



The development of motor behavior

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This article reviews research on the development of motor behavior from a developmental systems perspective. We focus on infancy when basic action systems are acquired. Posture provides a stable base for locomotion, manual actions, and facial actions. Experience facilitates improvements in motor behavior and infants accumulate immense amounts of experience with all of their basic action systems. At every point in development, perception guides motor behavior by providing feedback about the results of just prior movements and information about what to do next. Reciprocally, the development of motor behavior provides fodder for perception. More generally, motor development brings about new opportunities for acquiring knowledge about the world, and burgeoning motor skills can instigate cascades of developmental changes in perceptual, cognitive, and social domains. © 2016 Wiley Periodicals, Inc.

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INTRODUCTION

Motor behavior includes every kind of movement from involuntary twitches to goal-directed actions, in every part of the body from head to toe, in every physical and social context from solitary play to group interactions. The development of motor behavior bridges the entire life span from the first fetal movement to the last dying breath.

Although movements fundamentally depend on generating, controlling, and exploiting physical forces, managing forces requires more than muscles and biomechanics. At every point in development, adaptive control of movement relies on core psychological functions.^{1,2} Perception and cognition are required to plan and guide actions.³ Social and cultural factors spur and constrain motor behaviors.⁴ Motor behaviors, in turn, provide the raw material for perception, cognition, and social interaction.^{5,6}

Movements generate perceptual information, provide the means for acquiring knowledge about the world, and make social interactions possible.

According to a developmental systems view (see Blumberg, Development evolving: the origins and meanings of instinct, and Lickliter, Developmental evolution, *WIREs Cogn Sci*, also in the collection *How We Develop*), motor behaviors cannot be understood in isolation, divorced from the bodily, environmental, and social/cultural context in which they occur.⁷ Movements are inextricably nested in a body-environment system (see Oudeyer, What do we learn about development from baby robots?, *WIREs Cogn Sci*, also in the collection *How We Develop*). The body and the environment develop in tandem. New or improved motor skills bring new parts of the environment into play and thereby provide new or enhanced opportunities for learning and doing. Caregiving practices facilitate and constrain motor development. As a consequence, differences in the way caregivers structure the environment and interact with their children affect the form of new skills, the ages when they first appear, and the shape of their developmental trajectories.

New motor behaviors can emerge from a mix of interacting factors, some so pervasive that we mistakenly take them for granted, and some so subtle or

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nonobvious that we fail to recognize the link. Developmental changes in one domain can have cascading effects on development in other domains, sometimes far afield from the original accomplishment.^{8,9} Moreover, the context in which behavior develops can be very different for individual children, resulting in developmental pathways that sometimes converge at the same outcome and sometimes veer off in unique directions.

This article is organized around four basic action systems—posture, locomotion, manual actions, and movements in the face and head. We focus primarily on the infancy period, when basic action systems are acquired.

POSTURE

Posture is the most fundamental of motor actions. It is the foundation upon which other actions are built.¹⁰ The instant that any part of the body breaks from the support surface—merely raising an arm while supine or lifting the head while prone—torque acting on the body part creates disequilibrium. This is why novice sitting and standing infants lose balance just from turning their heads or lifting their arms. Posture must be sufficiently stable to allow movements of the extremities, and maintaining a stable posture sets up the necessary conditions for looking around, handling objects, holding conversations, or going somewhere. As such, the emergence of most skills—including those not obviously related to posture—must await the development of sufficient postural control. Like every action, posture is perceptually guided and maintained.

Overcoming Gravity

Gravity and the surrounding media (e.g., air, water, the ground beneath the feet) are so quietly pervasive, so hidden in plain sight, that these important factors are often overlooked as causal forces in development. But they are central for motor development. Before birth, the buoyant uterine environment supports a variety of postures. Large body movements—whole body flexion and extension, stretching and writhing, and vigorous leg kicks that somersault the fetus through the amniotic fluid—peak at 14–16 weeks gestation.^{11,12} As the growing fetus occupies increasingly more space in the uterus, the propensity for movement is masked until the fetus can no longer extend its limbs or turn its head. Many of the movements practiced by the fetus are present in the repertoire of the neonate,¹² but after birth begins the real struggle against gravity.

Postural development is the attainment of increasingly erect postures poised over an increasingly small base of support. Think of a newborn struggling to lift its head, a toddler's wide walking stance, and an older child dancing on pointe. Indeed, the most common images of motor development are milestone charts of postural development (Figure 1). The milestone charts suggest an orderly, age-related march through a series of stages, but developmental pathways can differ and individual infants do not strictly adhere to the normative sequence derived from average onset ages. Infants can acquire skills in various orders, skip stages, and revert to earlier forms.^{13–15} Moreover, the skills highlighted on the milestone charts reflect the cultural biases of the initial researchers and samples.⁴ In some cultures, for example, many infants do not crawl, or they do so after they learn to walk.¹⁶

Generally speaking, infants' gradual triumph over gravity precedes top down from head to feet. The top-down progression is especially striking in the development of sitting. At first, head and trunk control is so poor that unsupported infants fold in half, falling chest to legs. Increasing control moves slowly down the spine—neck, shoulders, waist, and hips.^{17,18} Infants eventually 'tripod sit' by stabilizing their torso with arms propped between their outstretched legs. Finally, around 6 months of age, infants sit independently with hands freed from a supporting role,¹⁹ and over the ensuing weeks gain sufficient stability to manage the destabilizing forces caused by turning the head, twisting the torso, and moving the arms. The skill progression is not locked to a strict maturational timetable. Differences in childrearing practices affect the timing and trajectory of sitting.^{4,20} In cultures where caregivers routinely exercise and massage their infants, the babies sit independently before 5 months of age, and they do so with such assured stability that their mothers regularly perch them on high furniture and leave the room to do chores.

Like sitting, standing typically begins with manual support of balance. Infants pull to stand and hold themselves upright by gripping furniture for support.¹⁵ Toward the end of the first year, they stand freely and cruise holding furniture for support.¹⁹ Locomotion in prone, sitting, crawling, and upright postures appears only after infants can keep balance in one place, and transitions between postures (shifting from prone to sitting, sitting to standing, and so on) typically emerge last.

