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A dynamical systems interpretation of epigenetic landscapes for infant motor development

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Abstract

This paper presents a unified dynamical systems theory of motor learning and development and addresses the normative order and timing of activities in the infant motor development sequence. The emphasis is on the role of intention in modulating the epigenetic landscapes to the emerging forms of infant motor development and how the evolution of attractor landscape dynamics in infancy arises from the multiple time scales of constraints to action. The development of prone progression in infancy is exemplified as a case study and experimental hypotheses of the theory of attractor landscape dynamics and infant motor development are provided.

Keywords: Infant motor development; Epigenetic landscape; Intention; Dynamics; Prone progression

The emergence of the fundamental movement patterns during infancy has long been recognized as one of the most central problems of human development (Weiss, 1941). Indeed, the study of the infant motor development sequence, in terms of the onset and progression of new posture and movement forms, has a rich and distinguished history (e.g., Gesell, 1929; McGraw, 1943; Shirley, 1931), and moreover, the last 20 years have witnessed a revitalization of interest in infant motor development. This zeitgeist has in large part been due to the introduction of the self-organization metaphor to motor development (Kugler, Kelso, & Turvey, 1982) and its theoretical and empirical instantiation through the concepts and tools of dynamical systems theory (Smith & Thelen, 1993; Thelen & Smith, 1994; Thelen, Kelso, & Fogel, 1987) and

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those of the related ecological approach to perception and action (Goldfield, 1995; Kugler, 1986; Kugler & Turvey, 1987; Newell, 1986). Today, these theoretical influences have been integrated to a considerable extent and the dynamical systems label is emphasized in both theoretical and empirical investigations of motor development.

A dynamical systems approach to motor learning and control has been appealing to students of motor development for several reasons (Kugler, 1986; Thelen, 1989). Fundamentally, it has been seen to provide a framework of principles that can describe and predict the changes observed in the development of the movement sequence in infancy. The framework can approach head on the challenging problem of the evolution and dissolution of the new movement forms of posture, locomotion and manipulation that are observed in the period of infancy. It also makes links to the concepts of stability and instability that have long been used to describe the pathway of change in the development of new movement forms (Gesell, 1929). Finally, the dynamical systems approach to motor development has been appealing because it offers a set of principles for the learning and performance of motor skills over the lifespan; the theoretical ideas are not confined to a particular age group or subset of motor skills as has been so often the case with theories in both motor learning and motor development (cf. Newell & van Emmerik, 1990). Nevertheless, many aspects of this comprehensive agenda remain to be examined experimentally leaving the dynamical systems approach to motor learning and development, to be interpreted by some as more metaphor, than an emerging theoretical and experimental framework (Van der Maas, 1996).

Adaptations of Waddington's (1957) metaphor of an epigenetic landscape for development have provided a heuristic schematic of the pathway of change in the development of the fundamental movement patterns (Connolly, 1986; Kugler, 1986; Muchisky, Gershkoff-Stowe, Cole, & Thelen, 1996). These landscapes of development can have a direct link to the attractor dynamics of movement forms as captured in a visualization of a state space analysis (Abraham & Shaw, 1984), although they have also been used to exemplify other biological phenomena and theoretical viewpoints to development (e.g., Meinhardt, 1982). Developmental landscapes have provided an image from a dynamical systems standpoint of the probabilistic pathway of the change in movement forms during ontogeny, and estimates of the relative stability and instability of the developing action capabilities of the infant.

To date, however; most of the technical development of a dynamical systems approach to motor control has come from the experimental tests and theoretical elaborations of the Haken, Kelso, and Bunz (1985) (HKB) model of inter-limb coordination (see also Kelso, 1995). This model captures many of the dynamical properties of inter-limb coordination but its' particulars have been largely confined to the attractor dynamics of a single action class with two biomechanical degrees of freedom. The problem of infant motor development is clearly one of harnessing the many degrees of freedom at multiple levels of analysis (Bernstein, 1967; Saltzman, 1979). When considered in a dynamical systems framework this gives added emphasis to the two essential components of a dynamical system: The role of the rule or function predicting where the system will be in a future instant of time, as well as the traditional focus on the state of the system at any moment of time.

This paper outlines a dynamical systems perspective to the observed order and timing in the emergence of physical activities in the infant motor development sequence. It builds on extant approaches of a dynamical systems framework to motor learning (Kugler & Turvey, 1987; Mitra, Amazeen, & Turvey, 1998; Newell, Liu, & Mayer-Kress, 2001; Newell, Kugler, van Emmerik, & McDonald, 1989; Schöner, 1989; Schöner & Kelso, 1988a, 1988b) and development (Kugler, 1986; Thelen et al., 1987), by addressing the role of intention in modulating the epigenetic landscapes of the attractor dynamics to the emerging forms of infant motor development. The role of multiple time scales of change to the emergence of the infant movement sequence is addressed, and in particular, the relatively shorter time scales of action goals and intentions on the dynamical landscape. The paper can be seen as a complement to our general paper on time scales in motor learning and development (Newell et al., 2001), but one that emphases the qualitative change in movement forms through the lifespan. The ideas developed are exemplified through a landscape analysis of infant prone progression and the outlining of general experimental hypotheses about landscape attractor dynamics and infant motor development.

1. The infant motor development sequence

Classic descriptive studies of motor development have shown that there is a relatively invariant intra- and inter-task sequence to the onset of the fundamental activities of posture, locomotion and prehension during infancy (e.g., Gesell, 1929; McGraw, 1943; Shirley, 1931). And, although the data from these studies are some 60 or more years old, there is still general agreement to the normative order in the development of the fundamental movement activities during infancy. Fig. 1 reproduces the schematic from Shirley (1931) showing the progression

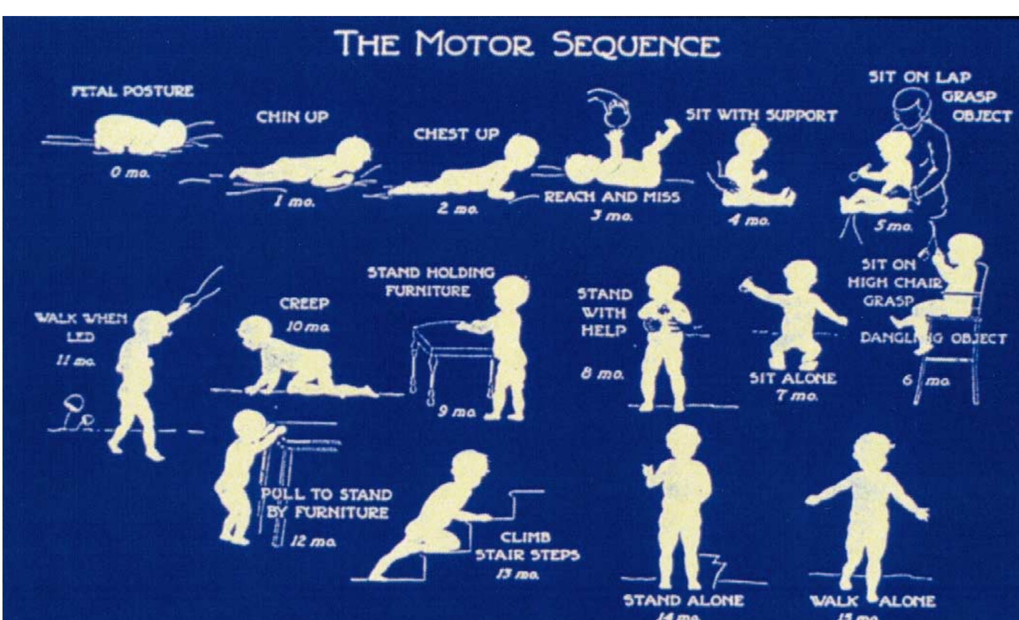

Fig. 1. The infant motor development sequence from Shirley (1931).

to the onset of the fundamental posture and movement activities as a function of infant age. Several studies of motor development have reported a mean and standard deviation of the normative chronological age of the onset of the activities in the sequence (see Gabbard, 2000; Haywood, 1993; Keogh & Sugden, 1985).

