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Abstract
All spatially and temporally coordinated behaviors are organized as action systems involving the coupling of perception and action. Some action systems are present at birth, but most will develop in the months and years to come; all of them will become better coordinated and tuned as a function of both neural development and experience. A number of key principles for explaining how perception and action are coupled are presented with specific examples from infant development, and followed by a discussion of specific change mechanisms responsible for the development of action systems.

Keywords
Action system, Affordance, Embodied knowledge, Goal-directed action, Imitation, Locomotion, Mirror neurons, Neural development, Perceptuomotor development, Postural control, Predictive tracking, Prospective control, Reaching, Self-organization, Spatial coordination
Biographical Sketch

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Perception and Action

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Introduction

Origins of Perception–Action Coupling

Perceptuomotor Behavior of Neonates

Adaptation to Changes in Brain and Body

Principles of Perception and Action

Reciprocity Between Perception and Action

Sensitivity to Surfaces and Objects

Sensitivity to Movements of the Body

Sensitivity to the Relation Between Self and Environment

Planning and Prospective Control

Significance of Future-Directed Information

Smooth Visual Pursuit Tracking

Reaching for Stationary and Moving Objects

Predictive Tracking of Briefly Occluded Moving Objects

Embodied Knowledge

Perception and Action are Context Specific

Coordination of Leg Movements

Scaling Perceptual Information to Motor Responses

Development of Reaching in the Light and Dark

Action Understanding

Common Coding of the Observation and Execution of Actions

Infants' Understanding of Goal-Directed Actions

Experimental Manipulation of Motor Experience

Coding Goals Versus Movements

Observation-Execution Matching of Non-human Actions

Developmental Origins of Common Coding

Change Mechanisms

Variation and Selection

Summary

Supplementary data

Further Reading

Relevant Website

Glossary

Action system Functionally organized action requiring continuous and dynamic perceptual modulation of the many factors (e.g., inertia of limbs, posture, direction, and distance of target) necessary for executing a response.

Affordance Perceptual information about an object or surface specifying a possibility for action. This information is only perceived if the action is within the motor repertoire of the actor.

Coordination and control Coordination involves organizing the multiple parts of a goal-directed action into proper relation with one another. For humans, coordination is a formidable task that involves almost 800 muscles that act to generate and dissipate energy at approximately 100 joints. Control involves tuning the specific parameters of a movement (e.g., displacement, amplitude, and speed of limb movements) to the local conditions in order to optimize coordination.

Embodied knowledge Pragmatic or sensory–motor knowledge about the physical or social world that enables a spatially coordinated action even when the goal is not conscious or continuously visible. This knowledge can be contrasted with symbolic knowledge that involves a representation of the world that can be mentally transformed and linguistically coded.

Haptic perception An active tactile process (pertaining to touch) that involves both sensory and motor systems to identify an object. In the human hand, tactile information is provided by the receptors in the skin, the muscles, and...
Newborn infants are capable of performing a number of actions that are regulated by perceptual information. For example, they can turn their eyes in the direction of a sound, visually scan differently in the light and the dark and concentrate their fixations near interesting objects. These actions are not just reflexes; they are goal-directed and perform various tasks such as finding food, avoiding predators, and establishing social bonds. This suggests that perception and action are not separate processes but are closely linked in the brain. The timing and force of motor actions are also influenced by sensory information. For example, reaching for an object is guided by perceptual information specifying the relation between the self and the environment. This information is necessary to maintain a balanced posture during the reach, but again the perceptual information changes as the posture is adjusted to that information. The sense of position and movement is derived from sensory receptors in the joints, tendons, and muscles. This information is used to specify the orientation of the body in space and the direction, extent, and rate of movement of the limbs.

In view of these many factors that must simultaneously contribute to the execution of a goal-directed action, it would be misleading to conceptualize perception and action as independent processes. Instead, it is much more parsimonious to view these processes as opposite poles of a functional unit or action system. The earliest developing action systems will be those related to the postural organization of the body and the control of locomotion. These systems are very important for the infant because they provide a means of maintaining stability and control during movement. The timing and force of motor actions are also influenced by sensory information. For example, reaching for an object is guided by perceptual information specifying the relation between the self and the environment. This information is necessary to maintain a balanced posture during the reach, but again the perceptual information changes as the posture is adjusted to that information.

The sense of position and movement is derived from sensory receptors in the joints, tendons, and muscles. This information is used to specify the orientation of the body in space and the direction, extent, and rate of movement of the limbs. The Russian physiologist, Nikolai Aleksandrovich Bernstein (1896–1980), was one of the first to recognize that spatially coordinated behaviors involved more than simply programming muscular responses, because other factors such as inertia of the limbs, reactive forces from the support surface, and initial postural conditions always combine with active muscle forces in producing complex chains of multisegment movements. All of these factors, or degrees of freedom, necessitate that active muscle forces are modulated by a combination of different sources of perceptual information specifying the self and the environment to ensure a functionally organized and goal-directed response.
high contrast edges, visually track moving targets, increase the frequency of hand-to-mouth contact following oral delivery of a sucrose solution, and show hand extensions toward a visible target. Until the availability of more sensitive instruments for measuring neonatal responses, these behaviors were often overlooked because they are quite fragile and inconsistent. For example, one reason that neonates show difficulty in tracking moving targets is that their heads are not yet independent of their trunks which are quite unstable and subject to intermittent movements.

It thus appears that newborns enter the world prepared to perceptually control some actions, especially those that are essential to their survival and adaptation. This preparation is a function of both the intrinsic organization of the brain, as well as behaviors that are practiced in the uterus. For example, the proprioceptive guidance of the hand to the mouth is established in utero by the beginning of the second trimester of pregnancy, and is readily observed in neonates. Furthermore, the mouth is more likely to remain open during arm movements when the hand goes directly to the mouth than when it first touches other portions of the face. The opportunity to practice this behavior in the uterus no doubt contributes to the degree of specificity that is present in its control at birth.

