Part I

Development of Perception and Action

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A Dynamical Systems Perspective on Infant Action and its Development

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Introduction

The study of motor development has again become one of the most active areas of infancy research, in part because a dynamical systems perspective has introduced new ways to address longstanding questions about the organization of motor skills and how these skills develop (see, e.g., the introduction by Lockman & Thelen, 1993, and other papers in a special issue of *Child Development* devoted to "Developmental Biodynamics"). The task for any general theory of motor development in infancy is to disentangle the complex causal and functional relationships between the motor repertoire of the newborn and the differentiated motor skills of the 2-year-old infant. Such a theory must address important questions like the following: Do primitive motor patterns (reflexes) prepare for the acquisitions of complex and apparently voluntary motor skills? If yes, how do they? If not, what happens to them after they "disappear"? How do qualitatively new forms and functions of coordinated motor action emerge from antecedent motor patterns with which they share neither form nor function? In other words, what do we mean when we speak about emergence, spontaneous pattern formation, and self-organization?

This chapter presents a dynamical systems perspective on motor development. We focus on the question, what are the sources of order by which new complex forms and functions emerge? This question has been of great interest for developmental scientists in several fields (see, e.g., Gilbert, 2000). The Darwinian view of the emergence of new forms is that selective processes act on a population of variant forms that express themselves in different ways given particular environmental opportunities (Mayr, 1982). Some developmental biologists (Kauffman, 1993, 1995) and neuroscientists (Gottlieb, 1992) have recently challenged the view that Darwinian selection is the sole source of emergent order in learning, ontogeny, and evolution. Kauffman, for example, proposes that self-organization arises in systems with very large numbers of interconnected elements (e.g., the genome, immune system, nervous system). Such systems can achieve organizational states ranging from ordered (highly resistant to change) to chaotic (i.e., subject to an avalanche of changes, or "damage"). Selection acts on this range of organizational possibilities to produce "complexity," a state that is ordered, yet poised near the edge of chaos. We propose that motor development is a process by which the infant's earliest behaviors (e.g., sucking, kicking, babbling) are self-organizing, and that the selective processes of active exploratory behavior transform these self-organizing systems so that they become useful for performing the "complex" adaptive behaviors that we call eating, walking, and speaking.

Self-organization and selection are heuristically powerful processes because they can account for both the small and the dramatic changes observed in motor behavior during infancy. Periods of relative stability in acquisition of a skill such as crawling allow the infant to introduce variations in performance (e.g., trying out a new way to shift weight onto the arms) without dramatic consequences, such as falling. By contrast, during periods of rapid organismic changes that are not under the infant's direct control, such as weight gain, similar modifications in behavior may result in a sudden loss of balance. Despite their best efforts, infants may suddenly find that former ways of successful locomotion are no longer effective. These changing organismic constraints on self-organizing processes open new opportunities for exploring how the body can be used to achieve particular goals.

The Dynamical Systems Perspective

The dynamical systems perspective on motor development stands apart from other developmental approaches in at least three ways:

- 1 It specifies how interactions among the parts of a system induce organizational changes in the whole (i.e., selforganization), without direction by an external agent (see, e.g., Wolff, 1987, 1991). For example, we show that there are lawful ways by which interacting behavioral rhythms (e.g., sucking, breathing, kicking, arm waving, babbling) influence each other to establish coordinated wholes, or synergies.
- 2 It specifies how selective processes work in conjunction with self-organization to induce new patterns of motor coordination. We view the selective process as the outcome of exploratory activity by the infant's interrelated perceptual systems (Gibson & Pick, 2000). So, for example, as infants kick, there is visual, proprioceptive-kinesthetic, and haptic information from contact between the foot and ground surface during vertical displacement of the body against the force of gravity. The exploratory process may be guided by caregivers, and the spatiotemporal regularities in feeding routines, games, speech intonation, and other "fields of promoted action" may play a significant role in motor development (see, e.g., Reed & Bril, 1996).
- 3 A dynamical systems perspective treats the nervous system as part of an embodied system (Thelen, 2000), in that: (a) the brain is considered a medium for imposing general laws that yield patterns of coordination, but the brain is not the sole source of coordination and control (Kay & Warren, 2001), and (b) the brain is "informationally coupled" to a structured environment (Gibson, 1966, 1979; Warren, 1998). So, rather than simply correlating changes in limb configurations with myelination patterns in order to explain developmental progress in locomotion, as in classic treatments by McGraw (1945) and others, we address how infants may use visual information to coordinate posture and gait as they negotiate inclines and avoid barriers (e.g., Adolph, Vereijken, & Denny, 1998; Kay & Warren, 1998, 2001). Similarly, when considering the development of reaching, we discuss how muscle activation (measured by EMG) capitalizes on the forces acting on the body (Spencer & Thelen, 2000), rather than identifying EMG correlates of behavioral change (Forssberg, Stokes, & Hirschfeld, 1992).