Given the established literature on the infant motor development sequence a comprehensive discussion of the movement and action phenomena in question is not required here. However; there are several key characteristics of the infant motor development sequence that any theoretical approach to infant motor development needs to accommodate. These are now briefly outlined to provide explicit recognition of the core phenomena of the invariant and variant characteristics of the infant motor development sequence.

1. There is a relatively invariant sequence to the progressive onset of the physical activities of posture, locomotion and prehension during infancy. That is, there tends to be a normative age-related order to the emergence of the fundamental movement activities in infancy.
2. There is variation in the timing of the onset of a given action within the motor sequence as a function of age. Within an individual, there is not necessarily a relation between the timing of the onset of one activity in the sequence with the timing of the onset of another activity in the sequence. This equivalence in the relative timing of activity onset in regard to normative standards extends also to the individual torso and limb movement components within the sequence of activities.
3. Not all infants universally follow the prescribed normative order in the development of the infant movement sequence. A particular activity may be either omitted from the progressive sequence of development or juxtaposed in the normative order.
4. There is a dependence on the development of a given activity in the sequence with the presence of a previously established activity in the sequence, but the co-dependence of the development of the activities in the infant movement sequence is not well understood.
5. The observed presence of a given activity in infancy can depend on the environmental support for action, leading to challenges in determining whether a given activity pattern has dissolved with development.
6. There appear to have been no systematic attempts to determine the degree to which infants can produce new patterns of coordination beyond those typically reported in the classic descriptions of the infant motor development sequence. New patterns of coordination refers here either to a qualitative movement form that has not been observed previously in the respective developmental group or more broadly in the lifespan of the human species, no matter the developmental age or stage.

The notion of a developmental movement sequence has been extended to the milestones of fetal movement progression (De Vries, Vissei, & Prechtel, 1983). Furthermore, the absence of more recent long-term systematic studies of the infant motor development sequence leaves it an empirical question as to the effect of cohort group on the traditional observations of the infant movement sequence. Nevertheless, there seems to be wide agreement on the nature of the qualitative properties of the development of the infant fundamental movement sequence (Gabbard, 2000; Haywood, 1993; Keogh & Sugden, 1985), although it is very difficult for observers to accurately record the onset and offset of new activities in the movement sequence without continuous 24-hr observation under a range of environmental conditions. Finally, it is important to note that the idea of a relatively invariant sequence in the development of behavioral change is also well accepted in the ontogeny of a wide variety of species.

Although the idea of a relatively invariant sequence to the progressive onset of physical activities in infancy is well ingrained in the motor development literature it is worth the reminder that many of these descriptive data sets were collected more than 60 years ago and the experimental work was driven in many instances by prescriptive theorizing of genetically motivated maturational perspectives. In contrast, the more contemporary self-organization metaphor for motor development introduced by Kugler et al. (1982) emphasized the coordination modes as emergent rather than prescribed properties. This viewpoint opens the door to a more flexible expectation of the emergence of the fundamental movement patterns as an adaptive function of the confluence of constraints to action (Newell, 1986). Thus, the degree of observed invariance in the emergence of the fundamental patterns may well be influenced by the extant constraints on infants in that cohort period, together with those on the experimenters given their theoretical expectation at that point in history.

2. Waddington's epigenetic landscape and infant motor development

Infant motor development has often been considered in the context of Waddington's (1957) metaphor of an epigenetic landscape (Connolly, 1986; Kugler, 1986; Muchisky et al., 1996). Waddington was interested in embryogenesis and the landscape model was a metaphor for considering the dynamics of developmental growth and change. The landscape model of Waddington, however, also captures to a large degree (and unwittingly it appears), principles outlined by Gesell (1929) within a biological maturational approach to motor development.

Gesell (1929) viewed growth and development as a unitary process mediated by innate processes that are laid down by genes. This position recognized the dynamic 'field like' processes that constrain physiochemical systems such as human species, where 'field like' refers to those neuromuscular and biochemical processes that operate within the body's soft tissue as a result of concentration differences, gradient, asymmetries and so on. Thus, Gesell's principles of motor development were based to some degree on what we would know today as dynamical or 'dynamical-like' system properties.

Fig. 2A shows a reproduction of Waddington's (1957) original epigenetic landscape metaphor for development processes. The landscape illustrates the pathways of developmental change, and when considered in the context of motor development, the emergence of the fundamental motor activities of infancy. Connolly (1986) has provided a full analysis of the theoretical implications of this landscape metaphor for infant motor development and so only the essential properties need to be outlined here. The three-dimensional image captures certain basic dynamic processes of human development and behavioral change; but it is important to note that the change evident in the three-dimensional landscape clearly emanates from the operations of a high-dimensional system.

The motion of the ball on the landscape reflects the developing phenotype. The fore to aft dimension is time or developmental age, the horizontal axis instantiates the emergence and dissolution of particular activities that hold dynamic equilibrium, and the slopes of the landscape surface capture the rates of developmental change. The stability of the system at

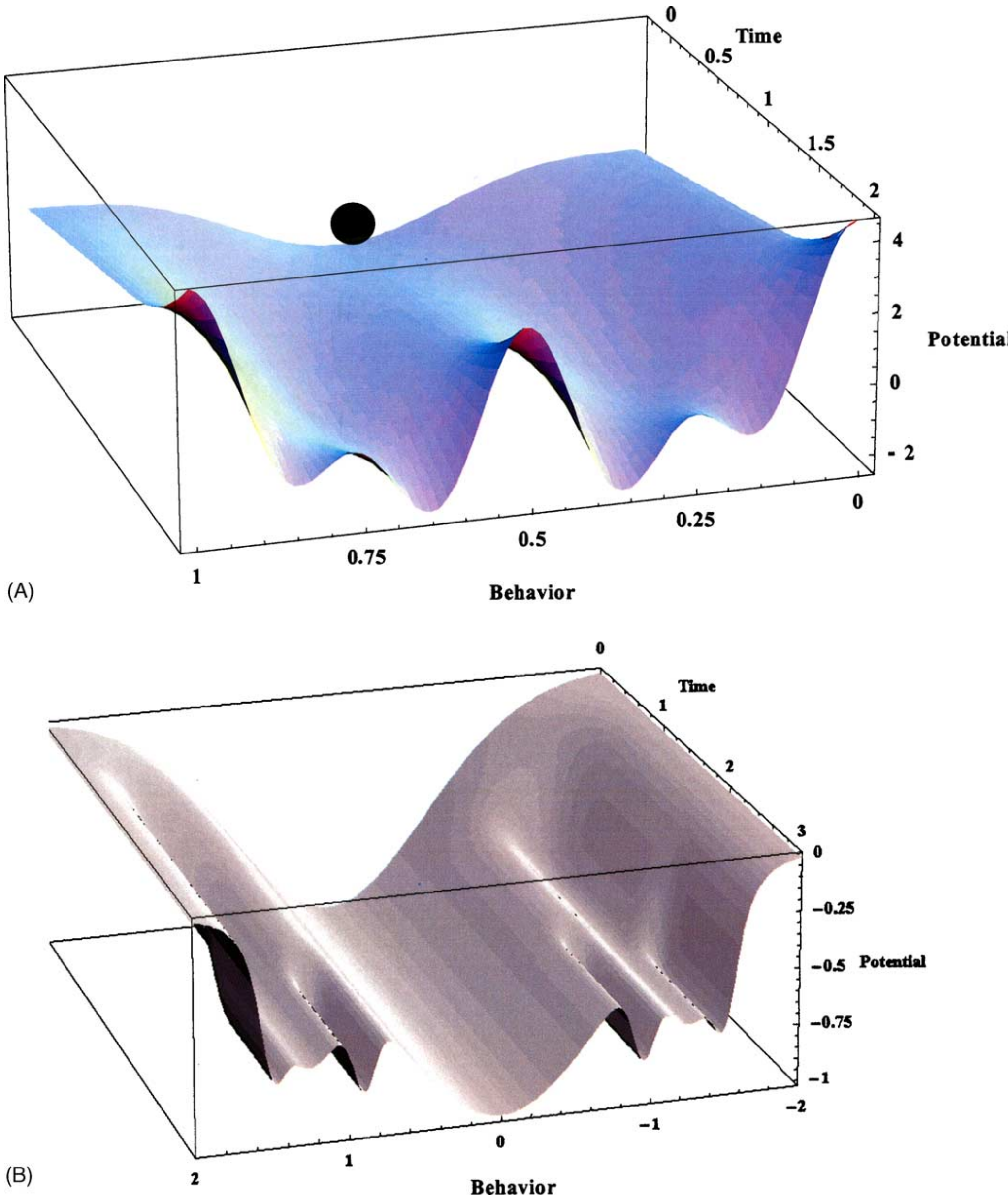

Fig. 2. (A) A schematic of the developmental landscape model of Waddington (1957) and (B) a revised formulation based on the same dimensions.

any given moment of developmental time is inferred from the depth of the landscape wells. In Waddington's (1957) theoretical approach to development, the properties of the landscape formation emerged through genetic control but the landscape metaphor for motor development can be extrapolated to include the full complement of environmental and organismal influences (Connolly, 1986).