Some behaviors may not be practiced in utero, but nevertheless show a rudimentary perceptuomotor coupling from birth that is necessary for their functioning. Indeed, newborns are intrinsically biased to move their arms in such a way that their hands remain in the field of view. While lying supine with arms pulled down by small weights, newborns will resist this force on the side of the body to which their head is turned (see Fig. 1). Interestingly, the resulting posture is consistent with a neonatal reflex, known as the tonic neck reflex, and is similar to the posture assumed by a person fencing. This behavior is not, however, simply a function of a reflex, because infants viewing a video monitor localized on one side but displaying the opposite hand, resist the weight with the hand opposite to the direction in which they are looking. Moreover, newborns viewing their hand in a dark room keep it positioned within a narrow beam of light and move their hand when the beam moves. This behavior is extremely adaptive because it biases infants to visually explore information that can be gathered by one of the principal information acquisition devices available from birth—the hands. In sum, infants are born prepared to coordinate their movements with perceptual information, especially when the coupling will benefit their acquisition of new information about themselves and their environment.

Even though some actions are spatially coordinated from birth, this coordinative pattern represents only a skeletal structure that will continue to develop for a long time to come. The development of perception–action systems involves a confluence of factors that include neural and biomechanical changes, as well as task and environmental factors. As infants continue to practice performing these actions, they will develop improved coordination and control. In the case of sucking, these changes take place very quickly. Within a few days after birth, the sucking system functions with considerable precision to optimize the intake of nutrients. Neonates learn very quickly to adjust the change in sucking pressure to the flow of milk that changes from suck to suck. They can also learn to modify their sucking in an experimental situation that provides them with access to their mother’s voice. By 5 weeks of age, infants can use sucking as a means to bring a picture into focus. These latter two examples show that even early action systems are not limited to specific biological functions and that they can be used as a means to an arbitrary goal, such as listening to the mother’s voice, as well as serving to fulfill an intrinsic goal, such as gaining nutrients.

### Figure 1

(A) An 18-day-old baby participating in the experiment. (B) Schematic representation of how the hands were measured in terms of x and y coordinates. (C) A typical time series showing the changing y-axis location of both arms waving without weights attached. Reprinted with permission from van der Meer, A.L.H., van der Weel, F.R., Lee, D.N., 1995. The functional significance of arm movements in neonates. Science 267, 693–695. Copyright (1995) AAAS.
Adaptation to Changes in Brain and Body

Although practice and experience are certainly necessary for the development of these action systems, they are not sufficient because the developing infant is also changing in body size and strength and the brain is developing as well. For example, the optical components of the eye are still growing at birth, the photoreceptors will continue to mature and migrate toward the center of the retina (i.e., fovea) during the first few months, and the synaptic connections between neurons of the central visual pathways in the brain will continue to develop for some time. These changes will improve the resolution of the visual image, which will contribute to improvements in the accommodation and convergence of the eye, as well as greater acuity for perceiving visual patterns. Likewise, the perception of relative depths and distances in the spatial layout will become more precise with the neural development of the visual system.

A more specific example of how the incompletely developed visual system constrains the functioning of an action system involves the saccadic localization of visual targets. When young infants detect a visual target flashing or moving in the peripheral portion of their visual field, they will move their eyes to center their gaze on the target. This movement involves a direct mapping between the retinal location of the target and the neuromuscular stimulation of the appropriate eye muscles, which changes as a function of the distance of the eyes from the visual stimulation. This mapping is present from birth, yet the localization process is imprecise and involves multiple saccades (rapid eye movements that jump from one location to another) before the target is foveated. It is not until 4 months of age that localization is accomplished with a single saccade. One factor contributing to this development is learning the precise relation between the neural pulse duration innervating eye muscles and the saccade magnitude necessary for rotating the eye to the correct position. Nevertheless, it is surprising that the calibration process takes over 4 months to complete, especially since it is estimated that infants make between 3 and 6 million eye movements by 3.5 months of age. It has been hypothesized that the reason for this lengthy process is that the mapping of retinal locus onto an oculomotor command is constrained by the changing distribution of photoreceptors on the retina. This situation makes it necessary for the infant to adapt continually to this changing sensorimotor relation during early development.

Although some action systems are present at birth, it is clear that many others will develop in the months and years to come, and all of them will become better tuned and coordinated as a function of both neural development and experience. In the remainder of this article, we will discuss some of the organizing principles by which this development occurs with illustrative examples from the different action systems that play a pivotal role in early development.

Principles of Perception and Action

Reciprocity Between Perception and Action

Sensitivity to Surfaces and Objects

Perceptual control of behavior depends on the detection of the relevant perceptual information, as well as the coordination of responses necessary for the action system. As simple actions, such as pursuit tracking of moving targets, saccadic localization, or hand–mouth coordination are practiced and repeated, they become better controlled and coordinated, which demands that the necessary perceptual information is detected with increasing specificity. An excellent example of this mutual reciprocity between perception and action is revealed by research on the minimum audible angle necessary for detection of a change in sound-source location. In this task infants are expected to turn their heads to the right or left of midline if they are capable of localizing the sound. The minimum detectable difference decreases rapidly between 8 and 24 weeks of age and then continues to decrease more gradually through 80 weeks of age. It is noteworthy that the most rapid improvement occurs during and just following the time that infants are developing independent control of their heads and torso. Until they develop enough control to stabilize their heads, it is not possible for them to localize a sound source with sufficient resolution to differentiate sounds that are close together.

Another compelling example of the reciprocity between perceptual development and the improved coordination of actions involves haptic perception. Adults detect many different properties of objects, such as size, texture, weight, hardness, and temperature, from haptic explorations. In the case of a blind individual, touch would serve as the principal means for learning about the material properties of objects. Some of these properties, such as size and temperature, demand minimal control of the hand and fingers, whereas other properties, such as weight and shape, require much greater control. Intriguingly, the ages at which infants first discriminate different object properties correspond to the developmental changes in the control of the hand and fingers. For example, infants discriminate size within the first few months, but texture, temperature, and hardness which involve tactile exploration are not detected until around 6 months of age, and weight and shape which involve grasping and lifting are not detected until even later.