Basis for Action

A stable postural base opens up new possibilities for acquiring knowledge and acting on the world. The

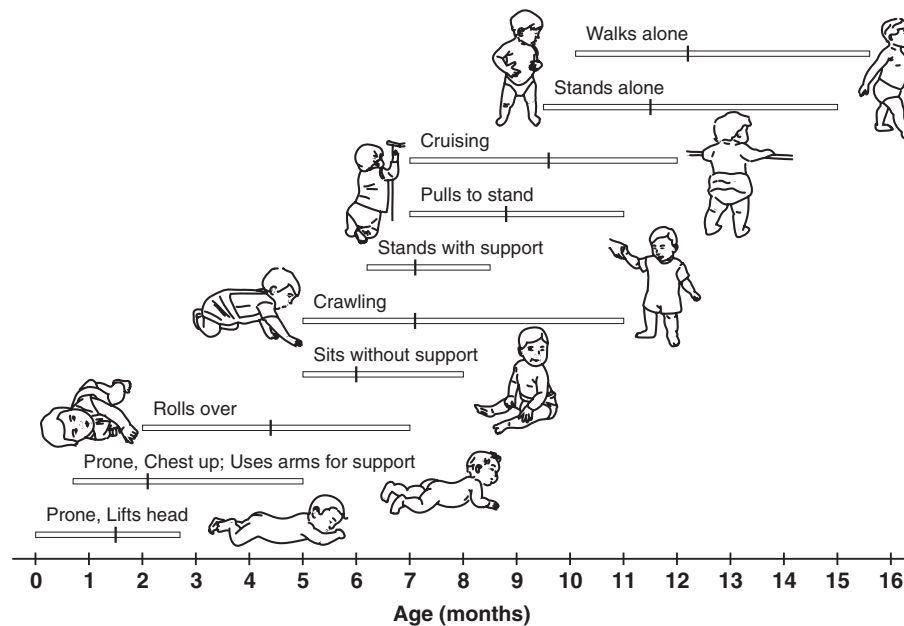


FIGURE 1 | Typical example of milestone chart illustrating age-related changes in postural development. (Reprinted with permission from Ref 4. Copyright 2010 Taylor and Francis)

ability to maintain head position while held in caregivers' arms allows infants to look around²¹ and maintain gaze with caregivers.²² The ability to sit and stand upright provides new vantage points for visual exploration.²³ Stability in a sitting posture frees the arms for reaching and the hands for manual exploration.^{17,24–26}

Indeed, reaching and manual exploration have different developmental trajectories for prone, supine, and sitting postures.^{25,27} While prone, bimanual exploration is difficult because one arm is occupied in holding the chest off the floor. While supine, infants struggle to raise objects against gravity and have difficulty exploring them visually. But while sitting, more sophisticated bimanual object exploration is possible because head, arms, and hands are more free to move.

Developmental changes in postural control instigate a cascade of far-flung changes: Independent sitting facilitates more sophisticated bimanual object exploration such as fingering, transferring, and rotating, which in turn facilitate learning about the three-dimensionality of objects.²⁸ Improvements in manual skills are also linked with shifts in infants' attention to changes in object appearance,²⁹ object size,³⁰ multimodal information about objects,³¹ and other people's intentions to grasp objects.^{32,33} The path from posture to prehension to perceptual learning is not immediately obvious, but it is there nonetheless.

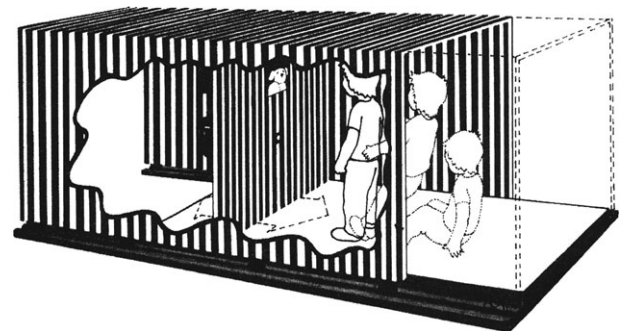


FIGURE 2 | Toddler losing balance in a 'moving room.' Child stands on a solid floor surrounded by walls that move back and forth along a track. Here, the walls move toward the child creating the visual illusion of the body swaying forward; the child compensates by swaying backward. (Reprinted with permission from Ref 37. Copyright 1989 American Psychological Association)

Dynamic Postural Control

Movement is ubiquitous in every posture. Even while lying down, the body is in motion. Similarly, sitting, crawling, and standing postures may appear stationary to casual observation, but they are not. Rather, the body gently sways back and forth within the base of support.^{18,34} A torque-induced sway in one direction must be met by a muscle-induced compensatory sway in the opposite direction. Standing infants are sensitive to perceptual information for body sway and can control swaying movements with merely a light touch of the hand on a support surface.^{35,36}

Visual information for body sway is extremely powerful. Slight movement of the walls around a sitting or standing infant in a 'moving room' creates the illusion of postural sway (Figure 2), and infants compensate for the visual information for body position by leaning in the opposite direction.^{37–39} However, infants do not use visual information for postural control as efficiently as older children and adults. While adults rock gently back and forth like puppets in tune with the wall oscillations, infants' compensatory sways are excessive and they often stagger and fall.

Summary: Posture

Posture is the core ingredient of motor skill. With no postural control, most motor behaviors are impossible. The development of postural control instigates a cascade of new skills and opens up new possibilities for looking, social interactions, manual actions, and locomotion. Postural development is partly a perceptual accomplishment because even while sitting and standing, the body is always slightly swaying and perception plays a key role in keeping the body inside the base of support. Postural control emerges from the interaction of a growing body dealing with the constraints of the physical environment—gravity, air, the properties of the support surface, and so on. Caregiving practices can speed up or delay postural control and the cascade of new skills that follow.