This landscape metaphor provides a number of insights into the dynamic processes of infant motor development that were under emphasized to varying degrees in the traditional maturation-learning debates about the motor development. Two points only are highlighted here. First, the emergence of stable states at the behavioral level, such as the physical activities of posture, locomotion and manipulation, involves potentially an element of chance in regard to the precise pathway traversed on the landscape over the passage of developmental time. Here by chance (often also called "noise", or "(stochastic) fluctuations") we mean all the influences that are not captured by the deterministic part of the dynamical model. Typically chance plays the most important role during a bifurcation, when new stable attractors emerge and the previous attractor becomes unstable. In the picture of the ball in the landscape this would correspond to a valley slowly turning into a peak. Without noise the ball would remain balanced at the peak but the tiniest chance fluctuations will make the ball roll down on one of the possible sides of the peak to a new stable resting point at the bottom of a new valley.

To push the analogy a little further we want to consider different factors that can determine the relative strength of the chance influences: For macroscopic objects (ball as ball bearing or marble, say) we can control laboratory conditions to minimize the noise influence of wind currents, ground vibrations, etc. As the ball becomes smaller, more noise fluctuations can become relevant. Particles that are barely visible to the naked eye can be observed to display random Brownian motion and at atomic and molecular levels, quantum fluctuations can become the dominant force of the dynamics as chance events that have to be expected. The presence of fluctuations has relevance to the observation that the exhibition of all the activities of the developmental sequence is not a necessary condition of infant motor development.

Second, the model shown in Fig. 2A reveals that the same developmental state can be realized over different pathways of change in the developmental landscape. This principle of equifinality has relevance to the observation that infants can have different orders to the development of the activities within the motor sequence. Reversals (e.g., Touwen, 1971) and omissions (e.g., Robson, 1970) can occur in the progression of the onsets of the unique coordination modes in the fundamental developmental movement sequence.

In summary, elaborations of the developmental metaphor of Waddington (1957), hold that there is a common dynamical ground to the processes of infant motor development, that can also lead to individual expressions in the timing with which physical activities emerge in infancy. And, as indicated earlier, many of Gesell's (1929, 1946) principles of development, particularly as they were applied to motor development, fit well within the Waddington framework. In short, Gesell and Waddington were essentially promoting informally some elements of a dynamical view of motor development, long before it became fashionable. Their ideas have been given fresh emphasis with the introduction of the dynamical systems approach to motor development (Kugler, 1986; Kugler et al., 1982; Thelen et al., 1987), and importantly, they are set within a biological framework rather than a purely context free systems approach.

3. Limitations of the landscape metaphor

The Waddington model was a metaphor of and for theorizing about the processes of growth and development in biological systems. And, as we progress to building a more formal dynamical systems account of infant motor development, based upon the concepts and tools of nonlinear dynamics, it is useful to note some limitations of interpreting the model too literally, or indeed, reading into it ideas that were never intended. The oft-published landscape of Waddington (1957) holds several limitations (at least in interpretation) that can be and have been passed over in discussions of its application to motor development.

First, the landscape image of Fig. 2A, shows that the most stable state at the beginning of phenotypical development is dissolved with the passage of time. Elaborating to infant motor development, this implies that arguably the most stable infant postural state, namely that of lying down, dissolves as a stable physical activity. This clearly is not the case. Lying down on a surface is a very stable state at all ages of human development, even if the sequential pattern and probability of engaging in that activity in everyday life changes over the lifespan. This is not to say that certain stable coordination modes do not or cannot dissolve, but rather that the probability of this happening depends on many factors, including that of the activity in question. In summary, the fundamental postural state of lying down remains a stable activity through the lifespan.

Second, the horizontal dimension captures qualitative stable states and these at the behavioral level of motor development are reflected in the fundamental coordination modes of posture, locomotion and prehension. Muchisky et al. (1996) have linked these to the order parameters in a dynamical systems perspective that define the unique physical activities (Haken et al., 1985). In this regard, it is useful to emphasize, however, after Connolly (1986), that the horizontal or activity dimension is multidimensional. This emphasis is not simply a reflection of the problem of representing many dimensions on a surface (piece of paper)—which it is in part. But, more importantly, that without considering the stable states of activity in a multidimensional framework, it is difficult to assess the relations *between* the stable states, because the order in which the states or activities are represented on the horizontal dimension is at best confined to intuition in the metaphorical model. The issue of dimensional representation of states has important implications for understanding the dynamical relations *between* activity modes and *how* these relations change over developmental time.

Third, the depth and slope of the landscape wells reflect respectively, the stability and rates of change in the state characteristics of an activity over time. However, the depth of a well in the developmental landscape does not alone determine the percentage or duration of times that a physical activity will be exhibited in infancy over a given period of time, as suggested by Zanone, Kelso, and Jeka (1993). The frequency of an instance of an activity is, however, relevant from a dynamical standpoint when considered in the context of the shorter time scale demands of infant goals and intentions.

Fourth, the model illustrates that the fundamental dynamical properties of the landscape change over developmental time. However, it does not show or even recognize that the dynamical landscape supporting physical activities can also change due to the shorter time scale influence of goals and intentions. Thus, while the Waddington model is not static in the context of motor development (cf. Connolly, 1986), it is typically not emphasized that the standard landscape metaphor does not capture sufficiently or even imply the wide range of time scale influences on behavioral change. In particular, it does not capture or reflect the relatively short time scale demands of the task, the local organism–environment interactions, and learning (Newell et al., 2001).

Fifth, the metaphor landscape of Waddington (Fig. 2A) shows the collection of states that are *possible* at a particular age, but it does not capture the relative dynamic properties of these states at any moment in time. It is a prototypical landscape showing the potential scope of stable states at a point in time of development rather than the nature of the landscape as it *evolves* in real time in the implementation of a given activity and the sequence of those activities that unfolds through the time course of the lifespan.

In Fig. 2B is shown a revised version of the Waddington metaphor that is still limited to the same three dimensions (activity, time, potential/stability) of Fig. 2A. However; the schematic of Fig. 2B preserves, in a motor development context, the fundamental stability of lying down over developmental time but still shows the evolution of new attractive stable states at points in time. As mentioned earlier; the stability of the activity dimension needs to be considered in a higher dimensional framework than that of a single dimension, if we are to understand the dynamical relations between activities and the changing landscape of development over time. In a later section we exemplify this point through an analysis of the emergence of the activities of lying down, sitting, creeping, crawling, standing and walking, all activities that make up the development of prone progression in infancy.

4. Dynamical systems approach motor learning and development

The Waddington (1957) landscape shown in Fig. 2A is a metaphor for development and its message through image captures some of the basic properties of a dynamical systems approach to development. This is the case with respect to concepts such as stability and instability, pathway of change in the landscape, and that the landscape changes over time. Furthermore, Waddington's (1957) landscape holds some similarities to the use of landscape potential well images in dynamical systems approaches to the representation of attractor and repeller states to the dynamics of state space representations (Abraham & Shaw, 1984).

