



SYMPOSIUM

Learning to Move in a Changing Body in a Changing World

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From the symposium “Biology at Birth: The Role of Infancy in Providing the Foundation for Lifetime Success” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2023 at Austin, Texas.

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Synopsis Infants of all species learn to move in the midst of tremendous variability and rapid developmental change. Traditionally, researchers consider variability to be a problem for development and skill acquisition. Here, we argue for a reconsideration of variability in early life, taking a developmental, ecological, systems approach. Using the development of walking in human infants as an example, we argue that the rich, variable experiences of infancy form the foundation for flexible, adaptive behavior in adulthood. From their first steps, infants must cope with changes in their bodies, skills, and environments. Rapid growth spurts and a continually expanding environment of surfaces, elevations, and obstacles alter the biomechanical constraints on balance and locomotion from day to day and moment to moment. Moreover, infants spontaneously generate a variable practice regimen for learning to walk. Self-initiated locomotion during everyday activity consists of immense amounts of variable, time-distributed, error-filled practice. From infants’ first steps and continuing unabated over the next year, infants walk in short bursts of activity (not continual steps), follow curved (not straight) paths, and take steps in every direction (not only forward)—all the while, accompanied by frequent falls as infants push their limits (rather than a steady decrease in errors) and explore their environments. Thus, development ensures tremendous variability—some imposed by physical growth, caregivers, and a changing environment outside infants’ control, and some self-generated by infants’ spontaneous behavior. The end result of such massive variability is a perceptual-motor system adept at change. Thus, infants do not learn fixed facts about their bodies or environments or their level of walking skill. Instead, they learn how to learn—how to gauge possibilities for action, modify ongoing movements, and generate new movements on the fly from step to step. Simply put, variability in early development is a feature, not a bug. It provides a natural training regimen for successfully navigating complex, ever-changing environments throughout the lifespan. Moreover, observations of infants’ natural behavior in natural, cluttered environments—rather than eliciting adult-like behaviors under artificial, controlled conditions—yield very different pictures of what infants of any species do and learn. Over-reliance on traditional tasks that artificially constrain variability therefore risks distorting researchers’ understanding of the origins of adaptive behavior.

Infants learn to move in a context of variability

Learning to move is a moving target. Infants of all sorts—human babies, rat pups, fawns, and chicks—learn to move in a context of tremendous variability. Some variability arises from developmental changes in animals’ bodies, some from newly emerging skills in their behavioral repertoires, and some from the natural variability of the everyday physical and social environment. Some variability is self-imposed, and some is externally induced. All the while, infants across species

must acquire the lifelong ability to cope with a changing body and changing skills in a changing world. They must tailor their behavior to local conditions. How do they do it? How do animals acquire the behavioral flexibility needed for everyday function and survival as independent adults?

We suggest that a reconsideration of variability provides new traction on such questions, and the answers are relevant for researchers in movement science, biomechanics, physical anthropology, organismal biology, developmental science, and so on—anyone

interested in the whole organism function of animals in their natural environments. To preview: Variability is not merely a problem to be surmounted. Rather, in early life, variability is also a critical component of the training regimen for future behavior. Indeed, infancy may be designed to trivialize performance errors, accommodate variability in performance, and capitalize on variable input to facilitate learning. Moreover, variability never goes away. Throughout the lifespan, bodies, skills, and the natural environment can change from moment to moment. Here, we use the example of walking in human infants to illustrate how rich, varied experiences in early life may lay the foundation for flexible, adaptive behavior in adulthood. More generally, we suggest that variability in early experience is a feature, not a bug.

Traditional perspective on variability

Traditionally, researchers consider variability to be a problem for skill acquisition and behavioral development (Harris and Wolpert 1998; Todorov and Jordan 2002). Variability in the body and the environment are viewed as challenges to be overcome, and variability in performance is treated as “noise” that reflects poor motor control. Indeed, infants’ movements—both cyclic and ballistic—are notoriously variable. With learning and development, variability decreases and movements become more consistent (Riach and Hayes 1987; Clark et al. 1988; Butterworth et al. 1997; Hausdorff et al. 1999; Berthier and Keen 2006; Chang et al. 2006; Hong et al. 2008; Saavedra et al. 2012).

Research from the traditional view assumes that infants are born with species-typical bodies and brains, including, simple neuromuscular coordination patterns. For human infants, the assumed innate endowment includes an anatomy designed for eventual bipedalism and the neural architecture for alternating leg movements—so-called “locomotor primitives”—that presumably lay the foundation for independent walking (Dominici et al. 2011). From this view, the simple locomotor primitives become linked with perceptual input and elaborated to maintain balance and cope with changes in the body and environment over time (Forssberg 1985; Dominici et al. 2011; Lacquaniti et al. 2012; Sylos-Labini et al. 2022). Thus, from the traditional approach, the complexity required for functional locomotion in a sea of change is constructed from simple, modular building blocks (Sylos-Labini et al. 2022). Alternating leg movements become transformed into varied locomotor patterns to navigate varied terrain. That is, “gait” appears earlier in development than gait modifications, and simple alternating leg movements remain the core essence of locomotion throughout the lifespan.