LOCOMOTION

Precursory locomotor movements are exhibited during fetal and neonatal periods, but locomotion is not reflexive or hardwired. Rather, locomotion is creative and infants must learn to control locomotion adaptively. Locomotion improves with practice, and practice can lead to extraordinary performance.^{4,7,40}

Newborn Reflexes

When newborns are held upright with their feet on a hard surface, they move their legs in an alternating pattern that resembles walking. This phenomenon is called the 'newborn stepping reflex' because the movements appear to be elicited by contact with the ground surface and do not require cortical control.⁴¹ Stepping typically disappears by 2 months of age and reappears at 8–10 months when infants begin walking with support. The fact that newborns produce alternating, upright leg movements led researchers to believe that walking is hardwired in the nervous system.^{42–44} Similarly, the curious disappearance and

reappearance of stepping was attributed to a hardwired developmental mechanism: Cortical maturation inhibits the reflex and increased myelination of the corticospinal tract allows stepping to return under volitional control.

However, the so-called stepping reflex is not, in fact, reflexive, and alternating leg movements do not, in fact, disappear. Newborns 'air-step' without an eliciting physical stimulus and they step in response to optic flow.^{45,46} Infants can deliberately modify their leg movements⁴⁷ in various configurations of alternating, simultaneous, and single-leg kicks.^{48,49} They spontaneously kick their legs while supine⁵⁰ and supine leg kicks are kinematically equivalent to upright steps, and are produced by the same muscle activations.⁵⁰ Moreover, supine kicking continues unabated throughout the period when upright stepping disappears,⁵¹ and upright steps instantly reappear when infants are held on a motorized treadmill^{52,53} or when their legs are submerged in a tank of water.⁵⁴ With daily practice in an upright posture, the stepping movements never disappear.^{55,56} Changes in the body, not the brain, explain the U-shaped trajectory of upright stepping: Between 2–8 months of age, gains in leg fat typically outstrip gains in muscle.⁵⁴ In an upright position, infants cannot lift their chubby legs against gravity, but in a supine position gravity helps to flex the legs; on a treadmill, the moving belt does the work of pulling infants' legs backward and in a tank of water, the medium alleviates the effects of gravity. Upright practice makes leg muscles stronger.

Creative Solutions

Individual infants find different ways to solve the problem of moving. Their first success at mobility likely involves a prone position with minimal balance constraints. They may log roll from place to place or pivot in circles using auditory information to calculate the shortest rotational distance to their caregivers.⁵⁷ As shown in Figure 3, some infants belly crawl, using limbs, head, and belly in various combinations for support and propulsion.^{58,59} The belly rests continually on the floor or bumps up and down during each cycle. Every form of precursory prone movement helps: Infants who pivot, belly crawl, and so on are twice as proficient when they begin crawling on hands and knees compared with infants who do not display the earlier forms.⁵⁸ In fact, simply spending a few minutes a day in a prone position accelerates the onset of rolling and crawling.⁶⁰

On hands and knees, balance constraints increase because the belly is off the floor. As a

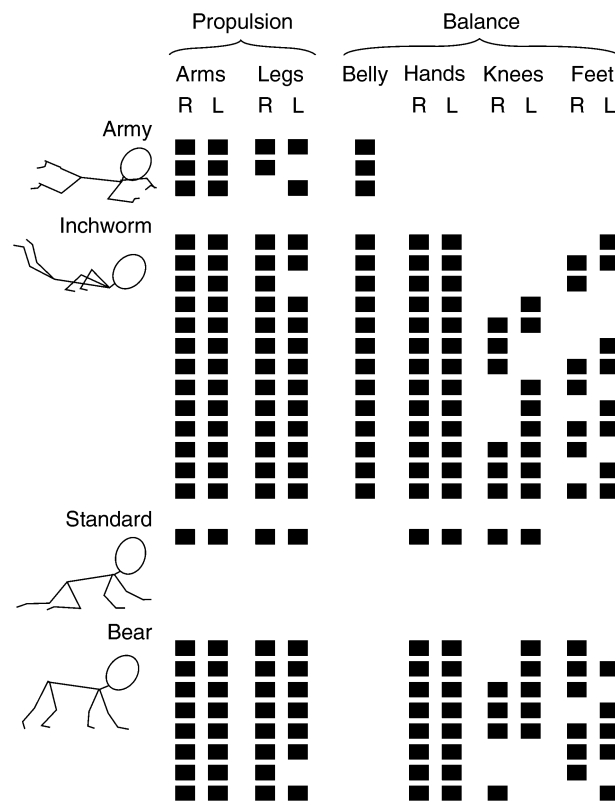


FIGURE 3 | Variations in infants' crawling patterns. Left column shows four different crawling styles: 'army' crawling with the abdomen continually resting on the ground, 'inchworm' crawling with the belly on and off the ground during each cycle, standard hands-and-knees crawling, and hands-and-feet 'bear' crawling. Center column represents combinations of arms and legs used to propel the body. Right column shows combinations of belly, hands, knees, and feet used to maintain balance. Each row shows a unique crawling pattern. (Reprinted with permission from Ref 58. Copyright 1998 Wiley)

consequence, most infants quickly settle into a relatively stable, near-trot gait pattern.^{58,61} But they also crawl on hands and feet, and combine hands, knees, feet, and buttocks into various forms of hitching and bum-shuffling positions that blur the line between sitting and crawling.⁴⁰ Balance constraints are more severe while upright, but learning to walk is likewise an exercise in creative problem solving with various falling, twisting, and stepping strategies for inducing enough disequilibrium to take steps but not so much loss of stability to cause a fall.^{43,62,63}

Generating new forms of locomotion can involve cognitive skills such as means-ends problem solving, representing goals and spatial locations, and tool use. As illustrated in Figure 4A, when confronted with challenging obstacles such as steep slopes, cliffs, and stairs, infants search for alternative means of descent—scooting, crawling, sliding, and backing strategies.^{64,66,67} Backing is most difficult