In the preceding two examples, motor development facilitated the perceptual sensitivity of infants to the properties of surfaces and objects over time. There are two other sources of perceptual information that are involved in the development of actions. One source is proprioceptive and it involves the positions, orientations, and movements of body segments relative to each other. The final source is the perceived relation between self and environment and it involves the position, orientation, and movement of the whole or a part of the body relative to the environment. Let’s consider how motor experience contributes to these two latter sources of perceptual information.
The development of self-produced locomotion on hands-and-knees involves a rather protracted period of development. Most infants begin to crawl with their abdomens on the ground by around 7 months of age. During this initial period of crawling, infants show considerable variability in their locomotor strategies and explore many different patterns of interlimb coordination, including pulling themselves with only their hands, or lurching forward by pushing up with their legs, or moving one limb at a time, or even moving all four limbs at the same time. The support of their abdomens on the ground enables infants to engage in any interlimb pattern of movement without risk of losing balance or falling. During this period of development, they are able to explore a wide variety of different interlimb patterns for locomoting.

Once infants develop sufficient strength to support themselves on hands-and-knees, they quickly converge on an interlimb pattern of moving diagonally opposite limbs (e.g., left arm and right leg) simultaneously and 180 degrees out of phase with the other pair of limbs. The selection of this specific pattern is a function of perceiving the optimal coordinative structure to ensure balance while minimizing the expenditure of energy. These are intrinsic goals that drive the infant to select the optimal locomotor gait pattern from among the many variations that were previously explored. This process by which behaviors go through a period of considerable variation before a stable new organization develops is repeated often in development, and is especially common in the development of motor skills, such as stepping, sitting, and standing.

The last source of perceptual information is concerned with the relation between the body and the environment. Does the development of self-produced locomotion contribute to infants’ sensitivity to this source of information? This question has been addressed by investigating whether prelocomotor and locomotor infants are differentially sensitive to whether a surface is traversable. Although some surfaces are more easily traversed than others, for example, a roadway vs. a narrow footpath along a mountainside, most afford some form of locomotion. One dramatic exception is a surface that ends abruptly at a precipice or cliff.

This type of surface has been simulated in the lab with a "visual cliff," which consists of a large sheet of plexiglass suspended 4 ft above the floor (see Fig. 2). A narrow board is placed across the middle, dividing the plexiglass into two sides. On one side (referred to as the shallow side), a textured checkerboard pattern is placed directly under the glass, so that it appears as a rigid and supportable...
### Perception and Action

Surface. On the other side (referred to as the deep side), the checkerboard pattern is placed 4 ft below the glass, so that this side simulates an apparent drop-off. In most studies, infants are placed on the centerboard and encouraged to cross to the mother who alternates standing across from the deep and shallow sides of the cliff. The question of interest is whether infants will be less likely to crawl across the deep side than the shallow side of this apparatus.

The visual cliff was designed originally to test depth perception, but more recent research suggests that infants are sensitive to depth information prior to the age when they begin crawling. If avoidance of the deep side of the cliff was specifically a function of depth perception, then all infants should avoid the deep side from the earliest age at which they could be tested. This is not what is observed, however. Infants’ avoidance of the deep side is related to their crawling experience—infants who have been crawling for 6 weeks are much more likely to avoid the deep side of the visual cliff than infants who have been crawling for only 2 weeks. Converging evidence come from studies measuring infants’ heart rate as they are lowered toward the deep or shallow sides of the visual cliff. Prelocomotor infants show heart rate deceleration (indexing interest and attention) to the depth information as they are lowered onto the deep side of the cliff. By contrast, locomotor infants with a few weeks of crawling experience show heart rate acceleration (indexing wariness or fear).

Why is perceptual information about the traversibility of surfaces interpreted differently by locomotor and prelocomotor infants? The answer is that the information specifying the apparent drop-off is only perceived as something to avoid when it is relevant to controlling the action of locomotion. If infants are not yet able to locomote, then this perceptual information can still be perceived, but it will not be perceived as a danger because this appraisal is specifically related to locomoting beyond the apparent drop-off. In essence, the visual cliff surface represents an “affordance,” or a possibility for action. This affordance is only perceived if the action is available to the infant. Thus, the perception of affordances and the motor status of the infant are intimately related.

Infants learn to perceive affordances for locomotion from their everyday crawling and walking experience. As infants acquire more experience with crawling, they become more accurate in perceiving whether or not these surfaces afford traversability. For example, infants become more accurate with experience in choosing which sloping surfaces can or cannot be descended. Moreover, their perception of the traversability of surfaces changes when the possibility for locomotion is manipulated by loading them with weights or extending their leg length with platform shoes. Similarly, varying the slant, friction, or rigidity of the support surface, etc., also alters the perceived possibilities for locomotion.

The preceding perceptual judgments are all scaled to the motor capabilities of infants. This is an important point to emphasize because it implies that the learning of specific perceptuo-motor skills cannot be generalized. The perceptual learning that accrues during the period of crawling is not transferred to upright locomotion. At the onset of walking, infants who avoid steep slopes when crawling show no hesitation in attempting to walk down these same slopes. Perceptual learning of affordances is highly specific and the mapping between vision and posture that emerges with the development of crawling will require a new mapping with the development of walking. This lack of transfer is not surprising given that each new form of locomotion involves a different set of response synergies that need to be coordinated and controlled by the perceptual information.

In sum, the development of perception and action is reciprocal. Improvements in the tuning of perceptual sensitivities enable finer control of motor responses. Likewise, changes in body size and shape, strength, postural control, and coordination of multiple body parts enable perceptual experiences that were heretofore unnecessary or unavailable. These changes in perception and action are cyclic and repetitive, and enable infants to continually improve their fit between their own action capabilities and the perception of their bodies and the affordances in the environment.