Accordingly, traditional methods for studying locomotion deliberately constrain variability to reveal the core properties of cyclical, periodic gait. Researchers record locomotion in infant and adult animals under highly controlled, artificial conditions. In the case of human infants, researchers observe babies taking continual, forward steps at a steady pace on a motorized treadmill or along a straight path over flat, rigid, uniform ground (left side of Fig. 1A, B). The primary agenda is to assess the maturity of infants’ gait patterns (McGraw 1945; Sutherland et al. 1980; Bril and Ledebt 1998; Ivanenko et al. 2004; Hallems et al. 2005; Ivanenko et al. 2005; Hallems et al. 2006). A century of research from the traditional approach yields consistent findings (for reviews, see Adolph and Robinson 2015; Adolph and Hoch 2019): In their first weeks of walking, human infants move slowly and inefficiently with short, wide, highly variable, and halting steps. Over development, speed and efficiency increase, and steps become longer, narrower, smoother, and more consistent, eventually reaching adult-like levels of proficiency after months or years (Sutherland et al. 1980; Sutherland 1997; Breniere and Bril 1998).

But the traditional approach can only assess the maturity and efficiency of animals’ gait patterns under artificial conditions. It cannot reveal the developmental pathway to functional locomotion in the real world, where movements must be continually adapted to cope with changes in local conditions. A focus on periodic gait to the exclusion of natural locomotion ignores animals’ real-world experiences (Gibb et al. 2022). Thus, the traditional perspective on variability leads researchers down the wrong path, or at best, yields a blurred, incomplete picture of the origins of adult-like, functional behaviors and how they develop.

An ecological, developmental, and systems perspective on variability

We propose a reconsideration of variability from an ecological, developmental, systems perspective. This view embraces variability and focuses on behavioral development in real-world, complex contexts (Adolph 2019). Variability is considered integral to and critical for behavioral development, such that changes in the body, skills, and environment can serve as both the foundation and impetus for development. Of course, variability in performance sometimes reflects noise and poor motor control, but it can sometimes be a creative solution for coping with variability in the body and surrounds. Regardless, variability is always important for, and informative about, learning.

How then does this view consider alternating stepping movements in human infants? Although alternating leg movements may appear similar in form