The instantiation of landscape dynamics is, however; not exactly the same in the Waddington and dynamical systems approaches to system development over time. An important issue is the nature of the dimensions that form the axes of the landscape, particularly the dimension(s) that capture the state of the system. This was never established clearly in Waddington's approach given its metaphorical status and this limitation was magnified given its elaboration from a model of embryogenesis to that of motor development. A dynamical systems approach requires the system to be described in a state space—a geometric space that captures the state of the system on certain dimensions at a given moment in time. Given the many physical degrees of freedom at many levels of analysis of the movement action system (Bernstein, 1967; Saltzman, 1979), the geometric representation of the state of the system is usually compressed into only a few dimensions or even one dimension—dimension(s) that are seen to capture sufficiently the order or state of the system. This leads to the notion of order parameters or collective variables to capture the distinctive pattern or qualitative state of the movement system (Gelfand & Tsetlin, 1962; Haken et al., 1985).

Fig. 3 shows the dynamic landscape of the HKB model (Haken et al., 1985) for the intrinsic dynamics of inter-limb coordination. The three axes to this figure are determined from the

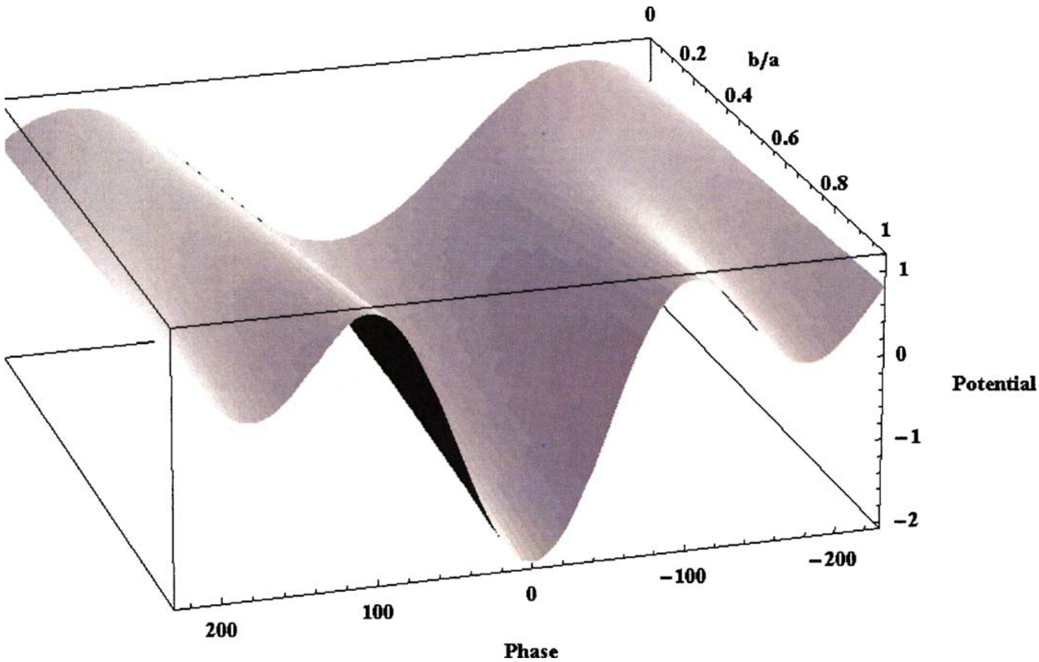

Fig. 3. The landscape dynamics of the basic equation of the HKB model (Haken et al., 1985) with the same parameters as in Kelso (1995, Figure 2.7).

components of the original basic equation:

$$V(\phi) = -a\cos\left(\frac{\pi}{180}\phi\right) - b\cos\left(\frac{\pi}{90}\phi\right) \qquad (1)$$

where V is the potential function, ϕ is the relative phase between the fingers and the ratio of a/b is related to the frequency of finger oscillation. Thus, the landscape emerges from the motion in a potential and the parameter values of the phase relation between the limb motions (order parameter) and the ratio of b/a that is related to the frequency of limb oscillation (control parameter). The landscape of this figure shows many of key features of dynamical systems in a variety of contexts, including the basin of attraction (the region of state space in which all initial condition converge to the attractor), multistability (the existence of more than one stable state for a given set of control parameters conditions), and how changes in the value of a control parameter leads to changes in the landscape and the emergence of bifurcations. The wells of the landscape are often called potential wells in reference to the potential for free energy of a corresponding physical system.

Thus, the informal developmental landscape of Waddington (1957) holds some qualitative similarities to the more formal landscape approach of dynamical systems. The dynamical systems framework provides the theory and techniques to characterize and measure important qualitative and quantitative properties of the evolution of the system over time (Abraham & Shaw, 1984). The wells and peaks in the developmental landscape of Waddington (1957) were deformed through genetic influences, but the dynamical systems approach considers a range of constraints to the development of action as reflected in the evolving landscape.

The constraints to the motor development of infants have a range of time scales from the relatively fast time scales of what are often termed ‘functional’ constraints to the relatively slow time scales of ‘structural’ constraints (Kugler et al., 1982; Newell, 1986; Thelen, 1986). A standard approach to the constraints of development has been to view the three major time scales of influence to the emergence of movement forms to be the very slow time scale of evolution, the more rapid time scale of ontogenetic development, and the much more rapid time scales of biological processes (e.g., Mittenthal & Baskin, 1992; Waddington, 1957). This traditional categorization, however, has tended to ignore or play down the role of task constraints and the relatively short time scale influence of intention to the changes in the landscape dynamics supporting action. However, there are many ways to organize the constraints to action and Eckhardt (2000) has provided a framework outlining the totality of environmental influences and population response over time.

5. Frames of reference for the landscape dynamics of infant motor development

In building a framework for the landscape attractor dynamics of infant motor development it is necessary to consider the mathematical frame of reference from which to build the dynamical relations. It is instructive to consider the approaches of other context domains to this frame of reference issue for attractor landscape dynamics.

Landscapes have been used as metaphors to describe the behavior under the influence of potential surfaces generated by different force fields. In the original sense of a landscape the elevation determines the potential surface generated by a constant gravitational force field. More complicated landscapes have been studied in the context of the curved space of general relativity, where massive bodies create indentations in an otherwise flat space visualized as an elastic membrane. Other potential surfaces are generated by distributions of charges and their electrical force fields. In these cases the forces have a long range and the corresponding landscapes have an only slowly decreasing slope as one moves away from the attractive center. Other force fields such as the ones generated by nuclear forces or those found in chemical or biological systems only have a short effective range. The slopes of their associated landscapes quickly go to zero within a short range.

For the general mathematical type of functions with these latter properties inverted Gaussian bell-shapes turn out to be natural choices for modeling short-range potential wells. They describe localized, attractive centers with variable strength (depth) y and range (width) σ_i. For instance, if the total number of attractive centers is N and if we approximate the behavioral order parameters with a two-dimensional landscape then we can present their coordinates as pairs $\Gamma_i = (x_{0i}, y_{0i})$ and the associated potential wells as

$$V_i(x, y) = -\gamma_i \, \mathrm{e}^{-\left(p_{i,1}\frac{(x-x_{0i})^2}{\sigma_{x,i}^2} + p_{i,2}\frac{(x-x_{0i})(y-y_{0i})}{\sigma_{x,i}\sigma_{y,i}} + p_{i,3}\frac{(y-y_{0i})^2}{\sigma_{y,i}^2}\right)} \tag{2}$$

Note that the width of the potential well can be quite asymmetric in x and y directions as determined by the parameters $\sigma_{x,i}$, $\sigma_{y,i}$. The orientation of the “potential valley” within the (x, y)-landscape is determined by the parameters $\{P_{i,1}, P_{i,2}, P_{i,3}\}$.

The range parameters $\sigma_{x,i}$, $\sigma_{y,i}$ introduce length-scales into the landscape in a way that is similar to the spatial frequencies in systems with periodic boundary conditions such as the well-studied HKB model (Haken et al., 1985). We can have both trigonometric and Gaussian function elements in the same model as long as the range introduced by the latter model is small compared to the shortest wave-length of the former (see, for instance, Newell et al., 2001).