### Planning and Prospective Control

#### Significance of Future-Directed Information

Our actions, like those of all animals, must be coordinated with the physical and social environment, and this coordination demands perceptual guidance and control. In walking along an unpaved, narrow path, for example, we select which surfaces to contact and which to avoid. Likewise, when reaching for a fork, we guide our hand to select this utensil and simultaneously avoid or inhibit our hand from reaching for the spoon or knife. These actions are accomplished in real time and their control requires more than feedback following their execution. It is only possible to modify a movement that has not yet been executed, which is why it is necessary to predict what will happen next and prospectively control the action. Information needed for the specification of upcoming events is available from the spatial and temporal changes in the optic and acoustic arrays. As adults, we readily appreciate the spatial and temporal components in the control of actions. For example, we know that it is necessary to be in the right place at the right time to catch a ball, meet a person, or give a lecture. Likewise, infants show considerable sensitivity to the spatiotemporal coordination necessary for the control of actions.

Unlike neonatal reflexes that are automatically triggered by specific stimuli (eg, Moro reflex—extensions of arms and legs with loss of support), actions are goal directed and they often involve multiple body parts that are hierarchically organized into a single system. For example, the eyes, head, and trunk must be coordinated when tracking a moving target that continues beyond the immediate field of view. Thus, actions must be scaled to the spatial and temporal changes in our body, as well as in the external world. Even a simple reach for an object requires the ability to predict what will happen next to the moving limb, as well as to the object that is to be grasped. Prospective control involves implicit knowledge of the body schema, as well as knowledge of the spatiotemporal regularities that govern physical and social events in the external world.
Smooth Visual Pursuit Tracking

What sorts of prospective information are available to infants and how is this information used for controlling their behavior? One of the earliest examples of prospective behavior involves the smooth visual pursuit of moving targets. In order to track an object smoothly it is necessary to anticipate its future position from its past history of movement, because the motor commands for moving the eyes in response to the movements of the target are not instantaneous but delayed by the inertia of the eye, as well as the rate of neural transmission. Smooth pursuit is present from birth, but it is intermittent and limited to large targets. As the eyes begin to track the target, infants’ eye movements become jerky because they are forced to execute corrective saccades (rapid eye movements from one fixation to the next). Beginning around 6 weeks of age, smooth pursuit improves rapidly and attains adult levels by 14 weeks of age for targets that move smoothly and gradually slow down before reversing directions. By 20 weeks of age, infants successfully track targets that cycle back and forth and abruptly change direction. This evidence for early pursuit tracking is even more remarkable when one considers that it often requires the coordination between head movements and eye movements. Some head movements are unrelated to fixation, and both visual and vestibular mechanisms are involved in compensating for these movements to some extent from birth. Between 3 and 5 months of age, head movements increase in response to a moving target, but for quite some time lag behind the target because of the greater inertia associated with the head. In order to stabilize gaze on the target, the eyes must lead the target to counteract the delayed head tracking. Thus, smooth pursuit involves the coordination of eye tracking and head tracking which continues to improve as infants develop better control of their heads and greater sensitivity to target velocity.

Reaching for Stationary and Moving Objects

A similar pattern of jerky and inconsistent movements accompanies the initial development of reaching which begins sometime between 12 and 18 weeks of age. When adults reach for a stationary object, they execute a single movement unit characterized by the arm initially speeding up and then slowing down as it approaches the target. The trajectory of the arm movement is smooth and precise requiring only a slight adjustment at the end to grasp the object. By contrast, infants initially execute multiple movement units as their reaching arm gradually approaches the object, each movement unit brings the hand closer to the object, but the reach takes longer and is more circuitous. Over the next few months, the reach becomes better scaled to the distance and location of the object reflecting the development of an ensemble of factors including neuro muscular mechanisms, the control of posture, improved distance perception, and a more precise mapping between perceptual information and the motor responses necessary for executing the reach.

At approximately the same age that infants begin reaching for stationary objects, they begin catching objects attached to a moving rod. By 4.5 months of age, infants can catch an object moving at 30 cm s\(^{-1}\), and by 8 months infants can catch objects moving at 125 cm s\(^{-1}\). Successful catching requires that the infant predict the future location of a moving object and program arm and hand movements to arrive at that location just prior to the arrival by the object (see Movie 1). Infants typically reach for a stationary object with their ipsilateral hand (corresponding to the same side of the body midline as the object), but they will often switch to their contralateral hand when catching an object oscillating back and forth in front of them. The choice of the contralateral hand insures more time to execute the arm and hand movement before the arrival of the object, and thus represents additional evidence of prospective control by infants.

Predictive Tracking of Briefly Occluded Moving Objects

One of the critical skills necessary for predictive tracking and reaching is the prediction of the future location of a moving target. If a moving target is briefly occluded, it is necessary for the observer to represent the object’s trajectory in order for the eyes to anticipate where the target will reappear. Tracking is predictive if, after following a moving target before occlusion, infants shift their gaze to the far side of the occluding surface before it reappears. This visuomotor behavior begins to emerge between 3 and 5 months of age depending on the width of the occluder, the duration of occlusion, and the velocity of the target. Jean Piaget suggested that predictive tracking is an epiphenomenon of motor persistence—the prediction of the reappearance of the target is a function of failing to stop tracking when the target disappears rather than a function of representing the continuity of the target’s trajectory. Recent evidence reveals, however, that motor persistence cannot account for such predictive tracking, as infants rarely track smoothly and continuously once the target disappears. Instead, they tend to stop and fixate on the occluding edge for a brief period of time, and then make one or two saccades to the other side of the occluder. In addition, infants predictively track along circular trajectories by 6 months of age, but this is also inconsistent with a motor persistence explanation which suggests that tracking should follow only a straight line trajectory.

Another possibility is that prediction develops from some form of contingency learning. Infants as young as 2–3 months of age learn to predict sequential alternations of targets appearing in two locations. This same type of learning is probably not sufficient, however, for explaining infants’ predictive tracking of a moving target, because the likelihood of this response increases following 2 min of visual experience with an unoccluded moving object. During this familiarization period, the moving object is always visible so there is no opportunity for learning the contingency that a target disappearing in one location would reappear some
time later in another location. Instead, it appears that infants extrapolate from the preceding spatiotemporal information to predict the reappearance of the target. In other words, infants represent the trajectory of the moving target to predict its future location.