These three distinctive characteristics of a dynamical systems perspective originate from an attempt to show how biological systems exploit physical laws to achieve complex organizational patterns. The physical laws include not only the fundamental laws of Newtonian mechanics that guide the field of biomechanics (see, e.g., Winter, 1990), but also the laws governing far-fromequilibrium systems (see, e.g., Prigogine, 1980; Winfree, 1980). The methodologies and mathematical tools adopted from these disciplines, such as topological analysis (Beek & Beek, 1988), mathematical modeling (e.g., Haken, Kelso, & Bunz, 1985; Kelso, Ding, & Schöner, 1992), and computer simulation (e.g., Saltzman & Munhall, 1989), are only now becoming part of the methodological tools of developmental scientists, so in the sections below, we take the opportunity to briefly describe how these methods can be used to address questions about infant motor development.

The goal of the chapter

The major goal of this chapter is to outline a dynamical systems perspective to the study of motor development by examining the core question of the sources of order by which new complex forms and functions emerge. Because this is a difficult and manyfaceted question, we unpack it to take the form of four related ones, used to organize the chapter:

- 1 What are the origins of order and flexibility in far-fromequilibrium systems that are characterized by fluid part– whole relationships among their component parts?
- 2 How do changes in the interactions between the parts of a complex system induce organizational change in the whole?
- 3 What is the relation between early forms of a behavior and later ones, e.g., between kicking and walking, or between pacifier sucking and breast- or bottle-feeding?
- 4 How do infants discover when to produce muscular activity in order to maintain an ongoing oscillatory behavior?

Our general strategy for each of the questions is to highlight a developmental phenomenon, introduce theory and methodology from a dynamical systems perspective appropriate to that phenomenon, and illustrate how some recent developmental research from the dynamical systems perspective has addressed it.

Four Questions Concerning Infant Motor Development

QUESTION 1 The origins of order and flexibility in complex systems

SELF-ORGANIZING SYSTEMS

A fundamental question about motor development concerns the ordering, or assembly, of component systems, during both ontogeny and performance, that makes possible the planning and control of stable, yet flexible, action (Saltzman & Kelso, 1987). The challenge in addressing this question was concisely articulated in a paper by George Butterworth (1993) on the causes of development:

The forms of the organism and its constituent subsystems (formal cause) distinguish the same organism at different points in development. Developmental theories, however, must not only explain the succession of static forms that can be observed, but also how forms change in a continuous progression. (p. 173)

We begin to address this challenge here by considering two sources of order (and flexibility) in complex nonequilibrium systems: self-organization and selection. The former refers to the integrated behavior of systems coordinating the actions of many elements. When systems are both complex and open to energy flux with the environment (i.e., far from equilibrium), this integration is due to the mutual interactions of the elements themselves rather than to any outside agent. Self-organizing systems are capable of forming patterns that have remarkable regularity, such as stripes in animal fur, and other aspects of morphology that have fascinated naturalists for centuries (see, e.g., Winfree, 1987). The question of interest for the study of infant motor behavior is whether self-organization, the emergence of patterns that are induced by the components themselves rather than by some outside agency, provides a parsimonious explanation of observed organizational changes.

NEWBORN SLEEP AND WAKEFULNESS

Observations of newborn sleep and wakefulness illustrate that even the earliest postnatal motor behaviors are stable self-recalibrating ensembles, what Wolff (1987) has called behavioral states. During "regular" (non-REM) sleep, the breathing rhythm is stable, the eyelids are firmly closed, and there is an absence of general body movements and vocalizations. By contrast, during "irregular" or REM sleep, breathing is irregular, and there are intermittent limb, trunk, head, and mouth movements. The awake infant may be in a state of quiet alertness: the eyes are open and make intermittent conjugate movements, the limbs and trunk are mostly at rest, and breathing is more stable than during irregular sleep.

Behavioral states are not merely different states of arousal. The temporary formation of each of these ensembles provides a distinctive organismic context for responding to environmental stimulation, and this has been experimentally verified in two ways. First, attempts to elicit "reflexive" behaviors yield different outcomes in each of the states. For example, during regular sleep and wakefulness, the Moro¹ and tendon reflexes are readily elicited, but during irregular sleep they are markedly diminished (Lenard, von Bernuth, & Prechtl, 1968). Second, the behaviors that define a state have different degrees of resistance against external perturbation, i.e., context dependence of behavior. Wolff (1966) found, for example, that a continuous monotonous sound converted irregular to regular breathing during irregular sleep, but the same "white noise" had little effect in modifying breathing during regular sleep.

We argue here that (1) the basis for the emergence of these ordered spatial and temporal patterns of sleep and wakefulness is self-organization, the tendency of the elements to "settle" into a small number of preferred configurations or states, called *attractors*, and (2) that the ensemble affects all of its parts just as each part contributes to the ensemble. To elaborate these points, the next section develops some of the concepts and techniques for studying attractor dynamics.

ATTRACTORS

One of the tools of dynamicists is the state space, a graphical means for displaying all the states that may be reached by a system, together with the trajectories for doing so. An attractor is a region of state space where trajectories come to rest. It can be a

¹ The Moro reflex occurs in response to a sudden loud sound or "dropping" the baby. The baby suddenly startles, throws its head back, and the arms and legs stretch out, and these quickly return to a central position.

point, cycle, or area of state space. For example, the behavior of a mechanical system, such as a clock pendulum, can be described completely by a two-dimensional state space, with axes of position and velocity. A distinctive property of attractors is their return to stability following an external perturbation: despite different initial conditions, trajectories will trace distinctive shapes as they settle, or come to equilibrium. With a point attractor, for example, the system is attracted to one point, and spontaneously returns to it after perturbation. The above example of the Moro reflex illustrates a system that exhibits point attractor dynamic: the elicited arm posture comes to rest at approximately the same endpoints. A limit-cycle attractor is a closed oscillation maintained by a competition between forces. Limit-cycle behavior is exhibited by a pendulum whose oscillation is sustained against the gravitational pull on the pendulum bob by the potential energy stored in a spring and released in "squirts" by an escapement. In later sections, we explore the possibility that behaviors such as sucking and walking exhibit limit-cycle attractor dynamics.

