 1991). By that age, alternation is so well established that it is preserved even when severely perturbed by placing infants on a split-belt treadmill that moves one leg twice as fast as the other (Thelen, Ulrich, & Niles, 1987). Alternation can thus be characterized as a stable, behavioral pattern that develops in the second half of the 1st year of life (Thelen & Ulrich, 1991).

The treadmill thus elicits a perceptual–motor pattern well in advance of the independent use of this pattern in erect locomotion. Given that the pattern itself shows a developmental course, we used this behavior to investigate the relation between individual movement characteristics and effects of training. First, if treadmill stepping is amenable to training, is training differentially effective depending on the initial stability of the infants' existing patterns? As we discussed earlier, dynamic theory predicts a stronger effect on unstable patterns. Second, are treadmill steps differentially affected by specific training conditions, in this case practice stepping versus practice standing and training on specific treadmill speeds? As outlined earlier, we predict that when the movement pattern to-be-learned matches what the infant does or prefers to do, that particular pattern will be enhanced leading to a specific learning effect, i.e., specific to the training condition. If the training condition does not match the infant's preferred pattern but competes with it, training will have few or nonspecific effects.

To test these predictions, we designed a training study that was heavily inspired by the Zanone and Kelso (1992) learning study. We gave month-long daily training to 3-month-old infants, whose step patterns are normally unstable, and 7-month-old infants, who usually step reliably in alternation, particularly at a fast treadmill speed. We trained the 3-month-olds at two speeds, fast and slow. The 7-month-olds trained at a generally not-preferred slow speed. Another group of 3-month-olds were trained in standing only. A fifth group was a no-training control group. Following the procedure outlined by Zanone and Kelso (1992), we regularly tested the effects of training by having all infants go through the entire range of treadmill speeds. Our detailed expectations were: (a) Training will be more effective when initial patterns are unstable, i.e., when infants initially perform few steps in several different patterns; (b) training effects will be specific to training condition (stepping versus standing) if initial preference for step type is unstable and does not compete with the training condition; and (c) training effects will be specific to training speed when initial speed preference is unstable or cooperating with the training speed.

Method

Subjects. Ten infants, 4 girls and 6 boys, participated in this study. There were eight 3-month-olds (mean weight: 6.6 kg., SD = .76) and two 7-month-olds (mean weight: 7.5 kg., SD = .28). All infants were white and from working- and middle-class families. The parents were identified through published birth announcements and invited to participate by letter and phone call. They were paid a small fee for their involvement in the study.

Apparatus. We trained infants on a small, motorized treadmill with adjustable belt speeds ranging from 11 cm/s to 29 cm/s. Two video cameras (one for each leg), positioned behind the infant at an angle of about 40 degrees, recorded the performance at 30 frames/s. Two spotlights, shining on the back of the infants, secured good visibility of the reflective markers taped to their heels. We conducted the training and test sessions in a mobile laboratory van parked near the parent's house.

Design. The eight 3-month-old infants were randomly assigned to one of four different groups. The two 7-month-olds were in a fifth group. The first group, labeled 3FAST, was trained on a fast-running treadmill (speed was 26 cm/s) four times a week for a total of 4 weeks. The second group, 3SLOW, and the 7-month-old group, 7SLOW, also had 16 training sessions, but on a slow-running treadmill (speed was 14 cm/s). By training the 7-month-olds on a generally nonpreferred slower speed, we tested whether their preference for faster speeds could be shifted toward a preference for slower speeds. The fourth group, labeled 3STAT, had 16 training sessions in which we supported them on a stationary treadmill. This group was included to control for muscle-strengthening effects of standing. Finally, we included a control group, 3CTRL, who received no training on the treadmill, but acted as a control for the normally expected developmental improvements in treadmill stepping (Thelen & Ulrich, 1991).

At the beginning and ending of the month of the experiment, all infants received a probe to test their stepping abilities at the full range of treadmill speeds (i.e., 0, 11, 14, 17, 20, 23, 26, and 29 cm/s). This allowed us to see whether training effects were limited to the particular training speed or generalized to the other treadmill speeds. In addition, the 8 infants who received training on the treadmill had these scalar probe sessions after every 2nd day of training. These infants thus received a total of 16 training sessions and nine scalar probe sessions. The 2 control infants received only the two scalar probe sessions.

Procedure. After the parent(s) entered the van with their infants, the experimenter undressed the infants and attached two reflective markers at the backs of the heels with hypoallergenic tape. Subsequently, the experimenter supported the infants above the treadmill, allowing them to bear as much of their own weight as they would, providing additional support and balance when necessary. The parents stood to the side of the experimenter in the infants' direct line of view.

For a training session, the treadmill was turned on for 2 min and 20 s, followed by a 2-min break in which the parents held their infants. We then supported the infants for another period of 2 min and 20 s on the treadmill.

The scalar probe consisted of eight consecutive, 20-s intervals. Every probe began with a baseline period of 20 s during which the treadmill was stationary. After 20 s, we turned the treadmill on at either the fastest (i.e., 29 cm/s) or the slowest speed (i.e., 11 cm/s). After every 20 s, we changed the speed in a stepwise fashion (decreasing or increasing the speed in 3-cm/s intervals) for a total of 2 min and 20 s. This was followed by a 2-min break and the second half of the probe, starting again with a baseline of 20 s, and stepwise speed changes of the treadmill after every other 20 s. The order of the speed changes (increasing or decreasing) was counterbalanced across both halves of each probe and across infants within each group.