One of the most important spatiotemporal properties of objects concerns the way they appear and disappear behind nearer objects. Consider, for example, a typical street scene where pedestrians and vehicles are continuously appearing and disappearing from view as they move, or you, the observer, moves. Adults interpret moving objects that disappear gradually behind an occluding surface as continuing to follow the same trajectory; moving objects that disappear abruptly or implode (shrink rapidly in size) are interpreted as not continuing or following a discontinuous path. In one of the first experiments testing infants' sensitivity to this information, 5- to 9-month-old infants were observed tracking these different events (see Fig. 3). The results revealed that they were more likely to predictively track a moving object that disappeared naturally (via occlusion) than unnaturally (via abrupt disappearance or implosion) (see Fig. 4). These results are significant because they show that infants predict the reappearance of objects based not only on their trajectories and the location of the occluding surfaces, but also based on the spatiotemporal changes associated with their disappearance. In a more recent study, 5- and 7-month-old infants were shown either the occluding or the imploping event for as many as 20 trials (see Movies 2 and 3). Both age groups revealed the capacity to predictively track the gradually occluded moving object from the first trial, but initially did not predictively track the imploping moving object. Over the course of the experiment, however, infants appeared to learn that the visual information specifying the discontinuity of the

Figure 3  The three horizontal panels depict the location and appearance of the rolling ball at different times during the stimulus event. (A) Occlusion. The ball gradually disappears behind the right side of the occluding surface (located in the center of the display), and then after 2 s reappears from behind the left side of the occluding surface. Note that the shaded portion of the ball is meant to depict its nonvisible portion behind the occluding surface. (B) Instantaneous disappearance. The ball abruptly disappears when it reaches the location of the white circle and abruptly reappears 2 s later at the location of the second white circle on the other side of the occluding surface. (C) Implosion. The rolling ball rapidly decreases in size as it approaches the occluding surface and rapidly increases in size as it reappears 2 s later on the other side of the occluding surface. Note that the ball completes disappearing or begins reappearing at the same exact time that the ball abruptly disappears or reappears in the instantaneous disappearance event. Reproduced from Bertenthal, B.I., Longo, M.R., Kenny, S., 2007. Phenomenal permanence and the development of predictive tracking. Child Dev. 78, 350–363, with permission from Blackwell Publishing.

Imploding object was contradicted by their recent visual experience, and as a consequence their predictive tracking improved over the course of the trials. This last finding is important because it suggests that even young infants can learn from brief experiences, and thus the possibility of unintentionally teaching them during an experiment needs to be considered when testing includes multiple trials.

Embodied Knowledge

Infants do not necessarily represent the identities and spatial locations of moving objects at the same age they represent the trajectories. Even 9-month-old infants sometimes fail to notice a change in the identity (eg, shape, color) of a moving object following a brief occlusion. (Interestingly, this finding is as true for adults as it is for infants because the same spatiotemporal information specifying the continuity of an object can sometimes obscure a change in its featural identity—a phenomenon known as change blindness.) Likewise, infants around the same age sometimes fail to represent the spatial location of a moving object during a brief occlusion. For example, 9-month-old infants can predictively reach for a briefly occluded moving object. If the object does not reappear, infants search in a variety of locations but do not search behind the occluding screen, suggesting that they do not represent the spatial location of the hidden object at the same time that they represent its trajectory. In sum, infants developing representations of objects emerge piecemeal rather than all at once.

In this section, we have emphasized prospective control of smooth pursuit and visually directed reaching, but there are many other examples of prospective control that develop within the first year. For example, infants learn to posturally compensate for a loss of balance, lean toward objects that are out of reach, anticipate the size, shape, and orientation of objects that they are attempting to grasp, and guide their locomotion around obstacles. It is often suggested that infants become successful across all these tasks as they develop the capacity to represent future events. This interpretation is partially correct, but it is not the whole story.

Knowledge of the future is embodied in the specific actions performed by infants. Prospective control depends upon the developing coordination and control of multiple body parts that are continuing to change in size, shape, flexibility, and strength in conjunction with the perceptual and cognitive information necessary to forecast future events and plan adaptive actions. Thus, future-oriented behaviors emerge piecemeal from specific experiences that infants encounter through their actions. It is the dynamic interplay between actions and goals in specific contexts and tasks that fosters the development of prospective control.

Perception and Action are Context Specific

As previously discussed, actions are a product of a multiplicity of factors including physical, physiological, and energetic components. Different tasks and contexts make different demands on these components, and thus the same action will not necessarily be observed in different contexts. For example, some neurologists report that pre-reaching movements by neonates are much better coordinated when the head is stabilized than when it is unsupported. This finding is especially important because it illustrates how passive support from the environment can interact with the active control and coordination of body movements.

Coordination of Leg Movements

One of the best examples of context specificity in the control and coordination of actions involves the alternating step-like movements of neonates when held upright with the balls of their feet touching a flat surface. Within a few months, these movements disappear when infants are held upright, but not when infants are lying on their backs or stomachs. These differences can be explained by a simple biomechanical calculation showing that more energy is needed to lift a leg to full flexion while upright than while supine. Although gravity is a constant force in the environment, it only becomes a constraint after the newborn period when infants begin experiencing rapid weight gains that decrease the ratio of muscle to subcutaneous fat in the legs. Experimental manipulations that change the weight of the legs or the resistance of the legs to flexion (eg, submerging infants in torso-deep water) show that the presence or absence of stepping is systematically related to the interaction between physical strength and leg resistance. These experimental manipulations highlight the importance of context in determining whether or not a specific action will be observed at a particular age.