The landscape metaphor also has been used in the context of chemical reactions and biological morphogenesis (Meinhardt, 1982) where the elevation of a point in the landscape determines if a certain gene is turned on (expressed) or not. The importance of catalysts for the deformation of reaction-landscapes was recognized already by Waddington (1957). The power of catalysts lies in the fact that they can rapidly lower potential barriers between potential wells and thereby induce effortless and fast transitions between them without affecting the asymptotic reaction balance. Later we will discuss ways in which behavioral intention can be metaphorically seen as introducing catalytic properties into the domain of transitions between behavioral attractors. In this case, however, the intentional change of landscapes will not only lower transition barriers but also significantly change the asymptotic outcome, i.e., the potential wells that will be stabilized.

More directly relevant to infant behavior; field potentials generated by electrical brain activity can be displayed by continuously changing landscapes. Here the elevation of the landscapes determines which neurons will fire and thereby trigger certain behaviors (Mayer-Kress, Barczys, & Freeman, 1991). Finally, the potential well of a single active neuron at a given point in time can be modeled by an inverted bell curve, indicating short-range interactions (in the average), thereby neglecting occasional long-range short-cuts that can have important consequences (Jung & Mayer-Kress, 1995).

The landscape of the HKB model (Haken et al., 1985) is based upon a trigonometrical mathematical framework due to the oscillatory nature of the finger motion. In this contextual situation the pendular properties of the finger motion insure a natural cyclical return of a finger to the same location. This provides a context in which trigonometrical principles can capture fully the resultant dynamics. However, in a system that moves its frame of reference in time, as is the case in human physical activity, the trigonometric framework to describe attractor dynamics holds limitations because we cannot assume periodicity. Thus, the mathematical frame of reference in our unified framework for the learning and development of motor skills, uses Gaussian bell-shaped functions to characterize the landscape dynamics.

6. Unified framework for the dynamics of infant motor development

In proposing a unified dynamical framework for infant motor development we follow the original intuition of Waddington (1957) for epigenetic landscapes: behavior is represented by the coordinates in the landscape. The influence of a given point in the landscape onto its neighborhood is determined by its elevation ("potential energy"). States in the immediate future of the system are determined by the slope of the landscape at a given point in the sense that the system will move in the direction of the steepest descent. One pitfall in the "ball-rolling-down-the-hill" metaphor of Waddington is that intuitively one would expect that the ball would pick up momentum and roll past the bottom of a valley uphill before it comes to a rest. In the dynamical systems interpretation the ball would not build up kinetic energy or momentum and it would come to a rest exactly where the slope is zero. A peak represents unstable behavior, the lowest point in a valley corresponds to attractive (or stable) fixed points.

Just as the collection of all genes in a biological species holds the potential for an array of phenotypes, the location of attractive centers determines a set of potentially stable modes of behavior. Many factors determine for a given cell which genes will actually be expressed to determine its function. For a motor development landscape, it appears that factors like intention and learning as well as organismic and environmental constraints will determine which, among a set of potential modes of behavior; will actually be expressed. Change in behavior can, therefore, been seen as a continuous switching on of goal attractive centers and simultaneous switching off of centers that are no longer the focus of the intention.

To be more precise, in the landscape metaphor the implicit assumption is that the system (child at a certain developmental stage engaged in movement activity) is represented by a point in the landscape that will move according to a gradient descent law. In other words, the direction and velocity of the movement depends on the local slope (more precisely, gradient) of the landscape. For a quantitative description this gradient is proportional to the accelerating force. Since for a fixed landscape this gradient is per definition independent of time, the dynamical system describing this motion only depends on the location in the landscape and not explicitly on time. These systems are known as autonomous dynamical systems.

In a time-independent landscape alone only the approach to local fixed points can be observed. Any transition, say, from sitting to standing would need extra terms in the dynamical description. A priori two options to this approach seem to be plausible. The first option is that intentional transitions could be accomplished by non-autonomous forces acting within the landscape, thereby "pushing" a point up-hill. This view seems to be especially suitable for uncontrolled random perturbations that are always present and that could be represented by a non-autonomous but stationary, stochastic process. The second option is that intentional dynamics is described by a rapid, non-autonomous change in the potential landscape itself. Through intention some of the attractors could be de-stabilized and turn into repellers while other local attractors suddenly become globally attractive in the sense that no-matter what initial condition the system starts in, it will always eventually approach the global attractor. With this option there is no need for hill climbing on the landscape between attractors and one could study how to minimize the energetics of searching.

Beek, Turvey, and Schimdt (1992) have discussed the potential role of autonomous and nonautonomous terms in a dynamical systems approach to movement in action. The theoretical assumptions of the ecological approach to perception and action (Kugler & Turvey, 1987) have led to the operational strategy of pursuing the possibilities of autonomous systems to their limits, *before* any consideration of invoking nonautonomous terms either theoretically or experimentally. The role of autonomous and nonautonomous terms is still a fundamental issue for dynamical systems accounts of motor learning and development, but is beyond the scope of this paper.

In Fig. 4 we consider the short time interval during which an infant can express one of the behavioral states available in her repertoire at the developmental stage represented by time $t = 1$ in the schematic landscape of Fig. 2B. During this behavioral expression we will observe a transition from an initial state (e.g., the "ground state" of lying down) to a target state (in our ex-

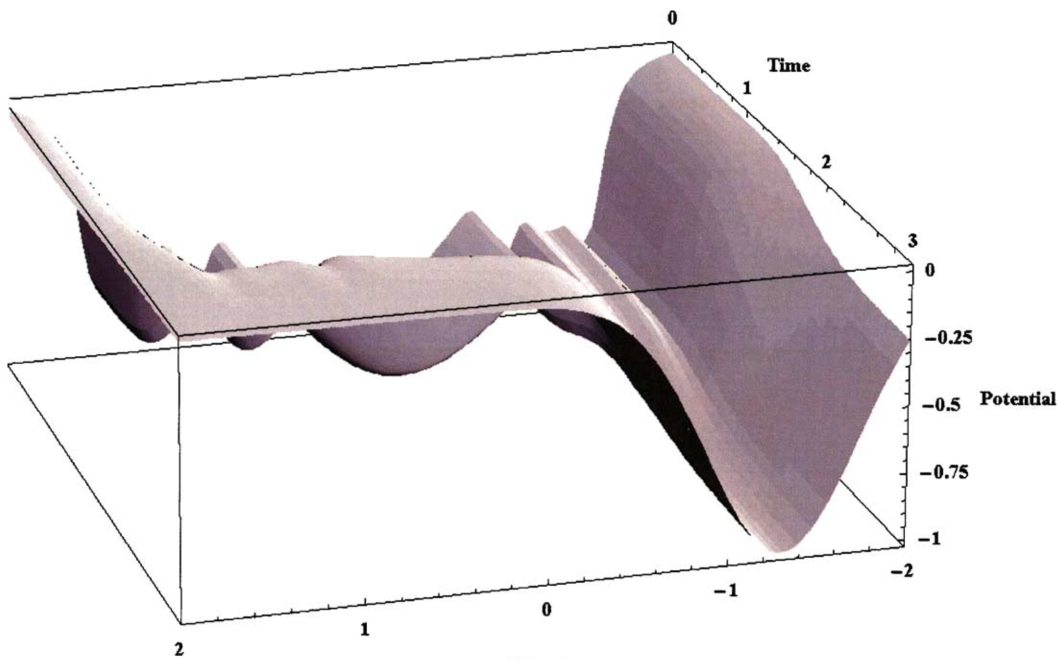

Fig. 4. A schematic of a developmental landscape with the shorter time scale demands of intention modulating the dynamics (see text for details).

ample this would be fixed point no. 1; the right most fixed point in Fig. 2B). Since this transition to a state like walking will typically take not more than a few seconds the time scales have been accelerated from a developmental level (order of month) by a factor of more than one million. Within our theoretical framework of dynamical behavioral expression this can be described with the following generic process: Starting from a (one-dimensional landscape) with seven potential modes of behavior (stable fixed points) we now assume that at time zero (in this shorter frame of reference) the target behavioral state (here fixed point no. 1) is identified through spontaneous or induced intention. Following the method of Schöner and Kelso (1988a, 1988b) we model the effect of this intention as a rapid change in the landscape structure as follows.