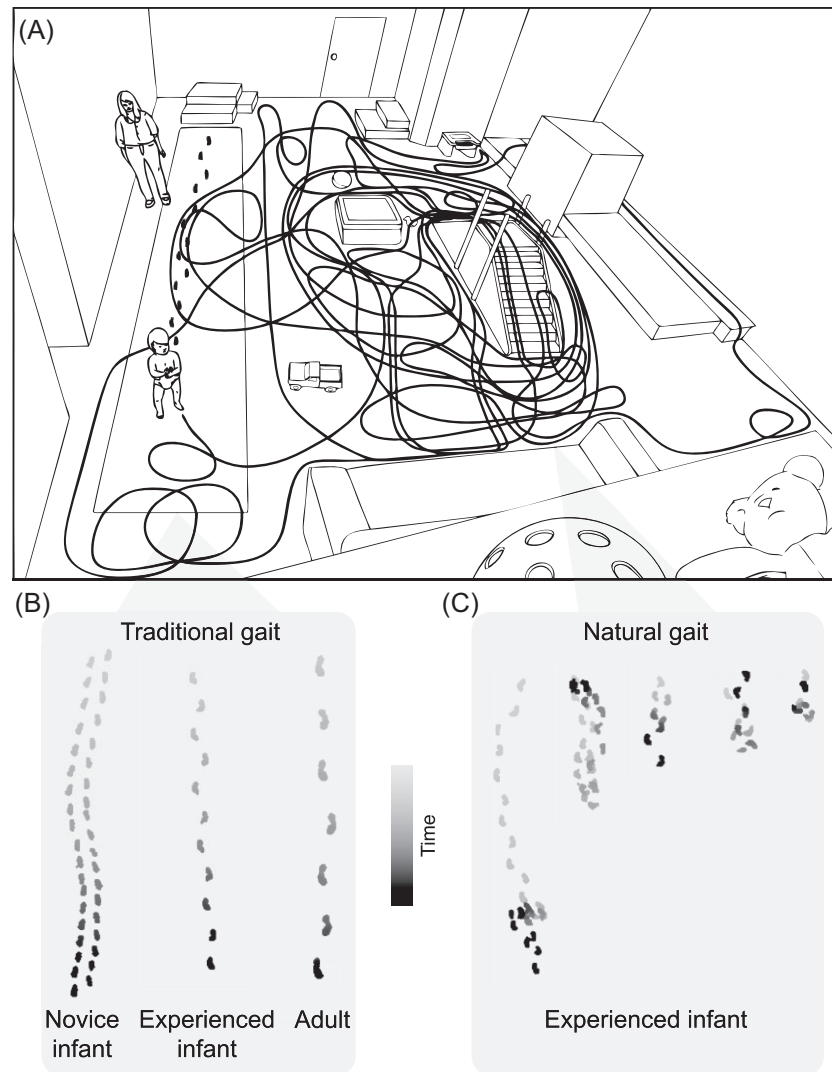


Fig. 1 Traditional gait and natural gait. (A) Traditional method constrains gait variability by encouraging infants to take continual, forward steps over a mechanized gait carpet (left side); ecological method allows gait variability as infants spontaneously produce intermittent bouts of omnidirectional steps on winding paths in free play. Footprints from an actual infant in the traditional gait task; thick black line denotes walking path of one 13-month-old infant during 10 min of spontaneous free play. Drawing adapted with permission from Adolph KE, Cole WG, Komati M, Garciguirre JS, Badaly D, Lingeman JM, Chan G, Sotsky RB. 2012. How do you learn to walk? Thousands of steps and dozens of falls per day. *Psychological Science*. 23:1387–1394. (B) Footprint paths showing improvements in gait patterns in novice and experienced infant walkers and adults obtained in the traditional straight-path task. (C) Footprint paths of the experienced infant walker in (B) during natural locomotion in free play. Data were obtained from bouts that spontaneously occurred on the gait carpet with infant walking in any direction or stepping in place.

to adult-like periodic gait, they have no assumed, preferential place in development. Rather than prioritizing adult-like forms of movement or “hard-wiring” them into the genetic endowment, alternating leg movements are considered to be merely one possibility among many. Everyone agrees that infants can move their limbs long before birth, including alternating “steps” and kicks. However, in utero and after birth, infants express a variety of movement patterns (Thelen 1979; Prechtl 1988; Cioni et al. 1989; Piek and Carman 1994; Hadders-Algra 2007). Depending on the context, some

coordination patterns are easier and more comfortable than others. For example, infants immediately switch from symmetrical leg alternation on a motorized treadmill to asymmetrical leg movements on a split-belt treadmill (Thelen et al. 1987; Yang et al. 2004); infants move both legs simultaneously when their legs are yoked with an elastic band (Thelen 1994); and they move only one leg when it causes an overhead mobile to jiggle (Rovee-Collier and Gekoski 1979). On this view, the immediate context of the body and environment determines which coordination patterns emerge. Or put

another way, infants learn to move in the body they have in the environment they're in (Blumberg 2009). Infants born without legs learn to walk on their arms; infants born with no limbs learn to move by rolling and scootching. And every infant learns to move over varied terrain that requires perceptual guidance and gait modifications to navigate obstacles and different ground surfaces.

Accordingly, methods for studying the development of walking from this ecological, developmental, systems approach involve experimentally inducing variability or embracing the variability inherent in natural activity (right side of Fig. 1A and C). Researchers record infants' movements in variable environments that require gait modifications and navigation (for reviews, see Adolph and Robinson 2015; Adolph et al. 2018; Adolph and Hoch 2019). Studies from this approach reveal that functional infant locomotion is complex and variable from the start. From their first walking steps, infants adapt to variability: Some sources of variability are imposed by factors outside infants' control (physical growth, caregivers' childrearing practices, and the environment). But much of it is self-generated by carrying objects and infants' spontaneous walking paths.

Using the development of walking in human infants as an illustration, we argue that the rampant variability and rapid changes so characteristic of infancy are not a noisy backdrop from which infants must struggle to extract a signal. Rather, variability is an ideal training regimen, and accordingly, infant development ensures variations in the body and environment. Infants cannot be learning fixed facts about their body or the world or rigid action patterns because their bodies, environments, and skills change from week to week, day to day, and even moment to moment. Instead, infants must be "learning to learn." They are learning to perceive which actions are possible and how to implement them as they make their way through the environment. Behavioral flexibility—built into the system from infants' first steps—gives infants the ability to cope with a changing body in a changing world, all the while acquiring more proficient walking skill (Adolph 2019; Adolph and Young 2021).

Infants learn to move in a variable body

At the same time that infants are learning to move, they must cope with frequent changes in their bodies and adapt their movements accordingly.

Endogenous changes in the body

Physical growth is a fact of development. As every parent knows, growth is especially rapid and dramatic in infancy. Babies get bigger, stronger, and more maturely

proportioned. The average newborn is about 50 cm long; a year later, the average toddler is about 75 cm tall (WHO Multicentre Growth Reference Study Group and de Onis 2006).

But few people realize the rapidity of change from infants' viewpoint. The continuous growth curves on the charts in the pediatrician's office are the result of mathematical smoothing between infrequent measurements (Lampl et al. 1992; Lampl 1993; Lampl and Thompson 2007). Daily measurements reveal that infants grow in short bursts of 0.5–2 cm in a single day separated by longer periods of no growth over 2–63 days. In fact, animal models indicate that most growth occurs when infants are lying down and their limbs are unloaded (Noonan et al. 2004). Thus, infants who were one size for weeks can go to sleep and wake up to suddenly find themselves in a bigger body. Changes in body size alter the biomechanical constraints on movement. With each growth burst, infants must recalibrate to new forces acting on their bodies.