The development of reaching in different postures is another example of the context specificity of motor control. Coordinated reaching is only possible in the context of a stable body posture that also enables stabilizing the visual target. When infants not capable of sitting without support (22–26 weeks of age) are placed in a fully supported posture (eg, supine or reclined), they tend to reach for objects with both hands. By contrast, infants capable of sitting without support (28–38 weeks of age) reach with one hand, regardless of body posture. The key finding here is that younger infants reach with only one hand when placed in an unsupported seated position, because they must compensate for a loss of balance by recruiting the other hand to help stabilize their body in this position. In this context, infants shift to a different response because the demands on balance are different, not because they have undergone a change in neural or muscular control.
Scaling Perceptual Information to Motor Responses

Another reason for the importance of context specificity is that successful performance requires scaling the changing perceptual information to a specific motor response. The scaling learned in one context does not automatically generalize to new motor responses in the same or different contexts. This lack of generalizability explains why crawling infants who have learned whether or not it is safe to traverse surfaces that are sloped at different angles are unable to transfer this learning a few months later to walking down these same surfaces. As a consequence, infants must relearn whether or not it is safe to traverse these surfaces when walking as opposed to crawling.

This same lack of generalizability is observed with regard to using visual information to control posture. In adults, posture is specified by proprioceptive, vestibular, and visual flow information. It is a goal-directed behavior, even though it is typically not consciously controlled. The goal is to maintain a stable body posture relative to some frame of reference usually specified by gravity and the surface of support. When a perturbation of this position is sensed, a postural compensation is initiated. This perturbation can be specified by one or more sensory inputs, such as visual motion, which is sufficient to induce a postural compensation. When an observer sways forward, visual information radially expands in the optic array, and this expansion typically leads to an automatic postural compensation in the opposite direction. Likewise, swaying backward results in visual information radially contracting and inducing a compensation in the opposite direction.

Some postural compensations are even elicited by neonates. When reclined newborn infants are stimulated by radially expanding patterns of visual information observed on video monitors, they show sensitivity to this information by pushing back with their heads. These compensations are detected by a pressure transducer and are scaled to the speed and direction of the visual motion. In other words, infants apply more backward force to their heads as the visual motion information is perceived as moving faster. Although this finding suggests that infants are already sensitive to optical flow information for controlling posture at birth, it is still necessary for them to learn how to compensate to visual motion information for controlling other postures, such as sitting and standing.

A good deal of the research on the development of postural control has involved a “moving room” (see Fig. 5). In this paradigm, the infant sits or stands on a stationary floor while the walls and ceiling move forward and backward. This movement produces visual flow information congruent with the head and body moving in the opposite direction, and induces a compensation of the infant’s posture. Sitting infants begin to show compensations at 7 to 9 months of age, a period that straddles the development of this posture. During this period infants show improvements in the speed and consistency of these compensations suggesting that some period of time is necessary to learn to regulate the amount of force necessary to compensate for the perceived displacement. Similarly, infants begin to show compensations while standing between 12 and 15 months of age, but these compensations are not present immediately with the development of independent stance. Some period of learning to scale the new response synergies to the optical flow information is required before infants show the ability to maintain their balance when perturbed by the moving room. In sum, infants must learn to modulate or control each new motor response de novo, even if the perceptual information (e.g., optical flow for specifying postural sway) is readily detected and processed.

Development of Reaching in the Light and Dark

Before concluding this section, there is one important caveat that should be discussed. Context specificity is important only if the changes contribute to the assembly of the action. At face value, this point is obvious, but there are many nonobvious examples in
development. Consider, for example, young infants reaching for objects in the light or the dark. Historically, the prevailing view has been that reaching is initially visually guided, but more recent studies show that infants reach as accurately in the dark for sounding or glowing objects as they reach in the light for the same objects.

In one longitudinal study testing infants between 6 and 25 weeks of age, infants first contacted the object in both conditions at comparable ages (light—12.3 weeks; dark—11.9 weeks), and they first grasped the object in the light at 16.0 weeks and in the dark at 14.7 weeks. Infants could not see their hands or arms in the dark suggesting that proprioceptive information was sufficient to guide reaching. Additional studies reveal that there are no differences in the reaching of young infants in the light and dark even when more precise kinematic measures (speed, number of movement units, straightness, etc.) are used.

By contrast, adults and even 15-month-old infants show significant differences when reaching in the light and dark. These differences are most likely attributable to the specificity of the reaches. Whereas adults and 15-month-old infants scale their reaching and grasping to the size and shape of the object, infants, just beginning to reach, apply the same undifferentiated response to all objects. Thus, contextual differences relating to the ability to see the arm and hand do not affect the reaching behavior of young infants because scaling the reach and grasp to match the size and orientation of the object is not yet integrated into the organization of this behavior.

Action Understanding

The perception and understanding of others' actions is foundational to how we communicate, learn about the social and physical world, regulate emotions, and develop attachments with others. By 5–6 months of age we see, or learn to see, others behaviors not as mere movements but as object-directed actions, and gradually appreciate that these actions are mediated by mental states (e.g., intentions, desires, beliefs). Unlike physical objects and events, mental states are not directly perceived, and therefore require additional levels of processing. One interpretation for this accomplishment is that it must await the development of higher-level cognitive skills necessary for conceptual inferences. It is difficult, however, to reconcile this interpretation with the precocious understanding displayed by infants. Accordingly, more recent interpretations have sought to identify mechanisms that would be available at younger ages. A number of these interpretations focus on the links that exist between the perception and execution of actions.

Common Coding of the Observation and Execution of Actions

Recent neurophysiological, neuroimaging, and behavioral evidence suggest that perception and action share a common representation or code for the observation and execution of actions. This common code implies that visual percepts of observed actions are mapped directly to our motor representation of the same action. As a consequence, an action is understood when its observation leads to simulation (i.e., representing the responses of others by covertly generating similar responses in oneself) by the motor system. Thus, when we observe a hand grasping a glass, the same neural circuit that plans or executes this goal-directed action becomes active in our own brain. Critically, the flow of information between perception and action enables more than an appreciation of the surface properties of the perceived actions. Actions are represented by the motor brain at multiple levels from muscle synergies to movement trajectories to the goals or effects of the movements. The activation of a motor representation enables an appreciation of the means (i.e., how the body parts are arranged to move) by which the action is executed as well as an appreciation of the goal or the effects of the action. During the performance of an action, the motor representation guides its execution, whereas during the observation of an action, the motor representation results in a mental simulation of the movement and its goal.