Instead of introducing an informational force that has an order of magnitude larger potential variation than the intrinsic forces (Schöner, 1989), we model the intentional transition or behavioral expression by lowering the potential of the target fixed point and simultaneously turning off the attractive potential for all other formerly attractive fixed points. This in done by raising the potential value for all attractive centers except for the target fixed point. Now we can simulate the transition by following the autonomous trajectory and study its properties.

It is interesting to note that this approach appears to be similar to the concept of motor programs (Keele, 1968; Schmidt, 1975), with the important difference that we have an operational procedure to systematically create and link the dynamical properties of different potential attractors especially including intentional transitions (or behavioral expressions) among them. The original metaphor of “motor program” does not introduce a natural geometry for this simulation tool.

It is proposed that the trajectory in a landscape to a stable fixed attractor is a suitable interpretation of the traditional notion of "motor program". To be more explicit: The concept of order parameters introduces coordination variables that significantly reduce the active degrees of freedom or dimension of the relevant state space. The autonomous time evolution of the order parameters is then implemented by (non-linear) dynamical systems which then introduce for each point in the order-parameter space an dynamical force field[1] that will then determine the trajectory of the whole system, including the fast ("slaved") variables that converge to the order parameters. The mathematical tools that are described here are ordinary differential equations. But those differential equations can also be interpreted (together with the process that led to the order parameters) as instructions inside of a symbolic program that are applied to all variables in the original state space all the way down to the vast numbers of individual motor units.

In a way we can see the dynamical systems description as an economical and visually intuitive approach to represent highly complex motor programs that would consist of instructions to all motor units during the entire duration of the movement. One can imagine that in any symbolic programming language the program for even simple coordinated movements could easily exceed the "kloc numbers"[2] of even very advanced programs written by humans. It might be interesting to note that for very complex computer codes one uses graphical (or even auditory) representations of instruction sequences or trajectories in our context.

In summary, whereas the original concept of motor programs makes it difficult to go beyond simple labeling of observations, the landscape structure allows one to introduce powerful mathematical structures in the space of motor programs. Those structures can be topological and geometrical which allows, for instance, the ability to define a "distance" between programs and make predictions about how the motor programs themselves will evolve under changing conditions.

For instance if new minima or maxima emerge or change their shape then from any given starting position we will be able to determine, which attractive center the system will approach along what path. Small changes typically will produce paths and thereby motor programs that are very similar. If a new maximum is created through development or other processes at a point that belonged to a well established path before then this new maximum will lead to a divergence of previously very similar paths. Consequently, we can predict not only that the resulting motor programs will become very different but we can also describe to a high degree of specificity where the programs will become most different. Since we now have a geographic representation of motor programs (instead of abstract symbolic ones) we can intuitively deduce many of their properties and make predictions about future developments. In summary, the unified dynamical approach outlined holds the potential to meld the self-organization and motor programming views to motor learning and control, through dissolving the artificial boundaries to these views that have been created by the emphasis on the distinctive constructs of symbols and dynamics.

7. Landscape dynamics and the development of prone progression in infancy

The infant motor development sequence contains a number of subsets of progression that pertain to particular classes of physical activity. These include progressions within the de-

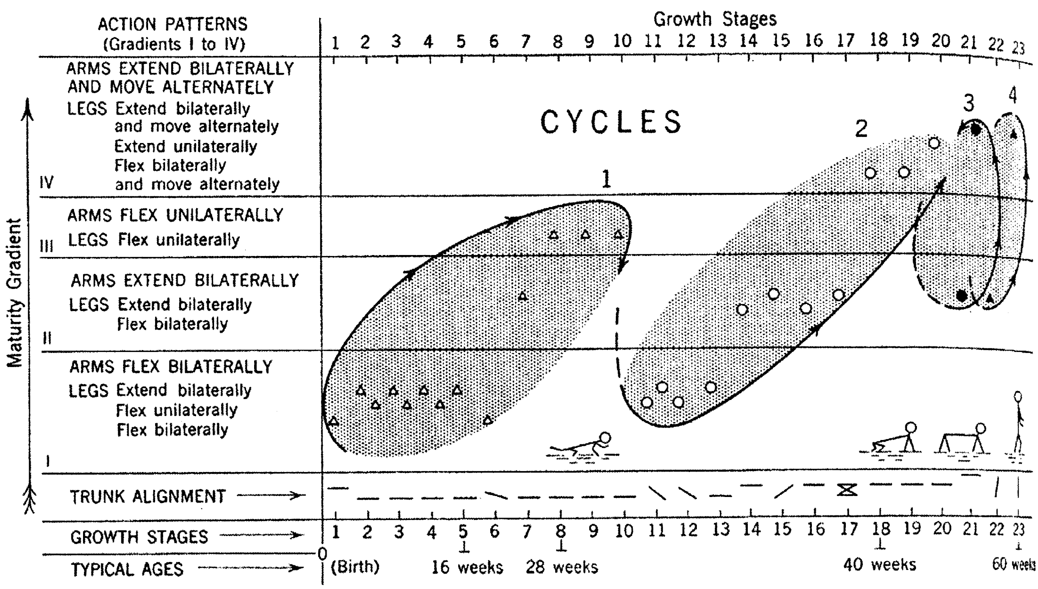

Fig. 5. The pattern of prone progression in infancy in relation to the demonstration of the component action patterns of the arms and legs (reproduced from Gesell, 1946).

velopment of posture, locomotion and prehensile functions. To make analysis and investigation of the infant motor development sequence from a dynamical systems standpoint more tractable it is useful to consider only a subsegment of the fundamental movement sequence. Invoking this strategy does not imply that there are not dynamical relations between activity subsegment classes, or that the principles advanced are not general to all action subsegments.

Here we consider one of the major activity categories in the developmental movement sequence; namely, that of prone progression. Gesell (1946) emphasized prone progression in his analysis of the infant motor development sequence. Fig. 5 shows the growth cycles observed by Gesell in the patterning of prone progression in the development of postural states in infancy. It illustrates the initial posture of lying down, and the subsequent emergence of chin up, crawling, creeping and standing, all in relation to the development of component action patterns of the arms and legs.

The developmental pattern of the age dependent onset of the fundamental activities of prone progression in infancy is shown to be nonlinear. For a given infant, the rate of the emergence of an activity and the time it takes to complete the development of the movement form is unique to each respective activity. The presence of a limb motion subcomponent in one activity does not guarantee that it will automatically be functional for another activity at the same point in developmental time. As the landscape metaphor of Waddington implies, there is an ebb and flow to the stability of the coordinative states over developmental time.