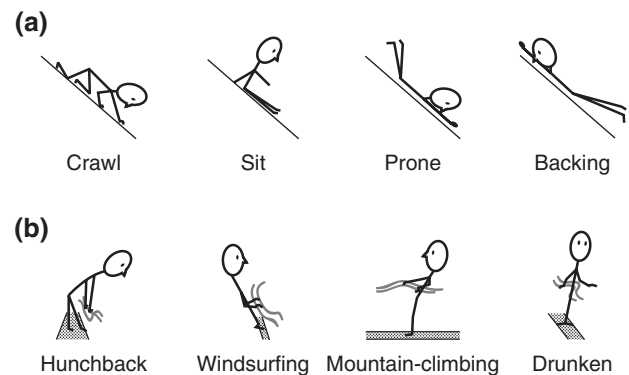


FIGURE 4 | (A) Some of the strategies infants use to descend slopes: Scooting down in a sitting position, crawling on hands and knees, sliding head-first while prone, and turning their bodies to back down feet first. (B) Some of the strategies infants use to cross bridges holding a wobbly handrail for support. Infants employ a 'hunchback' strategy by pushing down on the rail to make it taut, walk sideways while leaning backward as if 'windsurfing,' walking forward and pulling back on the rail as if 'mountain climbing,' and 'drunkenly' leaning against the rail as they staggered forward. (Reprinted with permission from Ref 64. Copyright 1997 American Psychological Association (APA) and Reprinted with permission from Ref 65. Copyright 2005 Wiley)

because it requires infants to initially turn away from the goal, coordinate backward movements, and steer without visual guidance. On narrow bridges, infants use a sturdy wooden handrail as a tool to augment their balance, but they reject the handrail if it is too far from the bridge.^{65,68,69} With only a wobbly rubber handrail for support, they test the potential utility of the rail, and invent various strategies for distributing body weight over the bridge and handrail (Figure 4B).

Learning to Walk

Infants take their first walking steps at 12 months, on average,¹⁹ but like all motor milestones, onset ages have a wide range (8–18 months). Walking onset awaits sufficient strength and balance to support the body on one leg as the other leg swings forward.^{43,70,71} Both experimental and cross-cultural studies show that experience standing, stepping, and moving upright facilitates gains in strength and balance and accelerates the onset of walking.^{4,7,40} A few minutes of daily practice with upright stepping causes infants to begin walking weeks earlier than infants who receive only passive exercise.^{55,56} Similarly, in Caribbean and African cultures where parents deliberately exercise their infants' upright skills as part of daily massage and bathing routines (Figure 5),

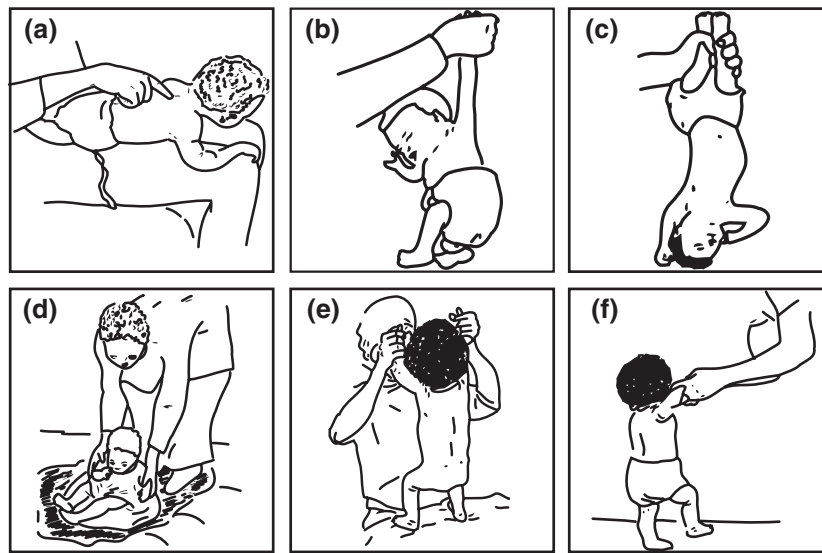


FIGURE 5 | Formal massage and exercise routines used in Africa, India, and the Caribbean that facilitate motor development. (a) Massage; (b and c) Suspending the infant from the arms and feet; (d) Mother providing sitting practice; (e and f) Practicing stepping in an upright posture. (Reprinted with permission from Ref 72. Copyright 1988 APA and Reprinted with permission from Ref 73. Copyright 2015 Taylor and Francis)

infants walk sooner than those from the same ethnic backgrounds who do not receive practice.¹⁶

Infants' first steps are wobbly and uneven, with a wide side-to-side distance between feet, a small front-to-back distance between steps, long periods when both feet are on the floor, and short periods when one foot is in the air.^{74,75} But soon the base of support narrows, step length increases, double support periods decrease, and infants are racing across the floor. The steep developmental trajectory for walking resembles the negatively accelerated performance curves characteristic of most motor learning tasks. Initial rapid improvements in the first 3–6 months of walking reflect infants' discovery of the relevant parameters that control upright balance and propulsion.^{74,76–78} A protracted tapering-off period ending between 5–7 years of age reflects subtle fine-tuning of gait parameters.^{70,79} Practice, not merely maturation, underlies improvements,⁷⁴ and infants accumulate immense amount of practice. In 1 hour of free play, the average toddler takes about 2400 steps, travels the length of about 8 U.S. football fields, and falls 17 times.⁸⁰

Sufficient practice can lead to improvements in endurance, strength, coordination, and balance far beyond the norm for Western walkers.^{4,40} Tarahumaran children engage in long-distance running as part of daily activity. As a consequence, endurance running exceeds the abilities of most Western ultramarathoners: Tarahumaran children routinely run 10–40 km in a few hours and adults race

150–300 km over 24–48 hours.⁸¹ From childhood, East African women and Nepalese porters of both genders carry prodigious loads on their heads. Adults in these cultures have learned to alter the biomechanics of gait so as to carry loads greater than their body weight with reduced energetic cost.^{82,83}