Although this theory for explaining how we understand actions dates back to the 1890s and the ideomotor theory of William James (1842–1910), direct neural evidence supporting this view emerged only recently with the discovery of mirror neurons in the ventral premotor cortex of the monkey's brain. These neurons discharge when the monkey performs a goal-directed action, as well as when the monkey observes a human or conspecific perform the same or a similar action. Thus, these neurons provide a common internal representation for executing and observing goal-directed action. Human neuroimaging and transcranial magnetic stimulation studies have shown activation of a homologous frontoparietal circuit in the brain during both the observation as well as the imitation of actions.

This neurological complement is furthered by recent behavioral evidence showing that the observation of actions facilitates or primes responding to similar actions. For example, people automatically and unconsciously mimic each others' gestures when they are casually talking to each other. At least in some situations, this mimicry is associated with liking or wanting to affiliate with the social partner. Also, people tend to respond more quickly to a stimulus when the response involves imitation as opposed to some arbitrary action. For example, participants respond more quickly to a hand opening or closing or to an index or middle finger tapping down when the response topographically matches the stimulus, and respond more slowly when the stimulus and the response do not match. Critically, this facilitation between the perception and execution of an action is most likely to occur when the action is already stored within the observer's motor repertoire. If, for example, an observer who is not a musician watches someone playing a violin, then the observed actions will not be mapped to an analogous motor representation because such a representation has not yet been developed in the observer. In this case, neither covert nor overt imitation of the violin player's actions will occur while watching the musician perform.
Taken together, this evidence suggests specialized processes in the human adult brain for mapping perceived actions to the motor system. Recent research measuring neural responses in infants suggests similar patterns of activation when they execute or observe goal-directed responses. It is currently hotly debated whether these findings are consistent with the human brain evolving to include a mirroring network for the observation and execution of action or whether this shared representation is the outcome of associative learning in early development. Either way, this mapping would present one mechanism by which infants could understand and predict others' goal-directed actions.

**Infants' Understanding of Goal-Directed Actions**

Some of the first evidence showing that infants' could perceive the goals and not just the physical movements of others' actions was based on looking time experiments. When infants were familiarized to a goal-directed action, such as reaching for a toy, their looking time to the event decreased over trials. Looking time increased when the goal was changed, but not when the reach trajectory changed suggesting that their representation of others' actions was structured by the relation between the agent and her goal. By 9–12 months of age, infants' looking times in similar experimental paradigms as well as their social responses in naturalistic and experimental contexts suggest that they understand others' intentions in acting. Furthermore, infants' begin pointing to absent or experientially defined referents making it clear that they understand that pointing is not simply a cue for attracting another's attention to a specific object, but instead is a means to orient them mentally to some shared representation. Infants also begin to show comprehension of pointing which requires more than merely following the direction of a pointing gesture, but instead understanding the communicative intent of the actor.

Converging evidence for infants' understanding of goal-directed actions is provided by eye tracking studies demonstrating that infants can anticipate the goal or the effect of an action. When adults perform a goal-directed action their eyes precede their hands in moving toward the goal. Likewise, when observing someone else perform a goal-directed action, the eyes move to the goal before the agent completes the action. In one of the first studies to test this behavior in infants, 12-month-old infants showed similar anticipatory eye movements when observing goal-directed actions (ie, placing objects in a container) performed by a human agent, but not when observing a “mechanical motion” event in which the objects moved without the intervention of a human agent. This latter result revealing differences between the observation of human actions and mechanical events is but one of a number of similar findings suggesting that the mapping between the observation and simulation of actions is restricted to the perception of human actions (but see later section on matching of non-human actions for a different interpretation).

Although early evidence suggested that infants' goal prediction of others' actions did not emerge until a year of age, more recent findings suggest that the goal prediction associated with direct reaching for a visible object emerges by 6 months of age. One rational interpretation for these discrepant findings is that infants' action understanding is linked to their motor experience. Whereas 6-month-old infants are already motorically capable of reaching for an object, they are not capable of placing an object in a container. This difference in motor experience could explain why infants' goal prediction does not emerge at one specific age, but rather emerges gradually as a function of the complexity and difficulty of the goal-directed action. Recall that an observation-execution matching system that involves the successful simulation of an observed action depends on the development of a corresponding motor representation. Consistent with this generalization are findings demonstrating that infants younger than 15 months of age are not very proficient when trying to press a small button with a single finger because they are unable to modulate the speed of their movement. Likewise, these infants are unable to predict from observing the velocity of a reaching hand with extended finger whether the target is a large or small button. Similar findings are observed when looking time measures have been employed. As we previously discussed, infants interpret actions as goal directed by 5–6 months of age, which is roughly the same age at which they begin to successfully reach for distal objects. For similar reasons, 9-month-old infants who understand the referent of a point are likely to also be able to point at distal objects. At 10 months of age, infants who are capable of pulling a cloth to retrieve a toy are more likely to understand the means-end structure of this hierarchical action.

**Experimental Manipulation of Motor Experience**

One problem with these findings suggesting that motor experience contributes to action understanding is that they are all correlative, and thus it is possible that some third variable could be responsible for the synchronous development of the motor response and its understanding by infants. One solution to this problem is to experimentally manipulate motor experience. This was accomplished in a fascinating study that fabricated Velcro-covered “sticky” mittens for 3-month-old infants. Although by this age infants are capable of extending their hands and arms and sometimes contacting objects, the objects are not grasped. Velcro-covered mittens constituted a “game changer” for infants because then they were able to apprehend Velcro-taped objects in their field of view. When infants were given experience with these sticky mittens prior to testing them for their understanding of the relation between an agent and her goal, they preferred looking at a novel goal as opposed to a novel means (arm movement to a different location) after being familiarized to a goal-directed action. Critically, infants who observed an adult wearing a Velcro-covered mitten reach and
approaching objects during the training phase, did not show any preference for the new goal or new location on the test trials suggesting that they did not understand the relation between the agent and her goal.