From Gesell's (1946) descriptive model of the development of prone progression we build a developmental landscape of attractor dynamics based upon principles of nonlinear dynamical systems (see Fig. 6). The landscape is created for the environmental context of a land-based surface of support, such as a floor in a house. The landscape would need to be modified for

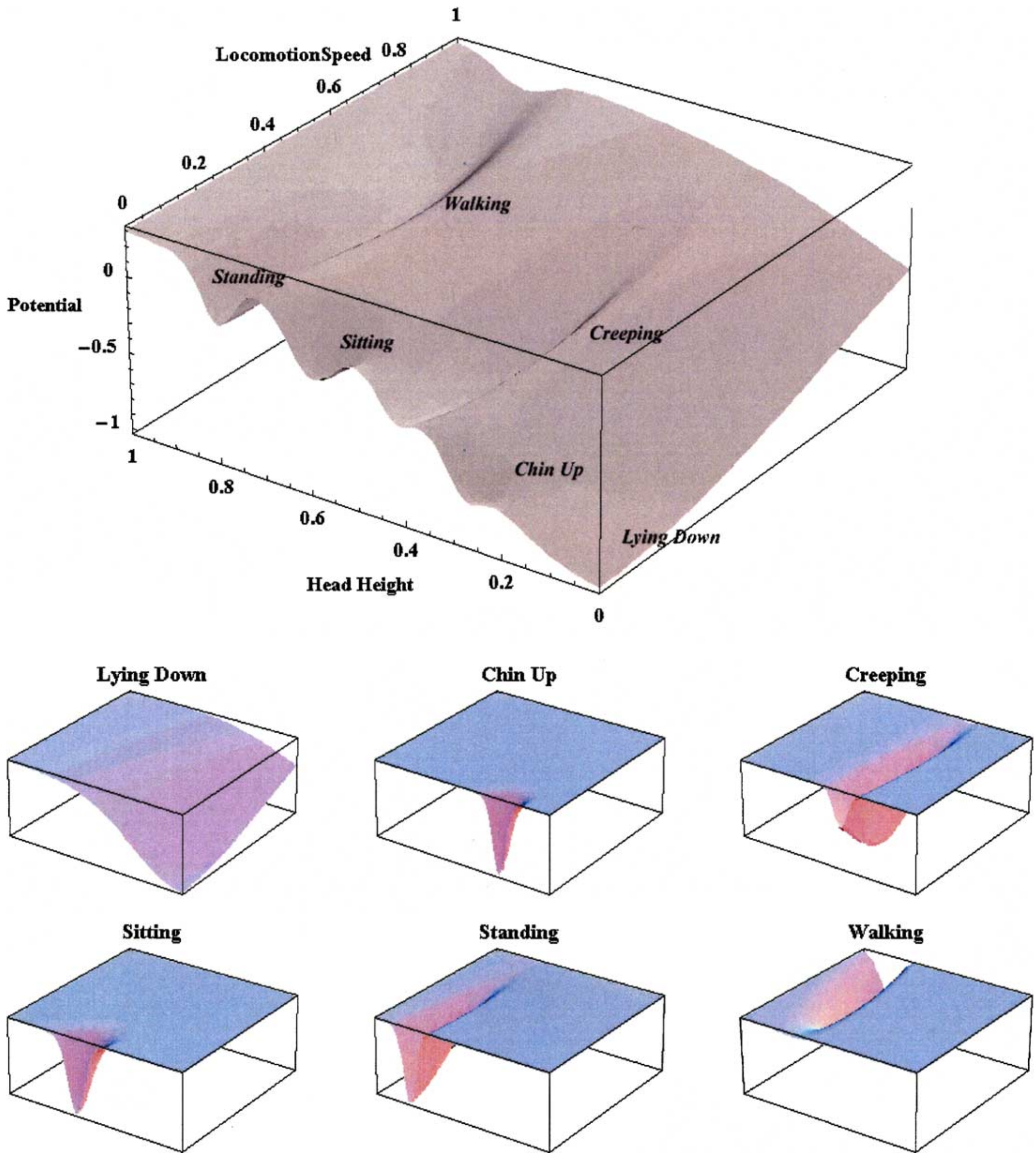

Fig. 6. *Upper segment*: The attractor landscape dynamics of the development of infant prone progression (see text for details of simulation). *Lower segment*: The figure shows the individual contributions of the attractors for each activity corresponding to the different behavioral attractors. If the contributions of these wells are superimposed, the landscape in the upper figure is the result.

other contexts, such as that of a gravity free environment, a water-based pool environment, and even the presence of supports or machines on a land-based surface.

Fig. 6 (upper segment) shows that the potential well dynamics of the attractor landscape are organized from the coordinates of head height from the ground and the speed of locomotion of transporting oneself from one location to another. The dimension of head height correlates

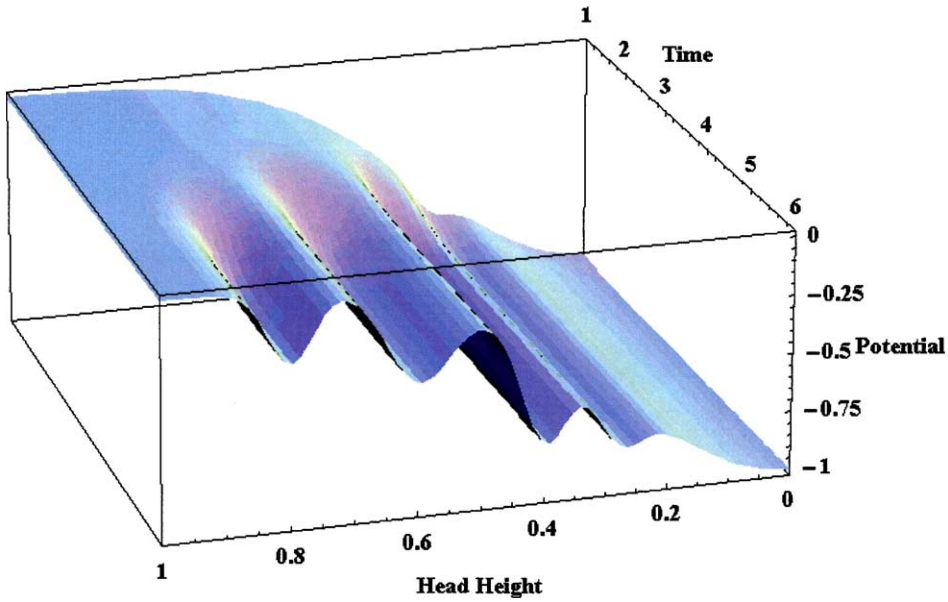

Fig. 7. One-dimensional version of the development of prone progression (omit speed). Onset times are 1, 2, . . . , 6 time-units.

with reaching height from the ground for prehensile activity and also the potential for picking up information from the environment. For the purposes of our model here, we do not attempt to unravel these distinctions in the dimension of the state space, but simply use head height and transport speed, as candidate variables organizing the development of prone progression.

The lower segment of Fig. 6 shows the contributions of the individual landscape wells for each activity to the total picture shown in the upper segment of Fig. 6. In the upper segment of Fig. 6, the value of the potential is calculated as the sum of the influences from all attractive fixed points as expressed by Eq. (2). For each of the six classic activities ("Lying Down", "Chin Up", "Creeping", "Sitting", "Standing", "Walking") we estimated their location in terms of the two order parameters of head height and locomotion speed. "Lying Down" has the lowest potential value in potential energy corresponding to the largest intrinsic stability. We also have chosen the largest values for range of attraction in both x and y directions. The slope in the y direction is larger than in x direction, representing the assumption that "falling down" (approach in y direction) happens faster than "coming to a sliding stop" (approach in x direction). For the other stable behavioral patterns we estimated the qualitative behavior in their neighborhood to illustrate the concept.

Detailed transition experiments between activity modes would be necessary to estimate the quantitative properties of the landscape. For instance in our schematic of Fig. 6 the transition from walking to standing would be less difficult (in terms of potential barrier) than a transition from walking to sitting. One advantage of this two-dimensional landscape compared to the more traditional one-dimensional landscape representation (see Fig. 7) is that we can illustrate multiple pathways between attractors. For instance there should be trajectories from "Walking" to "Lying Down" without having to pass through the "Sitting" or "Creeping" attractor.

One could argue that “head height” and “transport speed” can constitute external control parameters such as the oscillation frequency in the HKB model. Indeed, it is the case that one could come up with terms for the landscape coordinates exclusively expressed in behavioral variables such as combinations of phase differences between joint angles and their velocities to distinguish, say, between sitting and walking, and other activities in the prone progression sequence. These descriptive coordinates would be more complicated and less intuitive than the labels “head height” and “transport speed”, even though this level of analysis of the order parameter notion would be useful.

In the context of this paper we, therefore, treat these two coordinates as economical descriptors for high-dimensional sets of behavioral variables (“order parameters”) and developmental age as the only unspecific control parameter. As a result of this simplification we need to note that there might be many different “micro” states of behavior that lead to the same macro order parameter especially for zero speed. For instance, a head height that corresponds to a stable sitting configuration might also be assumed temporarily during infinitely many different transitions between the “standing” potential well and the “lying” attractive fixed point during the familiar process commonly known as “falling down”.