Obstacle Navigation

Perception-action coupling makes locomotion functional. To navigate the everyday cluttered environment, children must select the appropriate movements and modify them accordingly, whether crawling, walking, or riding a bicycle.⁸⁴ Children generate the requisite perceptual information through exploratory movements—looking, touching, and testing various options.^{7,64,85} The first studies of obstacle navigation tested infants on a 'visual cliff,' a drop-off covered in safety glass.⁸⁶ But infants in such studies can feel the glass and, after one trial, they learn that the drop-off is only illusory—and so they cross.⁸⁷ As shown in Figure 6, recent researchers have used real cliffs, bridges, waterbeds, foam pits, water pits, slippery surfaces, barriers, apertures, monkey bars, car-filled streets, and other obstacles to test the development of prospective control of locomotion.^{66,67,84,88–94} Because visual and haptic information are not in conflict on these apparatuses, children can be tested in dozens of trials (an experimenter follows alongside to ensure their safety). Many of the apparatuses are adjustable,

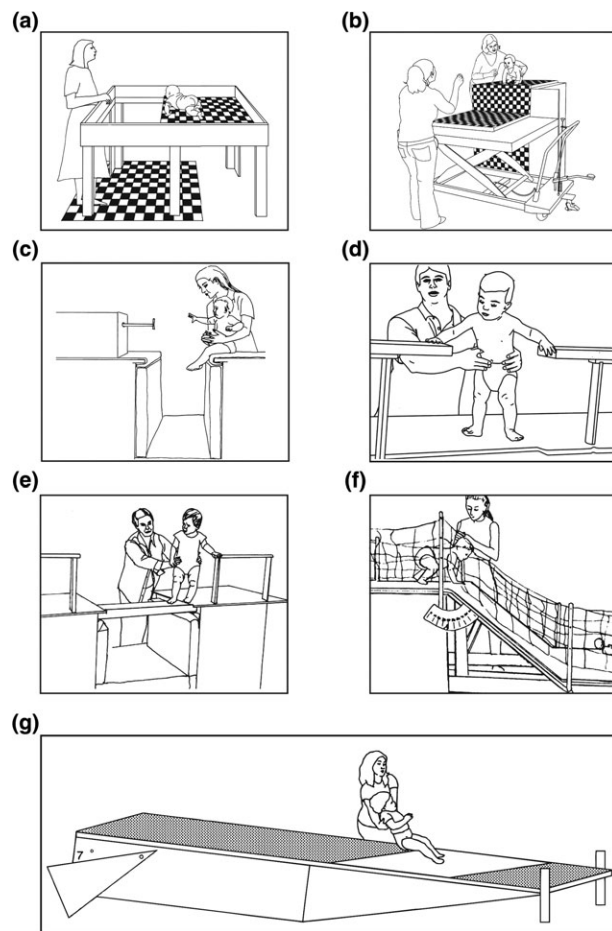


FIGURE 6 | (a) 'Visual cliff' with safety glass covering an apparent drop-off. (c) Real cliff with adjustable height of drop-off. (c) Sitting at the edge of an adjustable gap. (d) Cruising an adjustable gap in the handrail. (e) Walking across adjustable bridges. (f) Crawling down an adjustable slope. (g) Walking down a slope with a Teflon-coated section. (Reprinted with permission from Ref 73. Copyright 2015 Taylor and Francis)

allowing precise assessment of children's ability to gauge possibilities for locomotion.

Prelocomotor infants are sensitive to visual flow for heading⁹⁵ and depth information for a drop-off,⁹⁶ but sensitivity is not enough. Mobile infants must learn to navigate. In their first weeks after acquiring a new posture—sitting, crawling, cruising, and walking—infants plunge repeatedly over the edge of impossibly steep slopes, high cliffs, and wide gaps. Over weeks of experience with each posture, judgments improve so that infants attempt safe increments within their ability and avoid risky obstacles beyond their ability.^{7,40}

A surprising finding is that learning does not transfer from earlier to later developing postures. The same infants who perceive that a large gap

precludes scooting or leaning over the edge in an experienced sitting posture will repeatedly attempt to crawl over the gap in a novice crawling posture.⁹⁷ The same infants who perceive that a large cliff or slope is impossible to descend in an experienced crawling posture will repeatedly attempt to walk when tested in a novice walking posture.^{64,66,67} In a cruising posture, prewalking infants perceive precisely how large of a gap they can span with their arms, but not with their legs.¹⁴ Clearly, failure to transfer from earlier to later developing postures is not due to fear of heights because the gaps, slopes, and drop-offs are high above the ground in every posture.⁹⁸ Moreover, infants are not learning fixed facts about the environment or their abilities because possibilities for action change from week to week as locomotor skills improve. Instead, infants are learning to generate and use perceptual information about the current status of their body relative to the environment.^{7,40} They are learning the relevant parameters for each new posture in development and the relevant exploratory behaviors for calibrating those parameters in a new situation.

Summary: Locomotion

Fetuses and neonates can produce leg and arm movements that grossly resemble locomotion, but locomotion is not hardwired or reflexive. Instead locomotor development is tremendously plastic and responsive to caregiving practices. And locomotion is wildly creative. Every infant discovers a unique solution for their first crawling, walking, bum shuffling, or rolling 'steps.' And then they must learn to generate information for perception and cognition to find the right solution to suit the local constraints of the cluttered, obstacle strewn everyday environment.

MANUAL ACTION

Manual actions begin prenatally, but outside the womb, infants require a stable postural base to support arm movements and perceptual information to guide movements adaptively. Tools extend children's manual abilities.^{7,99,100}

Spontaneous Motility

Like all actions, manual actions appear long before birth. Ten-week-old fetuses flex and extend their arms, wiggle their fingers, and clench their fists.^{101,102} By 14 weeks, fetuses manually explore their own bodies, the umbilical cord, and the surface of the uterine wall.¹⁰³ By 16 weeks, fetuses bring

hand to mouth to suck their thumbs.¹⁰⁴ Even these early actions are perceptually guided and planned: Infants open their mouths in anticipation of, not in reaction to, the arrival of their thumb.¹⁰⁵

Spontaneous arm and hand movements continue after birth. Throughout the first year, infants flap their arms, rotate their hands, and wiggle their fingers, and exhibit bouts of rhythmical waving, rubbing, and banging while holding objects.^{51,106,107} Ironically, such so-called stereotypies may not be stereotyped at all. Infants' first banging movements are highly variable in terms of arm trajectory. Banging becomes increasingly uniform with the arm repeatedly tracing the same upward and downward path.^{100,108}

Reaching and Grasping

As in locomotion, the contextual influences of infants' bodies, physical environment, and social/cultural environment affect the development of manual skills. And individual infants forge their own developmental trajectories. Some infants learn to reach in the context of spontaneous arm flaps; they stiffen the arm joints to dampen inertial forces and direct the arm more in the direction of the target.¹⁰⁹ Other infants learn to reach more conventionally, by powering up their stationary arms in the presence of a target. In both cases, initial attempts are usually unsuccessful.