Measurements. We coded all the probe sessions for treadmill steps of both feet, that is, nine sessions for the 8 experimental infants and two sessions for the 2 control infants. We defined the initiation of a step as the video frame at which the marker on the foot reversed from moving backward on the treadmill to moving forward, signifying the start of a swing phase. The period between two consecutive reversals of the same foot marker was defined as a step.

We identified four different patterns of interlimb coordination in stepping: single, double, parallel, and alternate (Thelen & Ulrich, 1991). A single step was a step taken with one foot while the opposite foot was dragging on the treadmill belt or lifted up in the air. A double step was when one foot took two steps while the opposite foot stepped only once. When both feet were stepping with the same frequency, the relative timing between foot reversals determined whether a step was parallel (foot reversal initiated within 20% or after 80% of the step cycle of the opposite foot) or alternate (foot reversal initiated between 20% and 80% of the step cycle of the opposite foot).

Results

We present the results in four sections. In the first section, we check for possible order (or hysteresis) effects of the two probe halves and the direction of speed change within a probe. The second section presents the effects of training on stepping frequency as a function of training condition and initial pattern stability. In the third section, we investigate the development of preferred stepping patterns as a function of condition of training and initial pattern preference. In the final section, we pursue speed-specific effects of training on stepping performance in each of the speed intervals within a probe.

Effects of Probe Half and Direction of Speed Change. Each probe had two halves, each half consisting of a stationary baseline and seven intervals in which the treadmill speed was either increased or decreased. In order to test for possible effects of probe half and the direction of the speed change (increasing or decreasing) within a probe, we performed 2 Probe $\times$ Probe Half $\times$ Direction of Speed Change (1, 9 $\times$ 1st, 2nd $\times$ increasing, decreasing) repeated measures ANOVAs on the number of steps and the proportion of alternate steps (the developmentally most-stable pattern). There were no significant main effects for probe half and direction of speed change nor any significant interactions, indicating that there were no order effects for either measure of treadmill performance. Thus, we collapsed across probe halves and speed changes for all the following analyses.

Effects of Training on Stepping Frequency. To test whether daily training on the treadmill improved infants' frequency of stepping, we first compared the average number of steps per probe half between the first and last probe sessions at the group level. The results are presented in Figure 1. As can be seen, there was an overall increase in number of steps across all conditions. This increase was largest in the 3-month-old infants who received daily training on either a slow or a fast treadmill. Three-month-olds trained on a stationary treadmill did not improve frequency of step-

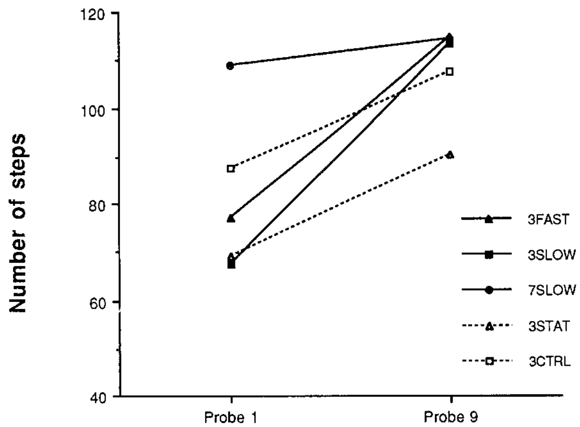

FIGURE 1 Increase in total number of steps from Probe 1 to Probe 9 for the five conditions.

ping beyond the normal rate of development as demonstrated by the control group. Training had little effect on the performance of 7-month-olds who performed near ceiling on the first probe.

A Condition × Probe × Speed Change (3FAST, 3SLOW, 3STAT, 3CTRL × 1, 9 × increasing, decreasing) repeated measures ANOVA on number of steps for the 3-month-old groups showed probe to be significant, $F(1,4) = 26.13$, $p < 0.01$. There were no significant interactions, indicating that there was no significant differential effect of training condition. An ANOVA with $n = 2$, however, has extremely low power. To further test for the effects of training versus no training, we collapsed 3FAST and 3SLOW in a training group and 3STAT and 3CTRL in a control group, and performed a one-way repeated measures ANOVA on number of steps. This design yielded a significant interaction between group and probe on number of steps, $F(1,6) = 4.22$, $p < 0.05$. This indicates that, within this small sample size, infants trained on a moving treadmill improve faster than the control groups with respect to number of steps. Treadmill stepping is thus amenable to training.

To test our hypothesis regarding the relation between initial pattern stability and magnitude of training effects, we plotted number of steps as a function of successive probes for each subject separately. In the top panel of Figure 2, the 3-month-old infants who trained on a moving treadmill are plotted together; the bottom panel shows the remaining infants. The values in the legend refer to improvement from Probe 1 to 9 in percentages of performance on Probe 1. Although there was considerable interprobe variability among individual infants, every 3-month-old trained infant who started out with few steps showed a large increase in number of steps with training (top panel). The 3 infants who showed stable performance on the first probe in terms of a large number of steps, i.e., CK in the 3FAST group (top panel) and both 7-month-olds (bottom panel), improved far less despite training. The Pearson correlation between number of steps on Probe 1 and improvement from Probe 1 to 9 (in percentages of number of steps on Probe 1) for these 6 trained infants was almost perfect, namely −0.95, $r^2 = 0.90$, and significant, $p < 0.01$.