There is a range of techniques for identifying attractors. As an initial verification, one can construct a state space, where the coordinate axes are the state variables of position and velocity. By measuring position and velocity of a marker on a limb segment, for example, it is possible to examine the convergence of a family of trajectories on a stable cycle (e.g., when a supine infant kicks a leg). For rhythmic kicking, a closed orbit of trajectories, with a certain confidence band, is suggestive of a limit-cycle attractor. Stronger inferences can be made about the identity of the attractor by examining whether its phase can be shifted in time by applying a mechanical perturbation, called phase resetting (Kay, Saltzman, & Kelso, 1991), and by measuring its dimensionality (e.g., Robertson, Cohen, & Mayer-Kress, 1993). It should be noted that the methodology for phase-resetting experiments and the mathematics for determining dimensionality are each nontrivial exercises, and this may account for the paucity of infant studies that have used these techniques.

BABBLING: AN ILLUSTRATION OF THE SELF-ORGANIZATION OF AN ATTRACTOR

One of the stunning features of motor development is the abrupt appearance of a new form of behavior: infants may suddenly stand up by themselves and take a first step, or begin to produce the repetitive vocalizations that we call babbling. For example, babbling begins at about 7 months of age. It is characterized by relatively rhythmic cycles of alternation between a closed and open mouth accompanied by phonation, or vocal fold vibration (Oller, 2000). A series of studies by MacNeilage and colleagues (e.g., Davis & MacNeilage, 1995; MacNeilage, Davis, Kinney, & Matyear, 2000) shows that across different languages there are only three particular couplings of vowels (V) and consonants (C) that emerge from all possible combinations during babbling and early speech: coronal consonants co-occur with frontal vowels (e.g., /da/), dorsal consonants with back vowels (e.g., /go/), and labial consonants with central vowels (e.g., /ba/). They argue that the cyclical CV alternation underlying a syllable reflects a tendency to organize speech according to basic biomechanical constraints of the mandible.

From a dynamical systems perspective, babbling is a consequence of changing patterns of interaction or "coupling" of components. Kent, Mitchell, and Sancier (1991), for example, argue that babbling emerges from the coupling of new capabilities in respiratory/laryngeal and supraglottal functioning. In respiratory/laryngeal functioning, infants become able to sustain phonation with possible interruption for phonetic segments, and in supraglottal functioning, infants are able to produce trains of repeated closant-vocant syllables. Thus, because the segments are produced in regular rhythmic fashion, and phonation is not disrupted by production of phonetic segments, the novel form of behavior that we call babbling may emerge from the coupling of systems with their own attractor dynamics. We next turn to concepts and techniques from the study of adult motor control for studying such attractor coupling.

SYNERGIES AS SELF-ORGANIZING SYSTEMS

Coordinated motion involves the cooperation of the following approximate numbers of degrees of freedom of motor subsystems: 10^2 in joint space, 10^3 in muscle space, and 10^{14} in neuronal space (Newell, 1996). Moreover, the components of these subsystems are of different sizes (neurons and muscles), interacting in many different ways (e.g., muscles acting as agonists or antagonists, and contracting by different amounts in equal time), and at different time scales. How, then, does cooperativity arise in such a complex system? One insight into this problem came from Bernstein (1967, 1996), who proposed that a system's degrees of freedom do not act independently, but rather are linked in such a way that they preserve a functional relationship to each other

during performance. So, for example, when a skilled marksman sights a target, the wrist and shoulder joints are constrained to act as a single unit, such that any horizontal oscillation in the wrist is matched by an equal and opposite oscillation in the shoulder. The term "synergy" has been used to describe a functional system in which there is a cooperativity of degrees of freedom and a damping out of faster variables by those with a slower time scale (Turvey, 1990). The concept of synergy may provide a basis for explaining how the earliest observable motor behaviors of infants become organized into coordinated patterns.

HOW ARE SYNERGIES FORMED?

The premier example of the formation of synergies at the time scale of observable motor behavior is rhythmical oscillation, apparent in behavior as diverse as fin oscillations in the fish Labrus (von Holst, 1939/1973) to the sucking behavior of human neonates (Wolff, 1991). Von Holst proposed that the oscillation of each fin of Labrus had a preferred frequency, and that there were three fundamental processes by which any two fins became coordinated: they could compete with each other, e.g., by continuing their preferred frequency (a maintenance tendency), they could combine in additive fashion (superimposition), or they could cooperate by achieving a common frequency with constant relative phase (magnet effect). The significance of the maintenance tendency is that it demonstrates the independent, autonomous nature of each oscillation. However, when the fins are active together, their mutual influences (maintenance tendency and superimposition) become apparent.