Goal-directed reaching requires perceptual information about the location of the object vis-a-vis the hand. Given appropriate postural support, neonates and young infants show precursors of visually guided reaching, extending their arms more frequently while looking at a toy.^{110,111} Successful toy contacts appear between 11 and 24 weeks of age,^{112–114} but reaches are jerky and crooked; the arm speeds up, slows down, and changes direction several times prior to contact. It takes years before children's reaches become as smooth and straight as those of adults.^{112,115} Infants 'reach' with their feet at a slightly younger age than they reach with their hands (Figure 7), showing that cephalocaudal (head to feet) development is only a rule of thumb, not an obligatory law of development.¹¹⁶

At about the same age that infants contact stationary targets, they show evidence of prospective control in dynamic situations by intercepting moving targets. As the toy moves along a horizontal path, infants time their arm movements so that their hand arrives at the location where the object will be, rather than where it was at the start of the reach.^{117–119} Visual information for frontally approaching targets is



FIGURE 7 | Three-month-old infant 'feet reaching' by contacting an object with the foot. (Reprinted with permission from Ref 73. Copyright 2015 Taylor and Francis)

different: The toy expands in the field of view. By 8–9 months of age, infants precisely gauge whether balls approaching at different speeds are catchable and they initiate interceptive arm movements based on visual information for time to contact.¹²⁰

Older children and adults rely on view of the hand as well as view of the target to guide reaching.^{121,122} However, young infants do not benefit from being able to see their moving hand. Researchers can measure the importance of continual visual feedback by turning off the lights once a reach begins (the toy glows to mark its location) or by occluding sight of the hand and arm with a cloth barrier. Infants begin reaching for objects in the light and dark at the same age, and are equally successful in both conditions.¹¹⁴ Moreover, the kinematics of infants' reaching trajectories in the light and dark are indistinguishable¹²³ and do not require sight of the hand.¹²⁴ In other words, infants' zigzag reach trajectories do not necessarily mean that they visually track their hand because infants display equally jerky reaches when they cannot see their hand. Jerky trajectories may result in part from postural constraints¹⁷ and unanticipated reactive forces.¹¹²

Much to infants' frustration, getting the hand to the right place is only part of the problem. Reaching precedes grasping because control of the arms precedes control of the hands. Normally, 3-month-olds merely swat at objects because they lack the requisite hand control for grasping and do not use perceptual information about object properties to plan the grasp. However, with the help of sticky Velcro mittens and Velcro covered toys, swats

are sufficient to pick up an object, thereby allowing 'pre-graspers' to reap some of the benefits of grasping objects that only older infants normally experience.¹²⁵ These early benefits have both immediate and long-lasting effects on manual skill.^{126–128} With increased hand/finger control, infants adapt their grip configuration to object properties, but they do so after contacting the object, not prospectively during the reach.¹²⁹ Prospective control of grasping based on visual information for object size, orientation, and substance appears months after infants begin reaching.^{130–133}

Exploring Objects

An object in hand opens up new opportunities for visual, manual, and oral exploration, and with increasing skill, object exploration becomes increasingly multimodal.^{134,135} At first, infants use their hands only to bring objects up to the face for looking and mouthing.¹³⁶ Increased grip strength allows infants to alternate between looking and mouthing, providing multimodal information about object properties. Soon, manual skills progress beyond mere holding. Infants heft, rub, squeeze, and finger objects.^{31,135,137} Later, infants coordinate visual and manual exploration by transferring objects from hand to hand and rotating them in front of their

eyes.²⁵ Hands begin to serve complementary functions, one supporting the object and keeping it in view, the other generating information about object properties by fingering or palpating.¹³⁸ Infants explore the relations between object and surface properties by banging a hard block against a rigid surface to make a noise or rubbing a soft block against the surface.¹⁰⁷

Extending Abilities with Tools

Tool use has its roots in early motor actions and relies on motor actions for its execution.^{99,100,108} Young infants' spontaneous banging and rubbing become preschoolers' hammering and drawing. Fetal hand-to-mouth behaviors become self-feeding with a spoon. Exploring relations between objects and surfaces sets the stage for using objects as effective tools.

Tool use requires infants to perceive that a goal is beyond their abilities, recognize that an object can serve as a means to augment their abilities, and execute the necessary movements to use the tool. Each of these steps in real time must first be acquired in development. For example, very young infants perceive when an object is out of reach.¹³⁹ Months later, they use hooks, canes, and rakes to acquire out-of-reach objects, but only if the target object is already placed inside the crook of the tool.^{140–142} And still