The resultant dynamical landscape of Fig. 6 reveals several important features about the development of infant prone progression. First, in concert with the earlier commentary on the Waddington landscape, the original stable state of lying down is still stable at the end of the time period marking the onset of walking. This is reflected in the general slope of the landscape being preserved over time and the attractor region of lying down also remaining a stable state. Second, this landscape is similar to that of Waddington (1957) in that it is a prototypical landscape of the potential stables states that exist over developmental time. It does not signify the changing landscape that relates to intention and the execution of action; hence, it does not capture the *real time* dynamics of the evolution and dissolution of activities over time. Third, the shape of the potential well for each activity is consistent with the behavioral properties shown by Gesell in regard to development and preservation of an activity over time. Fourth, the landscape as drawn suggests that over much of the first year of life or so, the task goal of a particular head height and transport speed combination leads to little equivalence about physical activities. In most cases, the infant has few and usually only one stable choice of activity to realize a particular coordinate point in this state space. This is consistent with the postulation that these macro level ‘functional’ constraints on action bring rapid compression of the many degrees of freedom in the conduct of physical activity.

The importance of a multidimensional consideration to landscape dynamics is revealed by a comparison of the landscapes and their meaning in Fig. 6 (upper segment) and Fig. 7. In Fig. 7, we characterize each of the behavioral fixed points of Fig. 6 by their “head height” parameter only, i.e., we ignored their difference in locomotion speed (e.g., “Walking” and “Standing”) now are represented by the same value of “head height”. The “Time” axis corresponds to developmental time. We note that the “Lying Down” attractor is always stable. Other attractors are turned on smoothly as the infant develops. In this representation the transition from, say, “Standing” to “Lying Down” would have to pass through “Sitting”, “Creeping”, and “Chin Up”. Thus, the two-dimensional framework of order parameters (head height and locomotion speed) is more revealing that the single dimension (head height). The additional dimension adds qualitatively to the dynamical description of the behavioral change.

In closing, it should be noted that the model of the landscape dynamics model shown in Fig. 6 for the development of prone progression is just as descriptive as that provided originally by Gesell (1946) using a different set of dimensions. Indeed, our dynamic model is phenomenological and based on the behavioral observations of Gesell. Nevertheless, the postulation of head height and transport speed as variables organizing the development of prone progression has introduced some interesting hypotheses for experimental test that are now considered in more detail.

8. Experimental considerations from landscape dynamics

The foregoing discussion on landscape dynamics and the infant motor development sequence leads to hypotheses and related operational considerations for an experimental program of research in this area. To a large degree most studies of the infant motor development sequence have been descriptive in nature, primarily charting the time course of the onset of particular activities within the sequence (cf. Gabbard, 2000; Haywood, 1993; Keogh & Sugden, 1985). Experimental manipulations within the context of the infant motor development sequence have been very limited, but a dynamical systems approach affords a number of experimental questions and hypotheses (cf. Thelen & Smith, 1994). Here we outline some specific experimental considerations in the context of our framework for landscape dynamics and infant motor development. The operational ideas build on the experimental program of Kelso and colleagues that has previously been focused to a large degree on the two degree of freedom inter-limb coordination task (Kelso, 1995).

8.1. Order parameters

The role of order parameters or essential variables was highlighted in the Haken et al. (1985) model of inter-limb coordination. Yet, strangely, there has been little attempt to discern the nature of order parameters of actions more broadly in motor learning and control, including infant motor development. The determination of order parameters for the fundamental physical activities of the infant motor development sequence would have broad ramifications for understanding motor control. Indeed, a systematic examination of the order parameters for the activities that make up the infant motor development sequence would be very instructive to both understanding the development of coordination in infancy, and to help provide a firmer theoretical basis for other experimental studies of motor control. It is generally viewed that the coordination of the multiple biomechanical degrees of freedom requires compression of these degrees of freedom to a lower dimensional control space or manifold (e.g., Gelfand & Tsetlin, 1962; Kay, 1988).

Here we projected the role of head height and transport speed as possible coordinates of the order parameters for the development of infant prone progression. As noted, these parameters are not defined in the same terms as that of relative phase in the HKB model, but we are suggesting that these functional demands on the state space provide a way to characterize the order in the resulting behavior. A description of the order parameters of each activity in terms of movement properties is a related but distinct experimental enterprise.

8.2. Control parameters

The variables that move the position of the system through state space are called control parameters in a dynamical systems framework. A wide range of variables could in principle act as control parameters in the reorganization of the system state space in motor development. Indeed, in principle, all of the features of the organism and environment that each has its own time scale could act as a control parameter that influences the emergence of the motor development sequence (Newell, 1986; Thelen, 1986). Parents and researchers of motor development have long searched for variables that will facilitate the onset of activities within the infant motor development sequence.

It should also be pointed out, however, that the distinction between the concepts of order parameters and unspecific control parameters is sometimes not so clear-cut, as maybe implied in the HKB model. For instance, in the classic example of the HKB model the unspecific control parameter "a/b" describes the amplitude ratios of functions that quite specifically influence certain modes in order-parameter space. In the HKB model the first parameter "a" corresponds to the strength of a fixed point at 0° phase difference. The second parameter "b" measures the strength or influence of an attractive fixed point at a phase difference of 180°. The "unspecific" control parameter a/b, therefore, depends implicitly on structures that are determined by qualities in order parameter space.

Finally, it is intriguing to question to what degree if any the emergence of the sequential properties of the fundamental infant movement patterns would be influenced by the introduction of more appropriate control parameters. By appropriate we mean here age and action parameters that increase the probability of inducing task relevant change in the organization of state space. An experimental examination of this issue is going to be very difficult with infants but without this theoretical goal, the pursuit of such creative manipulations is less likely to occur. The experimental evidence supports the proposition that the timing of the evolution (Zelazo, Zelazo, & Kolb, 1972) or dissolution (Thelen, Fisher, & Ridley-Johnson, 1984) of the activities can be influenced but not the emergence of a heretofore never observed qualitative movement form.

8.3. Switching between activity modes

A particular need is to understand the relations between the attractor dynamics of the physical activities in the infant movement sequence. Without such an understanding one cannot go beyond intuiting the relative positions (global dynamics) of the stable activity modes in the attractor landscape. In addition, such a research enterprise would reveal properties of the stability of the local dynamics of each attractor dynamic. Kelso and colleagues have used intentional switching between activities as a vehicle to understand the relative stability of the respective attractors supporting each activity (see Kelso, 1995).

It will be operationally difficult to instantiate a switching protocol with infants, particularly with younger infants, but this perspective should not prevent consideration of such an important experimental effort being conducted. A central feature will be finding the most relevant control parameters and goal states to guide the relevant behavioral change. The consequence would be through that an experimental protocol that induces infants to switch between activities in the prone progression sequence at different points in the lifespan would help reveal the dynamical relations between activities, their relative stability and how these relations change over time.

9. Concluding comments

In this paper we have reexamined the metaphor of landscape dynamics as a model for motor learning and development, and moved it to a more formal instantiation in terms of dynamical systems. The experimental focus was the infant motor development sequence and in particular the development of prone progression, but the theoretical ideas are part of a general dynamical systems framework for considering the role of time scales in the change of motor behavior (Newell et al., 2001). It was proposed that: (1) the traditional landscape metaphor has focused on the developmental time scale without sufficient consideration of the multiple times scales to action; and (2) that the selection of the most relevant time scales for action leads to a more useful interpretation of the landscape.

It is considered that the principles for time scales and landscape dynamics outlined here are not confined to infant motor development, but rather are general to the learning of all activities and behavioral expression across the lifespan. Thus, the acquisition of new coordination modes in adult physical activity can be experimentally investigated from the framework outlined. The development of higher dimensional landscapes to capture the dynamics of coordination and control may be useful to reconsider the central issues of learning, retention and transfer.

Notes

1. Note that we describe here the situation for a continuous-time model. For discrete time models the force (vector) field is replaced by an iterative dynamical map.
2. Kloc = 1000 lines of code, a traditional measure of the length of a computer code.

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