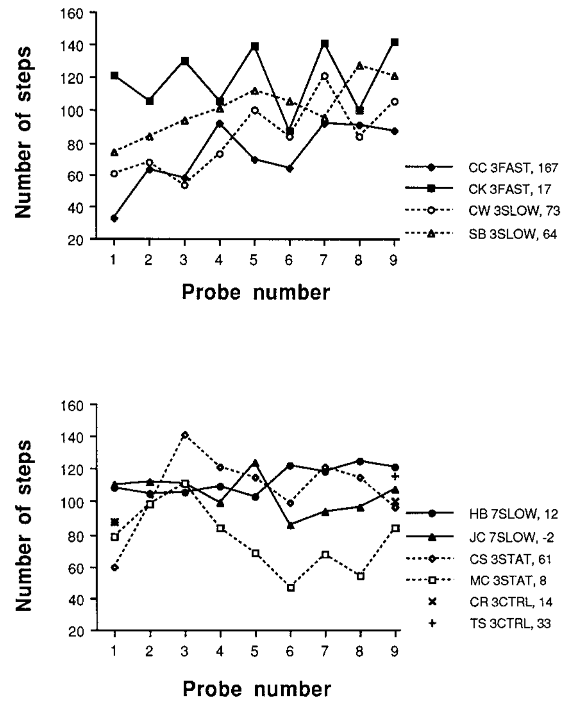

FIGURE 2 Number of steps for each of the 3-month-old training infants (top panel) and remaining infants (bottom panel) across the probes. The values in the legend refer to the improvement between Probes 1 and 9 in percentages of initial performance.

The 4 remaining 3-month-old infants all began with a small number of steps (bottom panel). Without training, the improvement in performance in the 2 control infants fell well behind that of the trained infants. Furthermore, in the 3STAT group (bottom panel) only 1 of the 2 infants had a large increase in number of steps with training on a stationary treadmill; both 3STAT infants showed a decrease after an initial increase in performance. With no training or training on a stationary treadmill, the Pearson correlation for these 4 infants between initial performance and improvement over time was lower than in the trained infants, namely −0.75, $r^2 = 0.56$, and not significant, $p > 0.05$.

Development of Preferred Step Patterns. Given that treadmill training in 3-month-old infants increased the overall number of steps, we next asked how training affected the changes in preferred stepping pattern as reflected in the proportion of each type of step across the probes, and whether this was dependent upon initial performance. Figure 3 shows how preferences for stepping patterns developed over the month of the experiment in each of the infants. All infants performed double steps only incidentally throughout all probes. Shifts in preference could be discerned, however, between the other three stepping patterns.

First, consider the 3- and 7-month-old infants trained on a moving treadmill (Figure 3, top 3 rows). On the first probe, all four 3-month-olds performed a mixture of mostly single and parallel, sometimes alternate, steps. The first infant (CC) trained on a fast treadmill (top row, left panel), performed predominantly single steps on Probe 1, along with a fair amount of parallel steps. With training, single steps decreased dramatically, alternate steps showed an increase, and parallel became the preferred pattern. In contrast, consider the second infant (CK) trained on a fast speed (top row, right panel). At the start of training, this infant stepped with about half of his steps alternating, and he maintained (and slightly increased) this strong preference for alternation throughout. He also showed a high proportion of parallel steps on the first probe, and this preference was largely preserved as well. In the slow treadmill condition, CW started out with predominantly single and parallel steps, and some alternate steps (second row, left panel). Over the course of the experiment, she showed a decrease in the proportion of single steps and an increase in alternate steps while maintaining parallel performance. SB began with a strong preference for single steps (second row, right panel). Throughout the course of training, this pattern mostly disappeared and alternate steps became the preferred pattern. With respect to the two 7-month-olds, HB maintained her strong and almost exclusive preference for alternate steps (third row, left panel). JC, in contrast, started with mostly parallel and single steps on Probe 1 (third row, right panel). His proportion of parallel steps slightly increased, along with alternate, whereas that of single steps decreased. Overall, training the 3- or 7-month-olds led to a decrease of single stepping whereas alternate and parallel stepping were either maintained or increased.

Like the trained 3-month-olds mentioned earlier, the 3-month-olds trained on a stationary treadmill and the control infants began with a mixture of step types. Infant CS had a small increase in alternation at the cost of single steps whereas his initial preference for parallel steps was further strengthened (fourth row, left panel). MC, who stepped less in later weeks of training, showed a small decline in single and alternation and maintained his mixture of parallel, alternate, and single steps (fourth row, right panel). One of the control infants, CR, while slightly decreasing the proportion of alternate, likewise maintained his mixture of step types across the month of the experiment (bottom row, left panel). The second control infant, TS, showed a decrease in her proportion of single steps and a slight increase in alternate and parallel steps (bottom row, right panel). In summary, compared to the trained infants above, we detected less regularities in the pattern of change for the infants who had no training or training on a stationary treadmill. Single steps could decrease but also increase, alternation increased in some infants and decreased in others, and the proportion of parallel steps could decrease, increase, or be maintained.

For all infants, regardless of training condition, we found a relation between the strength of the alternation preference and the overall number of steps taken. These are independent variables: Infants can step little and have all the steps alternate or they can step frequently and never alternate. Nevertheless, the overall Pearson correlation across all infants between number of steps in a probe and the proportion of alternation in that probe is 0.70, which is significant at $p < 0.01$. Individual correlations across probes for number of steps and proportion of step type are listed in Table 1 for the infants who were trained on either a running or a stationary treadmill. As can be seen, for each infant the correlation between number of steps and single steps was negative, whereas the correlation with alternate was always positive. Thus, for the groups and for the individual infants, the more steps taken, the more likely the pattern of coordination was alternating. In these correlations, no differential effect of training condition seemed to be apparent.