COORDINATION OF RHYTHMS IN EARLY INFANT BEHAVIOR

Respiratory and sucking rhythms are among the earliest organized behaviors of human infants. Decades of study have revealed that these rhythms have an endogenous origin (see, e.g., Wolff, 1991). However, the principles by which these temporal patterns influence each other are only now being elucidated. Goldfield, Wolff, and Schmidt (1999a,b) examined the dynamics of pacifier sucking and breathing among healthy and high-risk lowbirthweight infants who reached their term date, and in healthy newborns. We compared these three groups in order to determine whether measures of coordination could be used to identify how prematurity affected the developing nervous system. Our hypotheses were that in a high-risk premature group compared with healthy full-term or premature infants, (1) the integer frequency ratios of sucking and breathing would be lower (1/1 or 2/1, rather than 3/1 or 3/2) and (2) sucking frequency would have less influence on respiratory frequency (i.e., von Holst's magnet effect), as measured by differences in breathing during sucking bursts and pauses. The group of high-risk low-birthweight preterm infants produced simpler patterns of sucking and breathing (as measured by the ratio of their sucking and breathing frequencies) and sucking and breathing frequencies had less of an effect on each other than they did in the other two groups. Thus, all of the infants produced only a small number of different coordination patterns, and birth status was distinguished by simpler and less stable patterns.

In summary, a dynamical systems approach provides a unique perspective on the fundamental developmental question of the emergence of new behaviors. Rhythmic behaviors such as sucking and breathing are self-organizing systems capable of influencing each other so that they become coupled together in new ways. Most importantly, the coupling is induced by the components themselves, rather than from the outside. Ongoing research in our laboratory is beginning to address whether similar analyses can be applied to the respiratory and vocal components of babbling and speech.

QUESTION 2 Transitions between stable states

DEVELOPMENTAL TRANSITIONS

We have just seen that stable coordinative patterns may arise from the self-organizing dynamics of interacting oscillations, and next turn to the question of how transitions between stable patterns may arise from these same dynamics. Self-organization implies that particular patterns emerge from whatever components are available, and so the prediction for developing motor systems from a dynamical systems perspective is that infants should take multiple paths toward a developing skill. Consider locomotion. Classic studies of infant locomotion by Gesell (1946) and McGraw (1945) highlight the apparent stage-like sequence of prone progression in which crawling follows creeping. During creeping, both arms are extended, and both legs flex symmetrically. During crawling, by contrast, both arms are extended so that the hands are directly below the shoulders, and then each hand extends forward, alternately. At the same time the legs push the body forward, so that the arm and leg on opposite sides of the body move simultaneously. However, Adolph et al. (1998) and Goldfield (1989, 1993) have found that not all infants follow the same sequence: some creep before they crawl, others skip creeping all together and go directly to crawling.

Another illustration of multiple paths comes from the densely detailed longitudinal study of infant reaching, first reported by Thelen, Corbetta, Kamm, Spencer, Schneider, and Zernicke (1993). A remarkable finding in this work is that some infants begin the process of learning to reach by wildly flailing the arms, and only gradually achieve smooth trajectories; while others hardly move at all prior to reaching. The task of learning to reach is, thus, different depending upon the context of the limb's initial motion. In the former case, the infant must damp out energetic movements by stiffening the limbs, while in the latter, the infant must scale up the velocity and force of reaching. We see, then, that there are apparently multiple paths to crawling and reaching. Nevertheless, self-organization is still apparent, since for both reaching and crawling, all of the different paths do eventually lead to a common goal. But what, precisely, is the mechanism for change?

STABILIZING AND DESTABILIZING ATTRACTORS IN DEVELOPMENT

Thelen and her colleagues propose that locomotion (e.g., Jensen, Thelen, Ulrich, Schneider, & Zernicke, 1995; Thelen & Ulrich, 1991) and reaching (Spencer, Vereijken, Diedrich, & Thelen, 2000) are governed by a set of subsystem attractors. Consider, for example, a series of studies on the intrinsic dynamics of spontaneous limb movements (Jensen et al., 1995; Spencer & Thelen, 2000; Thelen et al., 1993) whose starting premise follows from Bernstein (1967): acquiring a motor skill (or, in dynamical terms, locating an attractor within a potential landscape and reducing instability) requires solving the problems of moving limbs in an environment of forces. Jensen et al. (1995) take a critical step in modeling the forces (kinetics) influencing muscular control by considering more closely the body's actual biomechanical properties, namely, the elastic quality of the muscles. Their developmental question was the nature of the transition from early, stereotypic leg flexions and extensions to the complex and differentiated control of the joints required for walking (e.g., flexion at the hip while extension occurs at the knee as the leg is oriented for the next footstrike). They found that this transition, roughly between ages 3 and 7 months, was made possible when the force of kicking relied less on simultaneously stiffening the leg at all of the joints, and instead began to modulate the spring-like stiffness of the leg (evidenced by increasingly differentiated slopes of lines depicting the relationship of peak velocity and amplitude). Thus, it is the combined influences of muscular forces and gravitational and other forces acting on the body that attract leg flexions and extensions into a stable attractor well.

Thelen's work captures the way that motor development follows multiple paths, and that there are multiple influences that push the developing motor system toward certain paths and not others. However, a difficult challenge in using a "landscape" of attractors to model developmental processes is that it requires specification of an attractor and its control parameter for many interacting subsystems (see, e.g., Muchisky, Gershkoff-Stowe, Cole, & Thelen, 1996). Another difficulty is capturing specific relations between musculoskeletal and neural subsystems. Can we, for example, identify specific influences of the brain on the organization of the body's intrinsic dynamics?