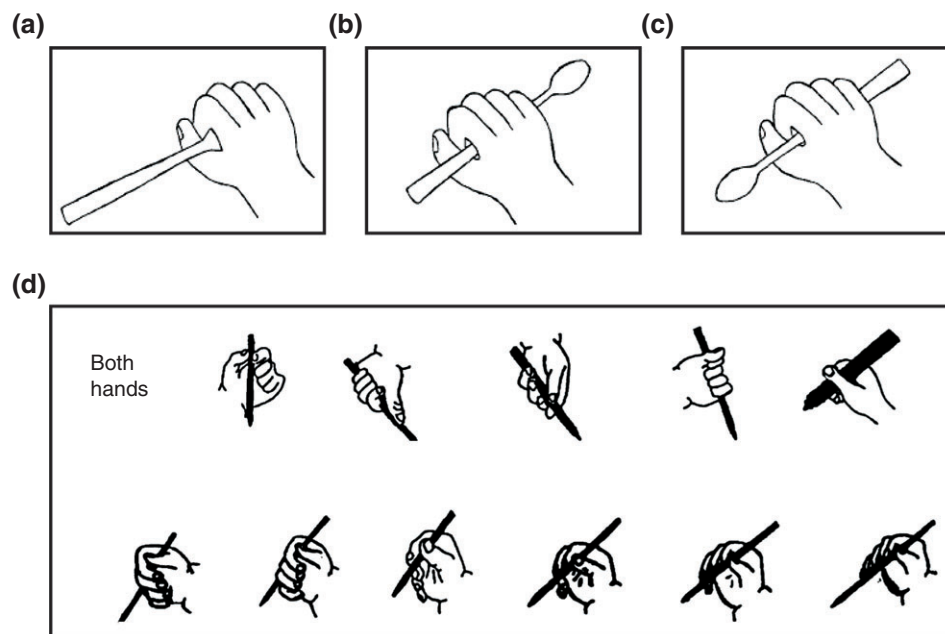


FIGURE 8 | Nine-month-old infant grasping a spoon (a) by the bowl or (b) with an ulnar grip that points the bowl away from the mouth. (c) An 18-month-old using a radial grip that correctly brings food to the mouth. (d) Variety of pen grips used by 3- and 5-year-olds and adults. (Reprinted with permission from Ref 143. Copyright 1999 APA and Reprinted with permission from Ref 144. Copyright 1998 Wiley)

later they perceive the full implications of the spatial relations by orienting the tools to place the target in the crook. Observing caregivers or other adults use a tool effectively provides a powerful impetus for learning.¹⁴²

Implementation often stands in the way of functional tool use. Nine-month-olds grasp a spoon filled with applesauce by the bowl end rather than by the handle (getting a handful of applesauce), or with a grip that points the food away from the mouth so that they cannot eat (Figure 8A,B). Eighteen-month-olds perceive the optimal grasp for delivering food to their own mouth and plan their grasp prospectively, but their planning is less efficient when feeding a doll (Figure 8C).^{143,145,146} Two-year-olds adapt their grasp to use a spoon with a bent handle.¹⁴⁷ But even 4-year-olds fail to realize that they must use an underhand grip to grasp a spoon or hammer pointing away from their dominant hand.¹⁴⁸ Implementing a writing or drawing instrument poses similar problems for older children.¹⁴⁴ Three-year-olds use 11 different grip configurations to draw straight lines (including using both hands to hold the pen) and individual children vary their grips from trial to trial (Figure 8D). Variability decreases by 5 years of age when most children begin formal schooling, and children converge on one of the two common adult grips.

Summary: Manual Action

Beginning prenatally, manual actions are perceptually guided and serve exploratory functions. Many of infants' spontaneous arm and hand movements are co-opted for goal-directed manual actions and tool use. Infants use vision to locate the target of a reach and to preshape their hand for grasping, but they do not require sight of their hand to get it to a target. Exploring objects is a multimodal activity involving eyes, hands, fingers, and mouth. Boosting up manual skills can jump start the cascade of opportunities for learning.

FACIAL ACTION

All the parts of the face begin moving prenatally, including the eyes while they are still fused shut. After birth, infants continue to produce spontaneous facial movements, but facial actions become integral to everyday function. The simple ability to swallow is critical for suckling, eating, and talking. Vocalizations and facial expressions are fundamental for communication. Head and eye movements provide the basis for visual exploration of the environment.

Swallowing, Sucking, and Chewing

Actions like swallowing are normally so innocuous that we do not recognize the tremendous coordination required. Fetuses make swallowing, sucking, and breathing movements, but since they do not breathe air or eat, the movements are not coordinated.¹⁴⁹ However, to nurse without choking or swallowing air, newborns must coordinate movements of tongue, jaws, and lips to create suction, draw liquid into the mouth, pull the liquid into the pharynx, and divert the liquid to the esophagus while pulling air into the trachea.^{150–152} Infants solve the timing problem by coordinating suck–swallow–respiration patterns at a ratio of 1:1:1 or 2:2:1.^{153–155}

Chewing solid food is more complicated because the food must be masticated before it can be swallowed. Newborns can mush up a small piece of banana and move it around the mouth with jaws and tongue.¹⁵⁶ However, infants rely on lateral jaw movements to do most of the work of chewing, whereas older children and adults use rotary jaw movements and incorporate more prospective actions of the lips and tongue.¹⁵⁷ Infants produce the same chewing movements regardless of the type of food, whereas older children select appropriate jaw movements and muscle forces based on the food consistency.¹⁵⁷

Facial Gestures and Speech

Facial expressions and vocalizations appear long before infants can convey feelings and communicate ideas. Fetuses produce smiles, grimaces, and facial movements that resemble adult-like expressions of laughter, crying, and pain.^{158,159} Neonates produce characteristic facial gestures to strong stimuli such as nose wrinkling and furrowed brows to noxious smells.¹⁶⁰ Newborns smile most while asleep, about one smile every 5 min.^{161,162} Awake infants begin to display social smiles and laughter by 2–5 months of age while gazing at caregivers or in response to positive stimulation.¹⁶³ Perhaps because they are so critical for social interaction, facial expressions are highly redundant so that muscles distributed throughout the face work in concert; eyebrows can convey basic facial expressions as effectively as the mouth. In fact, infants who lack the ability to move specific parts of their faces due to severe craniofacial anomalies, cleft lip/palate, or hemangiomas produce recognizable smiles, cries, and interested expressions.¹⁶⁴

The movements needed for speech production are perhaps the most complex movements children learn.¹⁶⁵ The jaws, lips, and tongue must be

precisely positioned to shape each sound as air travels through the oral and nasal cavities. Both speed and accuracy are major challenges in speech development. Adult-like speech is incredibly fast, encompassing up to 15 sounds per second.¹⁶⁵ As in the development of chewing, infants discover functional strategies to produce speech sounds, but their movements are not adult-like. For example, adults use quick simultaneous movements of the jaws and lips to babble (baba, mama), whereas infants rely primarily on jaw movements, which are easier to control.¹⁶⁶ Between 2–6 years of age, children gain better control over their lips and incorporate those movements into the previously established jaw movements, allowing them to produce a greater variety of speech sounds.¹⁵⁰