When infants performed more alternating steps, did they also improve the coupling of the two legs over time? In other words, did the delays between foot reversals (defined over each step

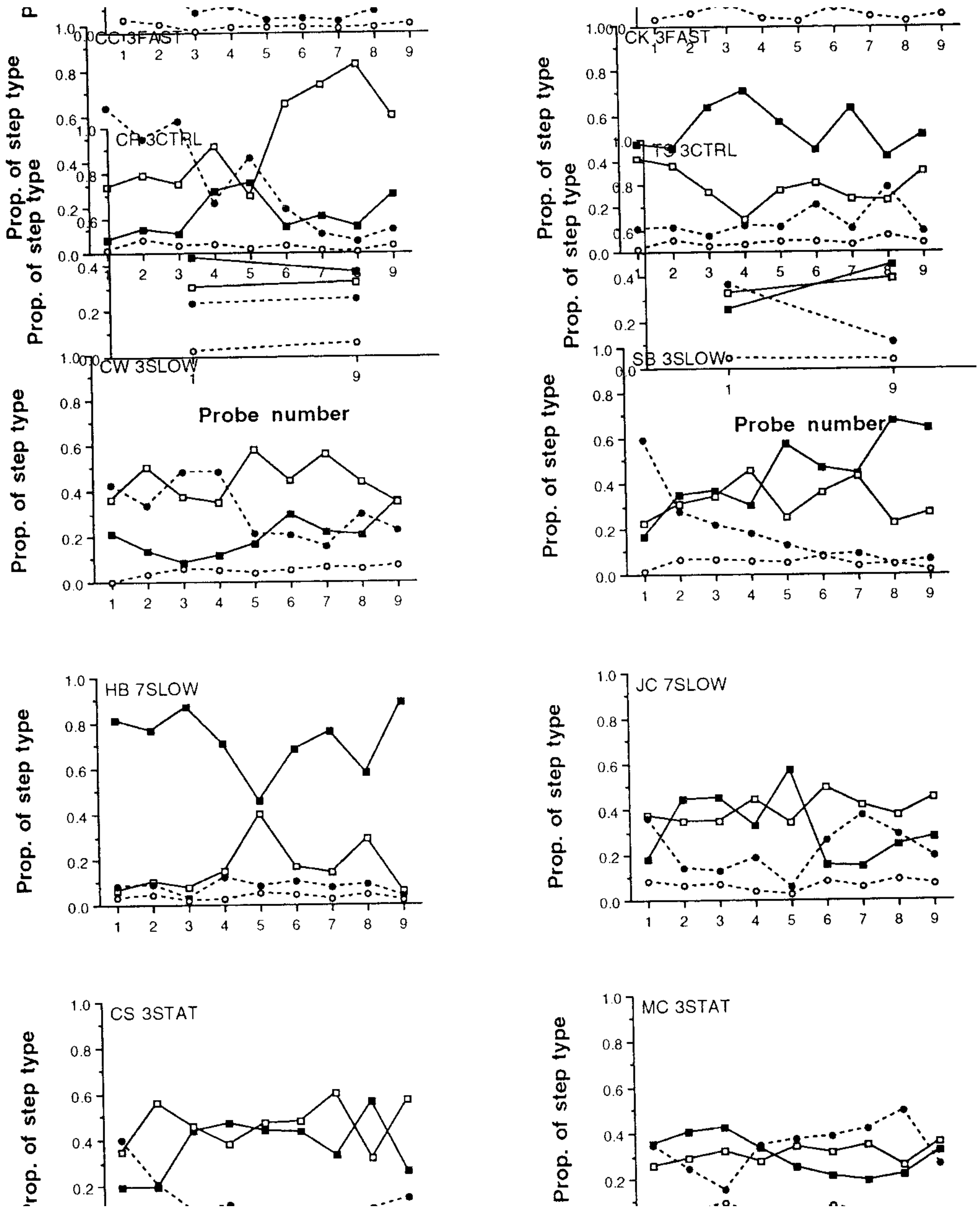

FIGURE 3 Proportion of each step type for each of the 10 infants across the probes. Filled squares refer to alternate steps, open squares to parallel steps, filled circles to single steps, and open circles to double steps.

Table 1. Correlations Between Number of Steps and Proportion of Step Type for the Experimental Infants Across the Probes

Infant	Alternate	Parallel	Single	Double
CC	.57	.69	−.88	−.12
CK	.44	.11	−.68	−.39
CW	.57	.53	−.87	.55
SB	.94	−.16	−.84	.07
HB	.04	−.03	−.03	−.10
JC	.81	−.75	−.64	−.44
CS	.66	.17	−.82	−.94
MC	.92	.08	−.90	.35

cycle) approach 50% over practice, indicating perfect alternation? To address this question, we looked at the delays between foot reversals of the alternate steps across the nine probes for all the infants. Overall, there was no convergence of this delay to 50% over the course of the experiment, either in terms of the mean or of the median value. There was also no systematic decrease in the standard deviations of the alternate step foot-reversal delays over the course of training. Although training thus promoted an increase in the proportion of alternation, within the criteria for alternating steps, we did not detect tighter coupling as a function of training. The only exception in this respect was SB who showed a clear decrease in SD over training. Note that SB was also the infant who had the largest increase in number of steps and proportion of alternate steps.