BREAKING SYMMETRY

A striking feature of vertebrate morphology is its bilateral musculoskeletal symmetry. Nevertheless, most humans use a preferred hand to perform certain skilled motor behaviors, such as writing. Hand preferences appear to be related to the functional organization of the brain: in right-handers, there is functional asymmetry of the motor cortex between the dominant and nondominant hand (Civardi, Cavalli, Naldi, Varrasi, & Cantello, 2000). Left-handers do not show this organization, but the epigenetic developmental process by which handedness becomes established may include a complex set of asymmetrical influences on the eye-head system that can account for both right- and lefthanded individuals (see, e.g., Michel, 1987). As we confront the question of transitions in motor development, the body's musculoskeletal symmetry and central nervous system asymmetrical biases may point to complementary roles played by the body and brain in maintaining a balance between stability and change. One possibility, for example, is that the self-organizing tendency of bilaterally symmetric pendula, masses, and springy tendons (like a suspended puppet being oscillated by a single spring) is to fall into stable synchronous patterns. Functional asymmetries of the nervous system may introduce biases in the

temporal recruitment of muscle groups on one side of the body that modify these synchronous patterns in order to introduce change in behavior. Is there evidence that synchrony is a strong attractor for intrinsic oscillation of symmetric systems, and that lateral asymmetries are involved in breaking symmetry?

To address this question, we turn to the mathematical modeling used by Turvey (e.g., Turvey & Carello, 1996) and others to study the dynamics of synergies, i.e., the nature of coordination between oscillations. The starting point is a limit-cycle attractor, described by a variable, relative phase. Relative phase is an example of an order parameter, a macroscopic quantity chosen because it captures the spatiotemporal details of a system and changes more slowly than the variables characterizing the states (e.g., velocity, amplitude) of the component subsystems. The mathematical model of interest (see Turvey & Carello, 1996, for details) expresses the opposing tendencies between coupling and competition among interacting effectors. The phase relation observed varies as a function of both the strength of coupling of the two oscillations and the size of their competition.

When competition between the two oscillations does not equal zero (such as when the preferred frequency of one oscillation is different from the other), the symmetry of the dynamics is broken. Broken symmetry results from the fact that the various components do not play an identical role in the coordination pattern. Consider, for example, the task of holding a pendulum in each hand and swinging them parallel to the sagittal plane about an axis in the wrist (Kugler & Turvey, 1987). Frequency competition is brought about when the lengths of the pendula are unequal, so that the swinging motion of each occurs at a different frequency. Kugler and Turvey (1987) find, for example, that frequency competition has different effects on deviations from a required phase during antiphase and in-phase oscillations. The critical point, here, is that when symmetry is broken, changes in coupling can bring about richly varied changes in the behavior of the synergy.

The analysis of pendular motion frequencies provides a natural extension to the oscillation of the body segments. Broken symmetry of pendular body motions, e.g., the way that the two hands contribute to bimanual tasks in different ways, may play a fundamental role in the development of skills. One possibility, for example, is that the left and right sides of the brain are characterized by coupling differences, such that there are lateral differences in the relative stability of attractors among limb segments (Byblow, Chua, & Goodman, 1995; Carson, 1993). Treffner and Turvey (1995) provide some support for this claim in a pendulumswinging experiment during which right- or left-handed adults oscillated pendula of the same length. Even when there were no differences in the oscillation frequencies of the two pendula, there was a small but reliable right-hand lead for right-handed participants, and the opposite was true for the left-handers. Handedness, in other words, broke the symmetry of pendular oscillation.

POSTURAL ASYMMETRIES AND ORGANIZATIONAL TRANSITIONS: CRAWLING

Goldfield (1989, 1993) examined the possibility that lateral asymmetries in hand preference might play a role in the developmental transition to crawling. Prior to crawling, infants use both hands to support the body as the legs propel it forward (Adolph et al., 1998; Freedland & Bertenthal, 1994). However, in order to change position along a support surface, one hand must be free to reach ahead to something that affords approach. These two functional capabilities of the hands, stance and transport, may compete with each other as the infant attempts to perform both at the same time: an attempt to reach promotes falling and using both hands for support does not change the body's progress toward the goal. Lateral asymmetry of hand use may resolve this competition by providing a division of labor: instead of performing stance and transport at the same time, stronger spatiotemporal coupling of synergies on the preferred side for reaching may allow the infant to use that hand for extending forward toward the goal, while the other hand maintains support (with the legs, an adequate tripod stance). The temporal sequencing of stance and support that we call crawling may, thus, result from broken symmetry.

A study by Goldfield (1989) provides some evidence for symmetry-breaking in the development of crawling. Goldfield (1989) observed infants in a condition during which they were encouraged by the mother to approach an object while seated independently on the floor. The infant's hand preference for reaching, scored during a separate task, was used to classify each infant as either predominantly right- or left-handed. A coder blinded to this classification scored the hand upon which the infant first landed when he or she fell forward to begin to crawl. There was a strongly significant association between the infant's hand preference and the hand that first contacted the floor: right-handed infants landed significantly more often on their left hand, and reached out to begin crawling with their preferred right hand. The converse was true for the left-handed infants. Thus, in falling from upright into a crawl posture, infants appear to be landing in a way that leaves their preferred hand free to reach ahead of them as they begin to crawl.