Externally imposed changes in the body

Moreover, infants' bodies change depending on how caregivers dress them. For example, something as seemingly trivial as a diaper can change the maturity of infants' walking gait (Cole et al. 2012). Compared with walking naked, infants take shorter, wider—less mature—steps while wearing a diaper. And the decrement is not trivial. On average, walking in a thin disposable diaper is equivalent to losing 5 weeks of walking experience compared to walking naked; walking in a bulky cloth diaper is equivalent to losing 8 weeks of experience. In addition, infants exhibit more missteps and falls while wearing a diaper compared to walking naked. Similarly, babies wearing pants take shorter, slower steps compared to walking in only a diaper or underwear (Theveniau et al. 2014). And infants wearing shoes take slower, wider steps compared to walking barefoot (Cole et al. 2022). Indeed, infants who come of age for rolling and crawling in winter achieve those skills at later ages compared to infants who come of age in the summer—presumably because bulky winter clothing impedes movement (Hayashi 1992; Benson 1993).

Self-imposed changes in the body

Not all functional changes to the body are externally imposed by caregivers. Infants create their own moment-to-moment changes by carrying and discarding objects. Infant bodies are small, so carrying objects changes the location of their center of mass and thus changes how they move (Adolph and Avolio 2000; Garciaguirre et al. 2007; Vereijken et al. 2009). Carrying heavy objects

raises the center of mass and pushes it forward or to the side. Even carrying light objects comes at a cost to infants' gait: Steps while carrying objects are shorter and slower than steps with hands free (Heiman et al. 2019). Nonetheless, during free play, infants carry objects in a third of their walking bouts, and they do so from the onset of walking (Heiman et al. 2019).

Thus, at the same time that infants are learning to move, they must cope with frequent changes in their bodies and adapt their movements accordingly. Every infant animal undergoes physical growth; many infant animals carry objects; and human infants have caregivers who alter their clothing and footwear. Regardless of the source, functional changes in the body alter the forces acting on the body during movement. For the developing infant, knowledge about the size and shape of the body cannot be prespecified or taken for granted. As a result, development produces a system that must be flexible in the face of change in its physical architecture.

Infants generate variable input for learning to move

Continual, forward steps on a treadmill or along a straight path is not how human infants—or nonhuman animals—walk in real life. Real locomotion occurs in complex, cluttered environments, over changing surfaces and elevations, around obstacles and conspecifics (Fig. 1). Consistent, efficient gait is insufficient for functional navigation in the messy, real world (Gibb et al. 2022). Adopting an ecological, developmental, systems approach—observing real behavioral development in real-world environments—provides leverage on how such complex behavior can arise.

In everyday life, infants generate their own input for learning to move. Infants' natural training regimen consists of immense amounts of variable, time-distributed practice. On average, human infants take 2400 steps an hour, approximately 14,000 steps over the course of a waking day (Adolph et al. 2012). If you string their steps together end to end, toddlers walk the equivalent of 8 American football fields per hour, or 46 football fields per day.

Variability in natural infant walking requires perception

Natural walking is not in straight, forward paths (right side of Fig. 1A and C). Instead, during spontaneous locomotion in free play, infants follow twisting, turning paths, looping around to visit, and revisit different parts of the room (Adolph et al. 2012; Lee et al. 2018). Most walking bouts (73%) are curved—with gentle serpen-

tine curves, abrupt zig-zags, or sharp “hooks” at the beginning or end where infants veer back the way they came (Fig. 2A). Frequently, infants don't follow any path at all. They dance about taking steps in place (Cole et al. 2016; Hoch et al. 2020). Moreover, most bouts are not comprised only of forward steps; half of walking bouts contain a mixture of forward, sideways, and backward steps, and a quarter of bouts contain no forward steps at all (Fig. 2B). Furthermore, infants don't accumulate immense step counts in long, continuous sequences. Rather, locomotion is distributed over time in small bursts of activity; infants are only in motion about 30% of the time (Adolph et al. 2012). Most spontaneous walking bouts are short—on average, about 8 steps. And a third to half of all walking bouts are only 1–3 steps long (Fig. 2C)—too short to even calculate gait parameters (Cole et al. 2016; Lee et al. 2018). Indeed, 4 alternating steps is the minimum for a walking bout based on traditional methods.

The variability induced by curved paths, omnidirectional steps, and frequent starts and stops is not a byproduct of immature gait or poor walking skill. As shown in Fig. 2A–C, the proportion of walking bouts containing curved paths, omnidirectional steps, and 1–3 steps is constant from the first week of walking until 9 months later when walking skill begins to asymptote (Lee et al. 2018). That is, swerving paths, backward steps, and short bouts are endemic in novice walkers with poor balance control, as expected in the traditional view, but also in experienced walkers after balance is well developed. Variability is characteristic of natural infant walking.

Moreover, the variability in natural, everyday walking yields insights into what infants are learning. Walking must be perceptually guided from the start, and gait modifications emerge concurrently with gait, not as add-ons or later elaborations as assumed by the traditional approach. Curved paths require the two sides of the body to do different things, whereas an innate coordination pattern of symmetrical, alternating steps would produce the same thing on both sides of the body. Frequent starts and stops require perceptual input to initiate disequilibrium to start moving, and then regain equilibrium to stop moving, whereas continual stepping on a motorized treadmill can be produced by anencephalic infants and decerebrate animals. Curved paths and omnidirectional steps mean that infants gain experience with asymmetrical forces acting on the body, controlling balance during acyclic, nonuniform maneuvers while generating disequilibrium and stability in all directions.