Speed-Specific Effects of Training. In the previous sections, we looked at the effects of training on stepping across probes. In this section, we ask whether differential effects of training can be discerned between the different speed intervals within a probe. Do infants develop, over training, a preference for their training speed? Is this related to initial speed preference? To answer these questions, we have to investigate changes in performance on each of the eight different speed intervals within a probe. We decided not to look at number of steps in each interval, as comparing absolute number of steps on a slow speed and a speed more than twice as high leads to misleading results. Therefore, we looked at the ratio of alternate steps to total steps at each speed within a probe. The data for Probe 1, the initial probe, Probe 4, midway in training, and Probe 9, the last test, are represented in Figure 4 for each infant.

In the 3FAST group, CC initially showed alternate steps at the faster speeds only (Figure 4, top row, left panel). On Probe 4, her proportion of alternate had improved overall. On the final probe, she performed the highest proportion of alternate steps at the training speed. CK, who was earlier seen to be quite good from the start in terms of number of steps and proportion of alternate, appeared to have a slight initial preference for the slower speeds (top row, right panel). This disappeared with training on a fast speed. Except on the slowest speed, he performed a high proportion of alternate steps across the intervals on Probe 9. In the 3SLOW group, CW initially showed variable performance across the speed intervals (second row, left panel). With training, she slightly improved overall, ending up on the last probe with the highest proportion of alternate on the slow training speed. Her pattern of performance on Probe 9, however, was variable. The second infant in this group, SB, greatly improved overall, with a variable pattern of performance at the end of the experiment (second row, right panel). The first 7SLOW infant, HB, performed a high proportion of alternate steps across speeds and probes (third row, left panel). JC, in contrast, did not show much improvement, and his fluctuations across and within the probes revealed no discernible differential effect of speed (third row, right panel). The two 3STAT infants had overall changes in performance across the probe trials, but no clearly discernible trend related to speed (panels in fourth row). One control infant, CR, performed the highest proportions of alternate steps on the slower and the faster speeds on Probe 1 (bottom row, left panel). On Probe 9, he had the highest proportion on the slower speeds. Infant TS began with a preference for middle speeds and seemed to develop, without training, a more variable distribution (bottom row, right panel).

These data are qualitative only, and should be regarded with proper caution. Nevertheless, there are indications for the development of a speed preference in the predicted direction in 2 of the 3-month-old trained infants. In a third trained 3-month-old infant, the initially preferred pattern competed with the training condition, leading to generalized improvement across all speeds. The last 3-month-old trained infant started with unstable performance, and also showed overall improvement. Training the 7-month-old infants did not yield a discernible pattern over speeds. The

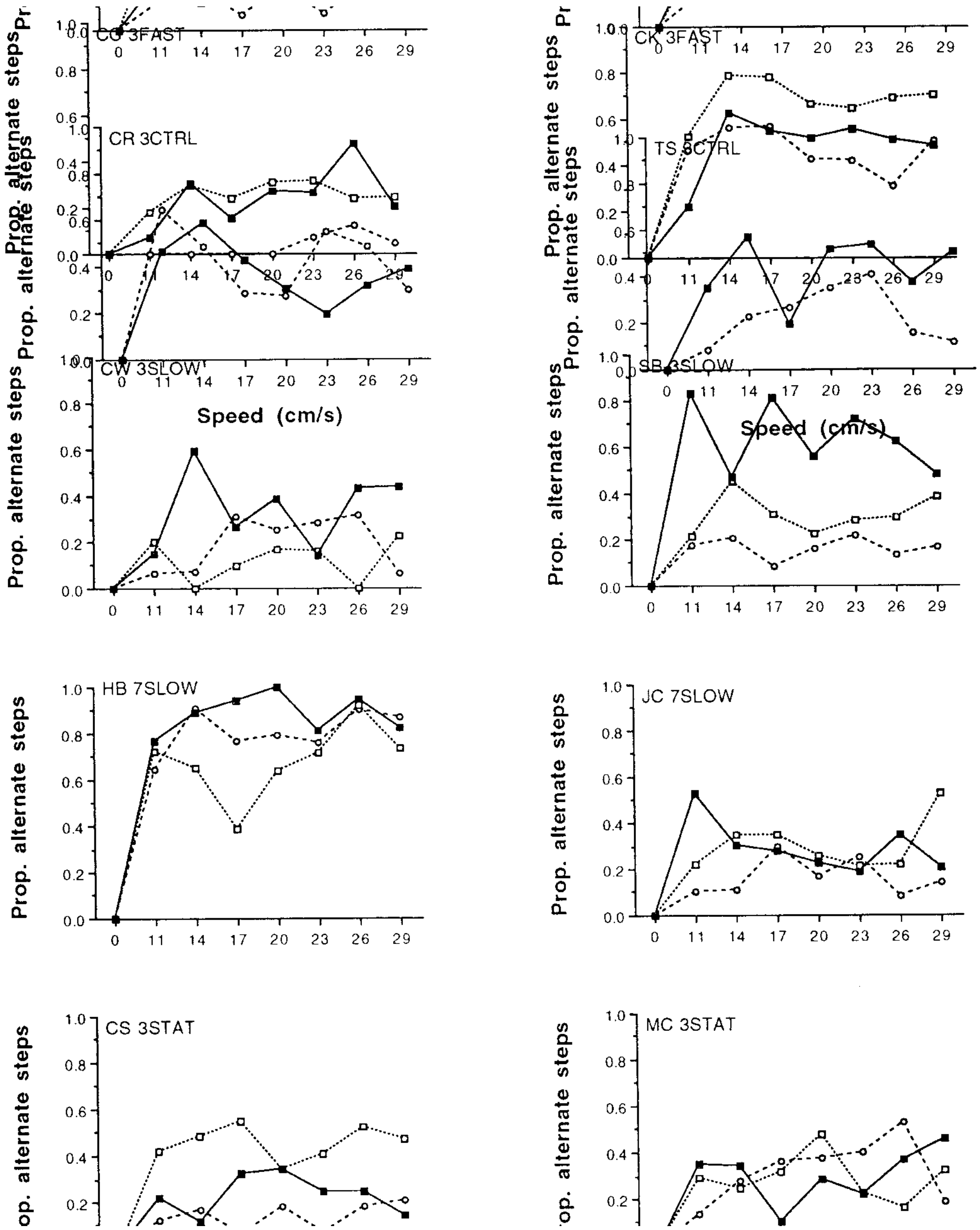

FIGURE 4 Proportion of alternate steps at each speed interval for each of the infants across the probes. Open circles refer to Probe 1, open squares to Probe 4, and filled squares to Probe 9.