To summarize, a dynamical systems perspective emphasizes that novel behavior emerges from unique combinations of interacting capabilities, each with its own rate of development. The particular functional system that emerges depends on competition and cooperation among its components. We next turn to the question of how newly emergent behaviors are related to their antecedents.

QUESTION 3

The relation between early and later forms of behavior: Selective processes acting on self-organizing systems

TRANSITIONS BETWEEN FORMS

Prechtl (1981) has highlighted the transient nature of many newborn motor behaviors, including rooting, sucking, palmar and plantar, and stepping "reflexes," and suggests that each appears to be "replaced" by more mature forms. For example, in the early form of orienting the head to receptor stimulation of the cheek, there is a somewhat frantic-looking rhythmic side-to-side headturning. Gradually, though, infants seeking the nipple will orient the mouth toward a source of milk, using multiple sources of information about its location (Prechtl, 1981). A fundamental question in development is how to characterize this relation between early and later forms. Here, we consider this question in the context of the relationship between self-organization of early oral motor behaviors and selective processes that are at work in eliminating certain patterns in favor of others.

TWO TYPES OF SUCKING BEHAVIOR

From a perspective that distinguishes "reflexive" and "rhythmic" behaviors (see, e.g., Gallistel, 1980), the non-nutritive sucking (NNS) behavior described earlier is an oddity. On the one hand, like the classic Sherringtonian reflex, it can be elicited by a particular means of stimulation, such as gently placing a finger inside the baby's mouth. However, once elicited, the infant continues to produce a 2 Hz rhythmic oscillation, pausing briefly

every few seconds, and continuing until the finger is removed or sleep ensues. Moreover, the careful observer can detect the same 2 Hz jaw oscillation during some periods of sleep, even with no oral stimulation. An additional feature that further blurs the classic distinction between sucking reflex and rhythm is the effect of milk flow on the sucking pattern. In experiments that control milk flow to an artificial nipple, when milk does not flow, infants produce the 2 Hz NNS pattern (positive pressure). When milk flow is initiated, the sucking frequency decreases to 1 Hz and there appears a negative pressure component coupled 1:1 with positive pressure. When milk flow is again interrupted, the negative pressure component dramatically decreases or drops out, and positive pressure returns to a 2 Hz burst-pause pattern. The implication of such experiments is that the motor system is organized in such a way that it is both capable of generating intrinsic dynamics and can be modified by the flow of milk from a nipple.

PHASE RESETTING

One way to conceptualize a motor control system that makes possible both earlier behaviors with intrinsic "reflexive" organization and later behavior that is modifiable by sensory information is with reference to a central "clocking" mechanism that can be adjusted by peripheral events. With such a mechanism as a foundation for motor control, the developmental phenomena of progress, regressions, and apparent disappearances might all indicate the relative degree to which central clocking can be influenced by feedback information about the current state of body articulators.

Experiments that have attempted to identify a central timing network that both drives the articulatory periphery and is influenced by feedback from the periphery have used a phaseresetting paradigm. During phase-resetting experiments, a sudden perturbation is applied to an effector participating in the rhythmic oscillation. The goal of phase-resetting analyses is to determine whether perturbations delivered during an ongoing rhythm have a permanent effect (i.e., a phase shift) on the underlying temporal organization of the rhythm. The presence of a phase shift indicates that coordination is not rigidly specified over the sequence, but rather evolves fluidly and flexibly. The methodology involves measurement of the amount of temporal shift introduced into a sequence, relative to the sequence's timing prior to the perturbation. For example, Kay et al. (1991) found that transient mechanical perturbations delivered to a finger altered the underlying temporal structure of oscillation by means of a phase advance, relative to where the perturbation occurred in the sequence. More recently, Saltzman, Lofqvist, Kay, Kinsella-Shaw, and Rubin (1998) have used phase resetting to examine the temporal control of successive opening and closing movements of the lips and the larynx in voiceless consonant production. They applied downward-directed mechanical perturbations to the lower lip during both repetitive and nonrepetitive utterances, and found that the lips and larynx were phase advanced as a relatively coherent unit. Both of these studies, then, support the claim that temporal control of both manual and oral sequences involves central clocking that both drives and is sensitive to peripheral dynamics.

CENTRAL CLOCKING AND PERIPHERAL TUNING IN ORAL-MOTOR BEHAVIOR

Finan and Barlow (1998) have examined whether infant nonnutritive sucking can be characterized by central clocking that both drives and is sensitive to peripheral dynamics. For this purpose, they developed an "actifier," a device for cyclic mechanical stimulation of oral peripheral mechanoreceptors in a way that mimicked the effects of natural movement. However, rather than using a strict phase-resetting paradigm, they instead examined whether they could modify the oscillation frequency of ongoing sucking so that it matched that of the mechanical stimulation. Some of the infants either increased or decreased cycle period so that it established 1:1 synchronization with the rhythmic mechanical stimulation. It should be noted that at the onset of stimulation, one infant simply stopped sucking, and three others raised or lowered the jaw while continuing to suck. At this point, then, while there is some evidence that the temporal organization of non-nutritive sucking can be modulated by rhythmic oral stimulation, further work needs to be done to firmly establish whether there is bidirectional coupling.