Thus, from their first steps, infants are practicing complex, perceptually guided behavior that allows them to adapt to varied terrain. The variability

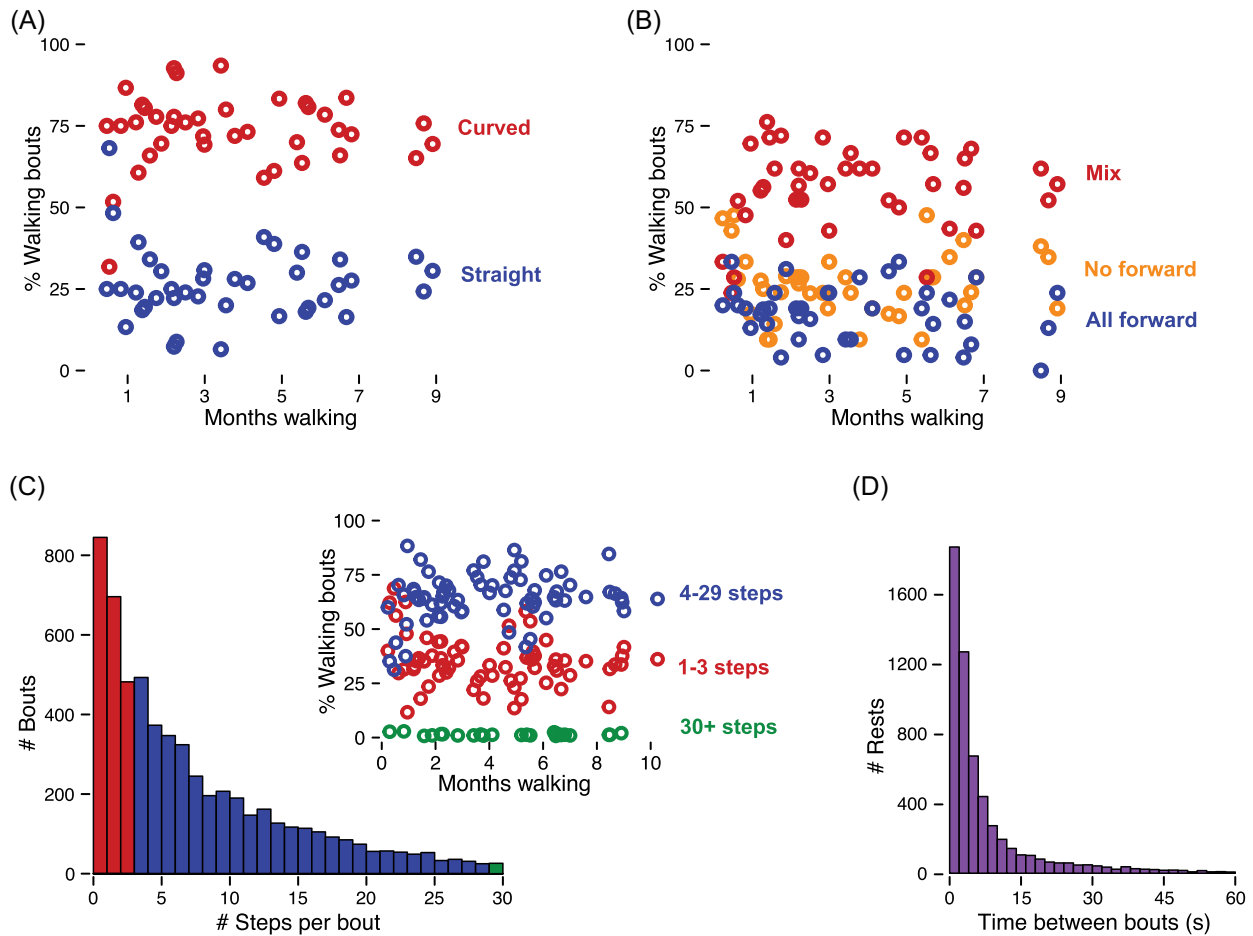


Fig. 2 Characteristics of natural infant walking during free play observed in 69 infants aged 11–20 months, covering the period from infants’ first week of walking until 9 months later, when walking skill begins to asymptote. Blue and green symbols denote data that conform to the traditional perspective on variability; red and orange symbols denote data only revealed during natural infant walking. (A) Small % of spontaneous, natural walking bouts that are straight (as assumed by the traditional approach) versus curved. (B) Small % of spontaneous walking bouts that contain only forward steps (as assumed by the traditional approach) versus bouts with a mixture of forward and not-forward steps or containing no forward steps. (C) Frequency histogram: Number of bouts that contain continual steps (at least 4 alternating steps, as assumed by the traditional approach)—bouts with 4–29 steps and bouts with 30 or more steps—versus bouts that contain only 1–3 steps. Histogram is cut after 30 steps for convenience. Inset: Percent of spontaneous walking bouts that contain 1–3 steps, 4–29 steps, and ≥ 30 steps. (D) Frequency histogram of “rests” between walking bouts (interbout intervals). Data in (A)–(C) were originally published in Lee DK, Cole WG, Golenia L, Adolph KE. 2018. The cost of simplifying complex developmental phenomena: A new perspective on learning to walk. *Developmental Science*. 21: e12615.

in infants’ self-produced, natural locomotion ensures that each bout of locomotion is different with different forces under different conditions, providing varied opportunities for learning to control balance and propulsion.