other 4 infants, trained stationary or control, predominantly showed variable performance across probes and speeds.

Discussion

Our goal in this study was to understand the effects of enriched motor experience on infants' performance. In particular, we asked (a) when training would be effective and (b) whether training effects would be specific to the training conditions. Working from dynamic systems principles of pattern stability, we predicted that training would not have the same effects on all infants. Rather, we contended that individual pattern preferences and their stabilities would interact with experimental conditions to yield differential results.

Our first analysis focused on the effects of experimental condition on the frequency of stepping. When we collapsed the training groups, we found an effect of training at the group level: The 3-month-olds who practiced on a moving treadmill had a larger increase in number of steps than infants of the same age who did not experience the moving treadmill. Within the limitations of the small sample of infants used in this intensive training study, we thus found that this early performance of a later coordination pattern is amenable to training. This finding is consistent with earlier research showing that enriched experience leads to an increase in performance (e.g., Zelazo et al., 1972).

By looking at individual characteristics, however, we also noted that training interacted with individual infants' own pattern preferences and stability. As we predicted, training was more effective when initial performances were unstable, both in 3- and in 7-month-olds. But we also noted that training changed the patterns of stability beyond what would occur during the natural developmental course of treadmill stepping. Compare the Pearson correlation coefficient between initial number of steps and training effect in the trained and in the control infants. In the 3- and 7-month-old trained infants, 90% of the variance in step increase was explained by the relationship with initial performance. In infants without additional training, only 56% of the variance in step increase could be attributed to initial performance, a nonsignificant correlation.

Likewise, both the training condition and the individuals' initial performance influenced the development of a preferred pattern of stepping (single, parallel, or alternate). In all trained infants, if single steps were performed on Probe 1, they dropped out by Probe 9. The proportion of alternate steps increased with training in all 6 trained infants, becoming the preferred pattern on Probe 9 in 4 of 6 infants. In the two exceptions, parallel steps were, and remained, the most performed step type. In the control infants, changes over time were less regular. The proportion of alternate decreased in half of the infants, single steps did not always drop out, the most performed pattern on Probe 1 (apart from single) did not have to become the preferred pattern by Probe 9, and the initial mixture of three different patterns was often retained. In comparison to the infants trained on a moving treadmill, the 2 infants trained on a stationary treadmill both developed a preference for parallel stepping. In 1 infant, parallel was the most performed pattern, after single stepping, on Probe 1. In the other infant, however, parallel ranked only third on Probe 1.

Training on a moving treadmill thus appeared to strengthen the stepping patterns that involved a coupling between the two legs (i.e., alternate and parallel) in comparison to other possible stepping patterns where the legs are moving independently (i.e., single and double). Alternate was the pattern that increased most with training, thereby increasingly becoming the preferred performance. In other words, training led to improved stepping performance on the treadmill, which in turn facilitated the transition from multiple stepping patterns to more dominantly alternate stepping. This is also indicated by a significant correlation across infants between the number of steps and the proportion of alternation. Over the relatively short time span of the experiment, no systematic changes were observed in the quality of the alternate steps. With the exception of 1 infant only, the infants did not converge to a delay in foot reversals of 50%.

With respect to speed-specific training effects, the results were variable and far from decisive. Bearing this critical note in mind, 2 of the 6 infants that trained on a moving treadmill indicated a preference for the training speed on Probe 9. One infant started with a slight preference for the training speed on Probe 1, which was subsequently strengthened by training. The other infant had unstable performance on Probe 1, and developed a preference for the training speed. Three of the remaining trained infants improved overall, and thus showed training effects generalized to all speeds. The initial performance of 1 of these infants indicated a competing speed preference on Probe 1. All 4 control infants showed variable performance across the probes and speeds.

A problem with the last analysis is the number of steps performed within a speed interval. Especially on Probe 1, both the total number of steps and the number of alternate steps were often very small. This makes it difficult to reliably establish initial preferences or to perform statistical analyses. These data should thus be regarded with caution and they do not provide hard evidence for our predictions regarding specific versus general effects. Nevertheless, they are largely consistent with our predictions and encourage further investigation along these lines. We did not test whether there is generalization of training effects to a different context, but the work of Zelazo et al. (1993) suggests that this might be limited.

Taken together, these results, although largely qualitative, are consistent with the dynamic systems' assertion that infants' initial performance and preferences interact with training to produce differential effects. Training condition alone was a much poorer predictor for outcome. In other words, what the infants brought into the experiment influenced their subsequent performance. To the extent that the initial performance was stable and competing with the training condition, training on the to-be-learned alternate pattern was less effective. This opens the way to further experimentation involving direct manipulation of initial pattern stability.