In summary, a dynamical systems perspective on the relationship between early and later forms of behavior emphasizes two roles for early forms of behavior. First, early-appearing behaviors serve an immediate adaptive role that ensures that the infant is motorically active. Second, these behaviors move the receptor surfaces of different body organs so that they reveal patterns of sensory input.

QUESTION 4 How do infants discover when to produce muscular activity in order to maintain an ongoing oscillatory behavior?

DYNAMICS AND THE ENVIRONMENT

Given the critical importance of receptor input in modifying dynamical systems so that they can adapt to a changing environment without losing their intrinsic stability, Butterworth (1993) and others (e.g., Goldfield, 1995) have turned to the work of James J. Gibson (1966, 1979) for insights into the nature of information. Gibson envisioned the actor/perceiver as being enveloped by fields that are patterned by the substances and surfaces of the environment. As animals and humans move through these fields, successive points of observation (in the case of vision) identify a trajectory of motion. On the one hand, this trajectory specifies the actor/perceiver's displacement during locomotion through the environment and, on the other, provides successive samples of the field that may be detected by the various perceptual systems (visual, auditory, haptic, taste-smell) during the displacement. By virtue of the evolution of nervous systems that vary in complexity, and of bodies that attain different sizes and forms, some animals are able to select information inherent to these patterns in a way that others cannot. For humans, the increasing selectivity from patterned fields during ontogeny is not only a function of development of the brain's receptor fields, but also due to increasing control of the means by which receptor organs are moved (Bertenthal & Bai, 1989; Bertenthal, & von Hofsten, 1998; Breniere, Bril, & Fontaine, 1989; Bril & Ledebt, 1998).

INFANT EXPLORATORY BEHAVIOR

In her influential theoretical and empirical work, Eleanor Gibson (e.g., Gibson, 1988; Gibson & Pick, 2000) has proposed that exploratory behavior is the primary means by which infants learn the relationships between their actions and the properties of the environment. Moreover, the selectivity of infant exploratory activity changes with the increasing postural control of the eye-head system and with mobility. So, due to limited eye-head and trunk control up until the age of about 4 months, infants explore only their immediate surroundings. They orient to sights and to the sounds that accompany visual events, and use haptic

mouthing to discover object properties. For example, Butterworth and Hopkins (1988) demonstrate the importance of the mouth as an exploratory organ in their observations of newborns bringing their hands to their mouths. Newborns will bring the hand to another part of the face, open the mouth in anticipation of the hand's arrival, and bring the hand to the mouth. When the hand is in the mouth, sucking has an exploratory function, as is evident in the types of active mouthing that are observed (Rochat, Blass, & Hoffmeyer, 1988).

Infants progressively explore more distal parts of the body, including the hands and the legs. We saw above that the reachinggrasping-handling system develops as the head and trunk are controlled more independently. Exploratory activity of the legs seems to be related to the body's axial (left-right) organization. For example, Rochat and Morgan (1995) used an experimental presentation of televised images of an infant's own legs to show that by 5 months, the infants detect the spatial discrepancy between an image that corresponds to what they experience while looking at their own moving legs and a spatially reversed image. Spencer and Thelen (2000) used kinematic and EMG data to examine the particular muscle combinations that were active within demarcations of a spherical region surrounding the infant's body. The study found a clear developmental relationship between movement within particular spatial regions and EMG activity: (1) early in the first year, infants moved through many spatial regions, including the one where the toy was located, but many of these early movements involved only biceps or triceps muscle activation, useful for moving the hand toward or away from the mouth; (2) after infants first learned to reach for toys at midline, the early muscle-activity patterns were replaced by deltoid-related ones, which served to move the hand toward the toy; and (3) infants increased muscle coactivity when near spatial regions in which the toy was located. Thus, over longitudinal observations of reaching, infants seemed to have learned which muscles moved their hand toward the toy, and which served to keep the hand near the toy's location. The variable being controlled appears to be end-effector position in body space.

As infants become more independently mobile during the first year, they begin to explore the relationship between their body orientations and the spatial layout of the environment. One way they do this is by using the arms and hands during crawling. According to a detailed longitudinal study by Adolph (1997), as infants move forward across the floor, they pause, pat the floor, and rock back and forth over their wrists. What does such

exploration reveal to the infant that may be useful for guiding locomotion? Using the hand to pat the floor is probably a means for testing the suitability of a surface ahead for locomotion. Indeed, studies on the visual cliff show that some crawling infants will reorient the body to extend forward the longest appendage, a leg, rather than the arm, to test a surface to be crossed (Campos, Bertenthal, & Kermoian, 1992). The use of the hands for exploratory purposes in the development of postural control has also been demonstrated in a paradigm developed by Barela, Jeka, and Clark (1999). During longitudinal measurements of independent upright stance (e.g., pulling to stand, standing alone, and walking), Barela et al. measured the force of infant hand contact with the surface of a small, suspended cube. They found that prior to walking, infants used greater force in touching the cube, indicating that they were using it for support (i.e., body sway occurred in advance of hand contact). However, once infants began to walk, hand contact preceded body sway, and was used prospectively to modulate sway before it occurred. Do infants use other types of exploratory activity to learn to walk?