Much of infant movement is not directed toward immediate goals

Much of infants’ movement occurs without a discernible, immediate goal. During spontaneous locomotion in free play, infant walking is not primarily characterized by walking to reach a destination, then stopping after arriving there. Of course, infants can

walk from point A to point B, and they sometimes do. But destination-directed bouts do not comprise the majority of infants’ natural walking experience. Most spontaneous walking bouts have no clear destination. Infants stop moving in the middle of the floor beyond arms’ reach of any recognizable person, place, or thing. Or they stop moving within arms’ reach of the same objects and places where they started (Cole et al. 2016; Hoch et al. 2020). When infants do stop at a new object, they rarely visually fixated the object before they began walking (Hoch et al. 2020). For infants, movement may be its own reward. Infants playing in an empty room with no toys or elevations walk just as much as infants

playing in a room filled with toys designed to elicit locomotion (Hoch et al. 2019).

Accordingly, during spontaneous locomotion in free play, bout length is not merely variable, it is random. And the randomness is independent of the layout of the environment. The distribution of infants' walking bouts closely follows a negative exponential function (Fig. 2C), such that the probability of a bout ending is largely independent of bout length (Cole et al. 2016). Very short bouts of 1–3 steps occur at elevated rates, but after infants take three steps, the probability of stopping remains a constant 10% for bouts of increasing length, such that the distribution is uniform. That is, taking one more step is just as likely after 4 steps as after 40 steps. The distribution of “rests” between walking bouts follows a similar negative exponential curve (Fig. 2D). A constant, uniform probability of starting and stopping indicates that decisions to start and stop walking are generally random. In principle, the random distribution of walking bouts could reflect a random distribution of potential targets. But even in an environment where the layout of potential targets is not uniform (e.g., infants' homes, lab playrooms with clusters of toys and furniture), infants' probability of stopping is uniform. Thus, the flat rate of starting and stopping is inherent to infant walking, not a response to a uniform layout of the environment.

Human infants are not unique in generating movement with no discernable, immediate goal. Spontaneous locomotor movements are characteristic of infant play across species, from the gamboling foal to the pouncing lion cub and tumbling puppy; even invertebrates such as octopuses and bumble bees engage in spontaneous motor play (Mather and Anderson 1999; Burghardt 2005; Dona et al. 2022). Locomotor play can account for 20% of animals' time and 10% of their energy expenditure (Fagen 1981). Why infants expend so much energy running around is a long-standing puzzle among developmental biologists (Fagen 1974; 1981; Burghardt 2005). Regardless of the immediate impetus, all that running around can have long-term benefits. For example, practice moving leads to improvements in locomotor proficiency and variable input likely provides experiences that support functional, goal-directed locomotion (Hoch et al. 2019).

Errors accompany variability, but most errors are trivial

Errors often accompany variable performance. Falling is a clear case of errors in walking. Human infants fall frequently, about 40 times per hour in motion (Han and Adolph 2021). But unlike falling in adults, infant falls are generally trivial. Because babies are small, low to

the ground, and move slowly, the impact energy generated by an infant fall is 18 times less than if infants were adult sized and walked at adult speeds. Moreover, infants spontaneously produce behaviors that mitigate the impact of falling: They take reactive steps, flex their knees, brace themselves on nearby supports, and outstretch their arms to arrest the fall. The impact of infants' falls is therefore diffused across multiple body parts and most falls are onto safe, padded body parts. When the head and torso do impact the ground, it is typically toward the end of a sequence of body impacts, when impact forces are dissipated.

Consequently, infants do not treat falling as an aversive penalty to avoid (Han and Adolph 2021). Infants rarely fuss after falling, and caregivers rarely show concern. Falling does not deter infants from walking, and infants do not avoid the objects or elevations that were implicated in a recent fall. In fact, fall frequency remains high after months of walking experience: Experienced walkers continue to fall despite dramatic improvements in balance control and walking skill. Why? Because infants continually ramp up their game (Han et al. 2021). New walkers fall because their legs collapse or they turned their head or lifted an arm. A few weeks later, they fall because they trip over their own feet or make a fast turn. Months later, they still fall because they are climbing on elevations, spinning, and jumping. New activities introduce new opportunities for error.

Variability in the input is a feature, not a bug

How does a variable practice regimen affect learning to walk? Is all that variability actually beneficial for learning? Human infants cannot be randomly assigned to particular everyday practice and falling regimens, but robots can. And robots provide a formal, embodied system for testing whether variability is a feature, as we propose, or a bug, as assumed by the traditional approach. Spoiler alert: Variability wins.