Looking

Visual perception involves pointing the eyes in the right direction. But looking usually involves more than moving the eyes. It involves coordination among body, head, and eyes to bring a desired location into view.¹⁶⁷ For newborns who can barely turn their heads, the control problem is simplified: They typically watch whatever happens to be in front of them, whether faces, hands, objects, or more complex scenes.^{168–170} Even after posture improves and infants can sit, crawl, and walk, much of what they see is opportunistic. Toddlers are less likely to tilt their head up to look at mother's face than to point their gaze straight ahead at her knees; they see what's in their hands or someone else's hands because the hands are already in their field of view.^{23,171–173}

Like other motor actions, looking is more functional and adaptive when eye, head, and body movements are controlled prospectively. To track a moving object, infants must anticipate its speed and trajectory to keep their eyes moving at the right pace. Large targets moving in predictable ways are easier for young infants to smoothly pursue with their eyes.¹⁷⁴ When the target moves too quickly, the eyes lag behind, so infants often make corrective saccades to catch up to the target. Over months of practice, infants track smaller targets at faster speeds,¹⁷⁵ resorting less often to corrective saccades. Initially, infants keep their eyes on the target, but their head lags behind. By 4–5 months, infants coordinate movements of eyes and head to smoothly follow moving objects.¹⁷⁶ While watching an object move repeatedly behind an occluder, 4-month-olds keep their eyes on the point where the object disappeared and then struggle to catch up to its motion after it

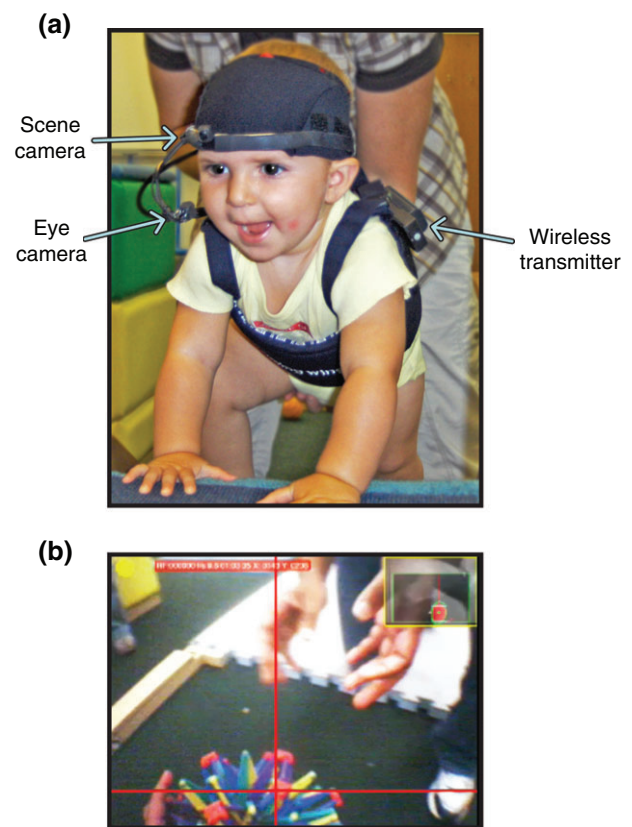


FIGURE 9 | (a) Head-mounted eye-tracker worn by a 14-month-old infant. An outward facing 'scene camera' records the infant's field of view, and an inward facing 'eye camera' records movements of the infant's right eye. Computer software calculates point of gaze. (b) Processed gaze video with red crosshair showing the infant's point of gaze. (Reprinted with permission from Ref 171. Copyright 2011 Wiley)

appears on the other side; 6-month-olds visually anticipate the location where the object will reappear, indicating their understanding that the object exists even when it is out of sight.¹⁷⁷

As in the case of walking, infants amass tremendous amounts of experience while learning to look. In 1 day, infants shift their gaze roughly 50,000 times.¹⁷⁸ By 2 months of age, infants have accumulated 200 hours of visual experience¹⁷⁷ and by 3.5 months of age, researchers estimate that infants have produced 3–6 million eye movements.¹⁷⁹ However, researchers know very little about what infants actually see outside of the laboratory. Head-mounted eye tracking provides a new method for observing infants' eye movements during unconstrained, spontaneous activity. As shown in Figure 9, infants wear two small cameras that record their eye movements and field of view for real-time gaze processing. Toddlers seamlessly distribute visual attention among multiple motor tasks, looking toward

obstacles to guide crawling and walking, fixating objects to guide the hand while reaching, and glancing occasionally at caregivers to initiate or respond to social interactions.¹⁷¹ Visual guidance becomes increasingly efficient over the course of development. Quick glances toward obstacles from a distance elicit more costly types of exploration such as touching.⁸⁵ Infants' short bodies serendipitously contribute to successful obstacle navigation because their field of view includes more of the floor compared with older children and adults, who primarily guide locomotion with visual information from the periphery.^{171,180}

Summary: Facial Action

Facial actions include many of our most prized and basic social skills—talking, facial gestures, eating and drinking, and looking at others and at the environment. And each of these skills sets off a new cascade of interactions. Infants' solutions for moving the various parts of their face often differ from those of adults, but they get the job done in that developmental niche.

CONCLUSION

The study of motor development is really the study of behavioral development. As such, it can provide a useful window into general processes of development because the topic of study—movement—is directly observable. Researchers in motor development have always recognized the importance of the bodily context.⁷ How could they do otherwise? Movements depend on physical forces and the moment-to-moment changes and developmental status of the body affect forces. The developmental systems perspective encourages researchers also to consider a larger context that includes the physical and social/cultural environment, and to view motor behaviors as potentially both cause and consequence of developmental change in other psychological domains (see Goldin-Meadow, Using our hands to change our minds, *WIREs Cogn Sci*, also in the collection *How We Develop*). Although prominent developmental theorists have long recognized the importance of motor development for psychological development more generally,^{5,6} only recently have researchers begun to systematically map out these developmental pathways.

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