LOCOMOTION WITH REFERENCE TO AN INVERTED MASS-SPRING PENDULAR SYSTEM

The human body under the influences of a gravitational field behaves like an inverted pendulum: any displacement away from the vertical (e.g., with the foot on a flat surface) causes an angular acceleration that must be compensated for by applying torque (i.e., force along a joint angle of rotation) at a joint (e.g., the ankle) (Woollacott & Jensen, 1996). The muscles and tendinous elements exhibit the additional properties of elasticity and damping. Based upon consideration of these constraints, Holt (1998) has developed a force-driven hybrid pendulum-spring model of the preferred gait patterns of adults. The model includes a periodic forcing function by which the muscles overcome dissipative (damping) losses across gait cycles, and two conservative forces, one due to the body's inertia in a gravitational field, and the other due to the spring energy return from the muscles and soft tissue. Whereas the Kay and Warren model probed the nature of the coupling of posture and gait, this model questions how each observed organization of the body's biomechanical properties - its segment lengths and masses, elasticity, and damping - reflects an optimal transmission of energy from the forceproducing muscles of the leg to the body center of mass of an inverted pendulum. Understanding how force production is

related to the dynamics of walking is crucial not only for healthy adults but also for adults and children with cerebral palsy.

The model addresses two well-documented findings for walking: (1) there is a preferred combination of stride frequency and length (a speed) at which energy expenditure per unit distance is minimized at approximately 0.79 cal/kg/m; and (2) any change in stride frequency or length away from this preferred combination results in increases in energy expenditure (Holt, Jeng, Ratcliffe, & Hamill, 1995). An account based on self-organization is that these findings reflect an actor's discovery of a particular frequency of limb oscillation at which a fixed force produces maximal amplitude (or, at which a minimal force produces a fixed amplitude). This frequency is called the resonant frequency of a system. A dynamical systems perspective predicts that the nervous system does not choose frequency or stride length; they are emergent properties of a linear oscillator operating in its resonant mode. To test this prediction, Holt, Hamill, and Andres (1990) experimentally increased inertial load by adding ankle weights during walking. If frequency is driven by the dynamics, then it should change according to the resonant period for the new inertial condition. The predictions were confirmed for adults and 9-year-olds.

DO INFANTS DETECT RESONANCE PEAKS IN THE FREQUENCIES OF THEIR OSCILLATORY BEHAVIORS?

We just saw that the fundamental property of a nonlinear oscillator, such as a mass attached to a spring, is that it requires a minimal amount of force to sustain oscillation of a mass when driven at its natural frequency. When a driver forces a mass-spring system, a peak occurs in the amplitude response near its natural frequency. At this peak, the system is said to "resonate" to the driver, and so this is called a resonance peak. On the basis of this work with adults, Goldfield, Kay, and Warren (1993) conducted longitudinal observations of infants learning the dynamics of a mass-spring system: their own body suspended in a harness with feet touching the floor from a spring of known stiffness and damping. Videotape recordings were made in the home once each week over a period of several weeks, as the infants learned to bounce.

Using a mass-spring model, Goldfield et al. tested the hypothesis that the infants we observed were controlling how much force to apply and how fast to apply the force of kicking. As in Holt's study, our model captures the optimality property of resonance. That is, the amplitude of the mass's oscillations is maximal at a specific frequency. It was further hypothesized that over longitudinal observations, infants were searching frequencystiffness space to find the resonant frequency. The resonant frequency depends upon the stiffness of both the spring and the legs, so in order to achieve maximum amplitude, the infant should match leg stiffness to spring stiffness. This was indeed the case. There was also an increase in amplitude over sessions, consistent with the hypothesis of exploration of a resonance peak, observed when a system is driven at its resonant frequency. More recently, Foo, Goldfield, Kay, and Warren (2001) examined what infants learned during this task by experimentally manipulating the system parameters of mass and spring stiffness once infants had already achieved their peak bout length while bouncing in the jumper. The major question was whether infants learned particular parameter settings per se, or learned the dynamics of the task, which would allow them to quickly adapt their leg stiffness and kicking frequency to new conditions. Both the mass and spring manipulations were effective in changing the bouncing frequency. One infant, for example, bounced at a frequency of 1.63 Hz at the session of the peak bout length; when an additional 2.30 kg mass was added to the bouncer, the infant bounced at 1.71 Hz; and when an additional spring was added in parallel, the observed mean bouncing frequency increased to 1.84 Hz. Moreover, at their first opportunity under each of the experimental conditions, infants began to bounce, indicating that they were exploring the dynamics of their actions rather than learning a particular parameter setting. Thus, as in the original Goldfield et al. (1993) study, after a period of exploring the stiffness by force parameter space, the infant is able to discover and exploit the stability of the attractor.

Conclusion

The foregoing account of a dynamical systems approach to infant motor development highlights the processes of self-organization and selection by which new behaviors emerge. Its promise as a unique approach lies in the methods by which new questions about motor development can be addressed. By developing mathematical models and computer simulations that attempt to capture neural, biomechanical, and environmental contributions to the emergence of new behaviors, the approach will continue to be useful for addressing the complexities of motor behavior. Its greatest challenge remains in providing ways to understand the relation between action and the domains that have traditionally been treated as separate human capabilities, namely, cognition, language, and social discourse.

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