These results suggest a different view on the well-known empirical fact of ceiling effects. Although the ceiling effect has been found in learning studies time and again, attempts to account for it have been ad hoc and unprincipled. In the dynamic systems view, the ceiling effect is an explicit prediction when trying to improve upon performance that is already stable. The dynamic systems' reasoning also proposes an explanation for reports in the literature that perturbations tend to enhance ongoing tendencies (e.g., Fentress, 1976). Dynamics labels this phenomenon *hysteresis,* which indicates that multiple behaviors are possible at the same time, and that the actual behavior is affected by your previous behavior. Whether this "redescription" is indeed an explanation awaits empirical confirmation by careful experimentation.

What Does Training Train? What then, does training train? To answer this question, we need to examine the dynamics of treadmill stepping more closely. Thelen and Ulrich (1991) suggested that the neuromotor pathways for stepping movements may be in place very early in life but that the behavior initially emerges only in the specific context of the moving treadmill. In particular, they hypothesized that it is the dynamic stretch of the legs provided by the moving belt that is the critical mechanism. Stretching the leg may have two consequences. First, given the spring-like qualities of the limb (Schneider, Zernicke, Ulrich, Jensen, & Thelen, 1990; Thelen, Kelso, & Fogel, 1987), the stretch provides the stored elastic energy for the spring forward, as is provided during normal locomotion as the weight is shifted forward over the stance leg. Recent evidence also suggests that the stretch is important informationally as well as energetically. Pearson, Ramirez, and Jiang (1992) proposed that the unloading of the leg at the end of stance and as it is maximally stretched provides the proprioceptive input that triggers initiation of swing and the bilateral pattern of alternating responses. When these investigators mechanically stretched the extensor muscles of one ankle in cats whose ankle extensor and knee flexor muscles were surgically isolated, they entrained bilateral locomotor patterning in the knee muscles corresponding to the frequency of their experimental rhythmical stretching of the ankle muscles. This suggests that proprioceptive information about the biomechanical status of the legs is used by the CNS to generate the characteristic muscle patterns of alternating swing and stance. The pattern emerges in a dynamic dialogue with the periphery, in this case, with the changing forces and loads on the limbs provided by the treadmill. Similar mechanisms may be at work in the animal literature and account, for example, for prefunctional stepping behavior in frogs (Stehouwer & Farel, 1984).

As Thelen and Ulrich (1991) suggested, in order for infants to enter into this perception–action dialogue with the treadmill, their legs must have the appropriate range of "springiness." The treadmill pull has no effect on legs that are too tightly flexed either because the infant does not make consistent contact with the belts or because the treadmill force cannot overcome the flexor bias. Conversely, legs that are flaccid cannot benefit from further stretch and may not receive the requisite energy or proprioceptive signals.

Under this scheme, training likely has the effect of influencing the general balance of tone and strength of the legs. Repeated stretching on the treadmill and swing forward may help release the 3-month-old infants from the flexor dominance of early infancy and particularly strengthen the extensor muscles that provide the stretch energy and information. Control and static-trained infants received less stretch exercise and their improvement may reflect the general extensor gains made from other, nontreadmill activities. Seven-month-olds are generally stronger and have already gained more balance between flexion and extension tendencies. Training did not further improve their treadmill performance.

As the younger infants became stronger and less flexed, they responded more consistently to the treadmill. If, as suggested by Pearson et al. (1992), there is a neural link between the stretch of one leg and the pattern in the opposite leg, any activity that promotes efficient stretch should also lead to a more alternating stepping pattern. This is what we found. The number of steps and the proportion of alternation were positively correlated. Thus, as stepping was facilitated, alternation emerged also as a preferred pattern.

Whatever the mechanism, we found that training on the new motor pattern of alternation competed with some infants' strong initial preference for parallel steps. This is consistent with what Zanone and Kelso (1992) observed in their adult subjects trained to a 90-degrees pattern of coordination in finger flexing. Some subjects immediately discovered the required pattern, whereas others had a more difficult fight against their highly stable 0- and 180-degree modes. Group data alone obscures this important insight about learning—that subjects come into the learning experiment with individual pattern stability that itself is a product of the organic status of the individual and his or her developmental history.

Treadmill Stepping and Independent Walking. What does treadmill training reveal about the natural process of learning to walk? Is there a relationship between the patterns elicited on the treadmill and walking? Normally, infants learn to walk without ever having seen a treadmill or having been trained on one. Additionally, our 7-month-old infants were good at treadmill stepping without prior training. This indicates that the developmental changes that lead to either good walking or good treadmill stepping without specific stepping practice may be a result of other, nonspecific activities that infants engage in that function to improve, for instance, extensor strength or balance of tone. At any time, the expression of specific neuromotor patterns is multidetermined. Facilitating any of the substrate systems, for instance through specific enriched experience but also through general training, can thus subsequently influence the expression. Note that the training here was simply to impose conditions favorable for eliciting stepping and thus to allow the system to assemble a stable and preferred pattern. In a sense, the same kind of process must underlie the onset of independent overground locomotion. Through infants' own explorations of their leg dynamics in standing and supported stepping, and with caregivers' assistance in creating a facilitative physical environment and providing postural support and stability, infants come to discover a pattern that works. As in the treadmill, the anatomic structure and neural substrate must be in place, but the cooperative assembly of these components is emergent in a particular context; in this case, the postural ability to provide dynamic stretch of one leg without losing balance. The ability to modulate current abilities of subsystems to new task demands is the fundamental process of development.