Simulated robots trained to walk on actual infant paths (with all the documented variability in infant path shape and bout length) outperform robots trained to walk in straight lines or other geometric path shapes (circles, squares) in repeated soccer matches (Ossmy et al. 2018). Why soccer? Roboticists test functional movement in “Robocup,” a platform that requires robots to flexibly adapt goal-directed movements to a changing environment filled with other agents, who have their own goals. The results of 1000 head-to-head matches between each pair of training regimens show a clear advantage for infants' natural, spontaneously generated input. Robots trained on real infant paths out-score competitors trained on geometric paths and win the most games.

When comparing training regimens based only on real infant data, robots trained on more variable infant paths (in terms of path shape, step direction, path length, and number of starts and stops) win more soccer matches than robots trained on less variable infant paths (Ossmy et al. 2018). Moreover, training on more variable paths leads to better learning on the trained path (robots travel faster and farther) and better generalization to untrained paths (Ossmy et al. under review).

In addition, while training robots to walk, systematic manipulation of the penalty for falling shows that no penalty at all leads to better performance on both trained and untrained paths (Ossmy et al. under review). Like human infants, simulated robots do not benefit from negative reward for errors. For infants, discounting errors likely maintains their motivation to practice and to continually push the limits of their developing skills. If newly walking infants were penalized for falling after turning their head, lifting an arm, or taking a step, they would never move at all. A robust system that is relatively impervious to errors—a bouncy baby that falls without incurring injury or cost—will continue to push the limits and to accumulate immense amounts of variable, time-distributed practice that facilitates behavioral flexibility and function.

Infants learn to move in a variable world

Motor behavior must be tailored to local conditions (Adolph and Young 2021; Gibb et al. 2022). Variable input while learning to move ensures that infants learn to tailor their actions to novel changes in their bodies, environments, and skills. Infants must learn to gather perceptual information and adjust their actions accordingly. That is, infants must learn to perceive possibilities for action—what Gibson (1979) termed “affordances.” Rather than learning fixed facts (e.g., “I’m a poor walker,” “slopes are risky”) or static solutions (e.g., slide down slopes in a sitting position), infants are learning to learn (Adolph 2019). They are acquiring the behavioral flexibility that will allow them to cope with novel challenges in the wider world.

For example, in their first weeks of walking, infants step right over the edge of impossibly high drop offs and steep slopes requiring rescue by an experimenter (Fig. 3). Over weeks of walking, infants’ judgments become increasingly accurate until experienced walkers can perceive affordances within a few centimeters of accuracy on adjustable drop-offs, bridges, and ledges and within a few degrees of slant on adjustable slopes (for reviews, see Adolph et al. 2018; Adolph 2019; Adolph and Hoch 2019). On increments well within their abilities, experienced infants walk straight over the obstacle. On

challenging increments around the limits of their abilities, infants slow down and shorten their step length as they approach the obstacle. They explore the situation by looking, touching, and testing different positions to generate perceptual information about the relations between their body and the environment, and then modify their gait to navigate the obstacle. However, on increments beyond their abilities, infants use alternative strategies such as backing feet-first, scooting, or crawling, and in extreme cases, they avoid going entirely.

Perception of affordances must be accomplished anew on each encounter. From week to week, infants’ walking skill improves, such that a risky slope or drop-off last week is safe the next. Infants update their judgments accordingly. When infants’ walking skill is experimentally altered from trial to trial by dressing them in Teflon-soled shoes or lead-weighted shoulder packs, experienced infants immediately recalibrate their judgments to the current situation (Adolph and Avolio 2000; Adolph et al. 2010). They treat the same degree of slope as safe, for example, while barefoot or while wearing feather-weight shoulder packs, but as risky in Teflon-soled shoes or while wearing lead-weighted shoulder packs. Such rapid adjustments to changing affordances indicates that infants are not learning simple, fixed associations. Likely, coping with variability from their very first steps lays the foundation for learning about changing affordances.

Infants do not need to experience all possible challenges they will face as adults to respond adaptively. Over the course of varied experience in infancy, they are instead learning to learn—learning to gather the requisite perceptual information and use it accordingly to adjust their actions. Such an ability is crucial for functional, adaptive locomotion. Rigid, innate rules cannot cover every situation. And infants cannot practice all possible permutations of the problems they will face in adulthood. For complex, adaptive behavior in the face of unknown challenges, animals need to acquire behavioral flexibility.

What about animals that move from birth?

Human infants are altricial (not independently mobile at birth). Locomotor development is protracted in altricial animals, taking weeks (in rats), months (in monkeys and lemurs), and years (in humans). In contrast, precocial animals such as deer and chicks can stand and take steps soon after they are born (e.g., Muir 2000). Does our proposal about the critical role of variability in acquiring functional locomotion apply only to altricial animals?