NOTES

We thankfully acknowledge the infants and their parents who gave so generously of their time and effort. Dexter Gormley, John Spencer, and the undergraduate students at the Infant Motor Development Lab were indispensable in data collection and analysis. Rob Bongaardt, Daniela Corbetta, John Fentress, and Pierre Zanone provided helpful comments on an earlier draft. This research was supported by HD223800 from the National Institute of Child Health and Human Development and by a Research Scientist Development Award from the National Institute of Mental Health Grant K05 MH01102 to Esther Thelen. Beatrix Vereijken was a research fellow of the Royal Dutch Academy of Arts and Sciences. Address correspondence to B. Vereijken, Department of Psychology, NTNU, N-7055 Dragvoll, Norway.

REFERENCES

Adolph, K. E. A., Vereijken, B., & Denny, M. A. (1997). Roles of Variability and Experience in Development of Crawling. Paper submitted for publication.

Bernstein, N. (1967). *The coordination and regulation of movement.* London: Pergamon Press.

Fentress, J. C. (1976). Dynamic boundaries of patterned behavior: Interaction and self-organization. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing point in ethology* (pp. 135–169). Cambridge: Cambridge University Press.

Fentress, J. C. (1981). Order in ontogeny: Relational dynamics. In K. Immelmann, G. W. Barlow, L. Petrinovitch, & M. Main (Eds.), *Behavioral development: The Bielefeld interdisciplinary project* (pp. 338–371). Cambridge: Cambridge University Press.

Gesell, A. (1945). *The embryology of behavior.* New York: Harper.

Gottlieb, G. (1991a). Epigenetic systems view of human development. *Developmental Psychology, 27,* 33–34.

Gottlieb, G. (1991b). Experiential canalization of behavioral development: Results. *Developmental Psychology, 27,* 35–39.

Kelso, J. A. S. (1990). Phase transitions: Foundations of behavior. In H. Haken & M. Stadler (Eds.), *Synergetics of cognition* (pp. 249–268). Berlin: Springer.

Kelso, J. A. S., Holt, K. G., Kugler, P. N., & Turvey, M. T. (1980). On the concept of coordinative structures as dissipative structures: II. Empirical lines of convergence. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior* (pp. 49–70). Amsterdam: North-Holland.

Kelso, J. A. S., & Schöner, G. (1988). Self-organization of coordinative movement patterns. *Human Movement Science, 7,* 27–46.

Kugler, P. N., Kelso, J. A. S., & Turvey, M. T. (1980). On the concept of coordinative structures as dissipative structures. I. Theoretical lines of convergence. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior* (pp. 3–47). Amsterdam: North-Holland.

Muchisky, M., Gershkoff-Stowe, L., Cole, E., & Thelen, E. (1996). The epigenetic landscape revisited: A dynamic interpretation. *Advances in Infancy Research, 10,* 121–159.

Pearson, K. G., Ramirez, J. M., & Jiang, W. (1992). Entrainment of the locomotor rhythm by group Ib afferents from ankle extensor muscles in spinal cats. *Experimental Brain Research, 90,* 557–566.

Schneider, K., Zernicke, R. F., Ulrich, B. D., Jensen, J. L., & Thelen, E. (1990). Understanding movement control in infants through the analysis of limb intersegmental dynamics. *Journal of Motor Behavior, 22,* 493–520.

Schoner, G. S., & Kelso, J. A. S. (1988). A synergetic theory of environmentally specified and learned patterns of movement coordination. I. Relative phase dynamics. *Biological Cybernetics, 58,* 71–80.

Schöner, G. S., Zanone, P., & Kelso, J. A. S. (1992). Learning as change of coordination dynamics: Theory and experiment. *Journal of Motor Behavior, 24,* 29–48.

Stehouwer, D. J., & Farel, P. B. (1984). Development of hindlimb locomotor behavior in the frog. *Developmental Psychobiology, 17,* 217–232.

Super, C. E. (1976). Environmental effects on motor development: The case of African infant precocity. *Developmental Medicine and Child Neurology, 18,* 561–567.

Thelen, E. (1986). Treadmill-elicited stepping in 7-month-old infants. *Child Development, 57,* 1498–1506.

Thelen, E., & Fisher, D. M. (1983). The organization of spontaneous leg movements in newborn infants. *Journal of Motor Behavior, 15,* 353–377.

Thelen, E., Kelso, J. A. S., & Fogel, A. (1987). Self-organizing systems and infant motor development. *Developmental Review, 7,* 39–65.

Thelen, E., & Ulrich, B. D. (1991). Hidden skills: A dynamic systems analysis of treadmill stepping during the first year. *Monographs of the Society for Research in Child Development,* Serial No. 223, 56(1).

Thelen, E., Ulrich, B. D., & Niles, D. (1987). Bilateral coordination in human infants: Stepping on a split-belt treadmill. *Journal of Experimental Psychology: Human Perception and Performance, 13,* 405–410.

von Holst, F. (1939/1973). *The behavioral physiology of animals and man.* Coral Gables, FL: University of Miami Press.

Zanone, P. G., & Kelso, J. A. S. (1992). The evolution of behavioral attractors with learning: Nonequilibrium phase transitions. *Journal of Experimental Psychology: Human Perception and Performance, 18,* 403–421.

Zelazo, P. R. (1983). The development of walking: New findings and old assumptions. *Journal of Motor Behavior, 15,* 99–137.

Zelazo, N. A., Zelazo, P. R., Cohen, K. M., & Zelazo, P. D. (1993). Specificity of practice effects on elementary neuromotor patterns. *Developmental Psychology, 4,* 686–691.

Zelazo, P. R., Zelazo, N. A., & Kolb, S. (1972). ‘‘Walking’’ in the newborn. *Science, 177,* 1058–1059.