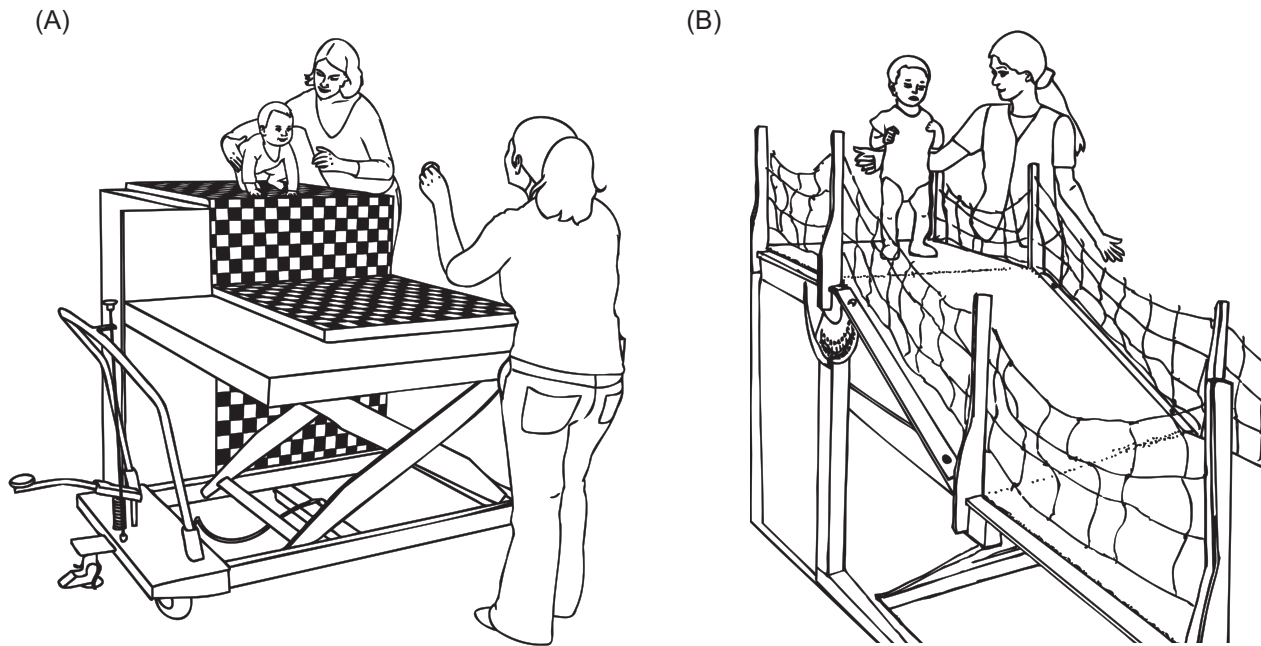


Fig. 3 Examples of apparatuses to test infants' perception of affordances for walking. (A) Continuously adjustable drop-off (0–90 cm). Caregiver encourages infant from bottom of landing platform. Experimenter follows alongside infant to ensure their safety. Reused with permission from Kretch KS, Adolph KE. 2013. Cliff or step? Posture-specific learning at the edge of a drop-off. *Child Development*. 84:226–240. (B) Continuously adjustable slope (0–90°). Caregiver (not shown) encourages infant from bottom of landing platform. Experimenter (shown) follows alongside infant to ensure their safety. Reused with permission from Adolph KE, Joh AS, Eppler MA. 2010. Infants' perception of affordances of slopes under high- and low-friction conditions. *Journal of Experimental Psychology: Human Performance and Perception*. 36:797–811.

To date, research with precocial animals is limited to the traditional approach and thus cannot speak to the role of variability or the acquisition of behavioral flexibility. Rapid attainment of adult-like locomotion is based on measures of gait maturity, as animals step on motorized treadmills or take continual, forward steps along straight paths on flat, uniform ground surfaces. Likely, chicks, fawns, kids, and so on, produce omnidirectional steps in short bouts on curved paths during spontaneous everyday locomotion, just as altricial infants do, but such descriptive data are not yet available. Similarly, the extent to which precocial animals flexibly adapt their movements to changing conditions shortly after birth is an open question. Regardless, both precocial and altricial infants acquire locomotion in a body and environment that is continually in flux. The real question is whether infants accommodate to variability by elaborating on pre-existing movement patterns or incorporate variability as part of the learning process.

Conclusions

We suggest that learning to move in the context of ongoing developmental changes ensures a variable training regimen (Fettters 2010; Adolph et al. 2015). As infants'

bodies grow and their motor skills improve, the accessible environment expands. For human infants learning to walk, everyday childrearing practices induce variability in the body and environment, and babies create their own training regimens to induce variability in the body and environment.

However, variable bodies, environments, and behaviors are not only a defining feature of human infancy and are not limited to learning to walk. Every animal must cope with a changing body and environment and adapt their behavior to changes in local conditions. Thus, we suggest that an ecological, developmental, systems perspective on variability may prove useful for understanding functional behavior in any animal in its natural environment. And our proposal that variability in development is a feature, not a bug, may facilitate understanding the origins of behavioral flexibility. In coping with variability at every step of development, behavioral flexibility can be built into the system from the ground up.

Acknowledgments

We thank the organizers of this symposium, Rebecca German and Christopher Mayerl, for including us in "Biology at Birth: The Role of Infancy in Providing the

Foundation for Lifetime Success.” We thank Jesse Young for discussions about research with precocial animals.

Funding

This work was supported by grants to KEA from NICHD R01HD033486 and DARPA N66001-19-2-4035.

Conflict of interest statement

The authors report they have no conflicts of interest.

Data availability statement

There are no new data associated with this article.

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