Although these findings represent an important step in the right direction, they were not conclusive because motor experience necessarily involves associated visual experience which might be different than the passive observational experience provided to the control group of infants. This difference between active and passive visual attention is readily appreciated by all of us when driving a motor vehicle to a destination as opposed to being a passenger in that same vehicle. One gallant attempt to resolve this ambiguity was to employ a “yoked design” in which 3-month-old infants in the observational condition received training that was matched to the experience of the infants in the active condition. This design would presumably equate the visual experiences of the infants in the active and passive conditions, but the infants in the passive condition were still deprived of correlated visual-motor experiences which is necessary for the development of spatially coordinated behaviors. Further reservations about these findings were revealed by a follow-up experiment in which the training objects differed from the test objects. Unlike the findings from previous experiments, 3-month-old infants did not selectively prefer the new or the old goal events suggesting that they had not encoded the agent–goal relation. It thus appears that the visuomotor experience that contributes to action understanding is very specific, at least at young ages, and highlights the reciprocal role of visual attention and motor performance. In related research, two- to 3-month-old infants were given much more experience playing with blocks while wearing sticky mittens (ie, 2 h of object directed training over a 2 week period) and this training resulted in improved reaching behavior as well as changes in their visual exploration of agents and objects. Infants who watched their parents playing with the blocks for an equivalent amount of time did not show much of a change in manual or visual behaviors. These latter findings further support our claim that visual attention and motor performance are reciprocally related.

As infants continue to develop beyond the first few months, their visual attention becomes more selective and more often guided by their own goals and intentions. Early on, infants’ orienting to stimuli in the environment is primarily under exogenous stimulus-driven control, but gradually they begin to also develop endogenous control over their attention. This means that attention is no longer governed merely by object salience, such as a face-like stimulus or a moving or sounding toy. Instead, infants begin modulating their attention in response to the actions of their social partner as well as the context. Indeed, this is exactly what is necessary for infants to distribute their attention between a social partner and the referent of their gesture or gaze. By learning how to modulate attention, infants become better tuned to the critical information communicated by the actions and social cues of social partner. This is why even at 6 months of age infants show predictive looks to the mouth when observing a person grasp a cup and to the ear when they see someone pick up a phone. In this case, it is unlikely that motor experience is responsible for infants’ goal predictions, but rather it is the repetitiveness and consistency of these events that enable infants to begin learning the statistical regularities that will guide their attention and predictive gaze.

**Coding Goals Versus Movements**

In theorizing how motor experience contributes to action understanding, it is important to consider that actions are represented at multiple, hierarchically-nested levels ranging from specific muscle synergies to more abstract distal goals. It is often assumed that the mapping between observed and executed actions occurs exclusively at the level of the goal or the effects of the action. Most of the research with infants assume that they code actions at this same level of analysis, because goals can be represented more abstractly than movements, and thus infants can generalize their representations more readily to others’ goal-directed actions even if the specific movements vary.

In spite of the attractiveness of the preceding logic, we wish to caution against dismissing the importance of movements, per se, in mapping the observation of actions to their execution. Giacomo Rizzolatti (1937–) and his colleagues who discovered mirror neurons speculate that there may be two distinct resonance mechanisms in humans: a high-level resonance mechanism coding actions in terms of goals, and a low-level resonance mechanism coding the movements of an action. An example of this low level mechanism in humans involves recording motor evoked potentials from arm muscles while participants observe a hand reaching and grasping an object. The recorded motor potentials from the participants vary systematically with the changing size of the finger aperture as the hand approaches the object. As such, this finding is consistent with the motor representation coding the manner in which the action is performed over time rather coding its goal or end state.

Some of the best evidence for this low-level resonance mechanism in infants comes from observing their perseverative search errors. In the classic, Piagetian A-not-B error, 8- to 12-month-old infants first search correctly for an object they see hidden in one location (A-location) on one or more trials, but then continue to search at that same location after seeing the object hidden in a new location (B-location). Recent accounts of this error emphasize the role of repeated reaching to the initial location biasing infants to continue reaching to the same location even when no longer correct. If infants are capable of mapping observed movements to their motor representations, then they should commit the same search error even when they only observe someone else finding the object on the initial A-trials. Interestingly, this prediction has been repeatedly confirmed with 9-month-old infants, but only if the experimenter who recovers the hidden object on the A-trials reaches with his ipsilateral hand (ie, the hand on the same side of the body as the object).

Why should infants be more likely to covertly imitate or simulate the actions associated with an ipsilateral than a contralateral reach (ie, the hand crosses the body midline when reaching for an object)? One likely reason for this finding is that infants begin to reach contralaterally about 2–3 months later than they begin to reach ipsilaterally, which starts around 4–5 months of age. This
developmental lag translates to infants’ showing a bias to reach ipsilaterally throughout their first year and results in a less developed motor representation when tested for the search error at 9 months of age. Some support for this interpretation comes from a training study where 9-month-old infants were familiarized with an experimenter reaching repeatedly for toys with only his contralateral hand, and then searching for the hidden toy on the A-trials of the search task with only his contralateral hand. Unlike the results from previous studies, infants searched in the incorrect location even though contralateral reaching was observed. In a follow-up experiment, a new group of infants was tested following familiarization with ipsilateral reaching. Even though the goal was the same in this new condition, infants did not search significantly more often than chance at the incorrect location. Critically, the goal which is to recover the hidden object remains the same in both conditions. It thus appears that encoding the goal of the reaching action cannot explain these differential results. Instead, focusing infants’ attention on the movement increases the likelihood that the action will be covertly imitated.

Additional findings testing infants’ goal predictions following ipsilateral and contralateral reaches suggests an advantage for predicting ipsilateral reaches. Infants between 6 and 12 months of age were tested with an eye tracking system while observing an actor facing them while sitting at a table and reaching either ipsilaterally or contralaterally for an object situated in front and to the side (see Movie 4). At least through 10.5 months of age infants were more likely to predict the goal on ipsilateral than contralateral trials (see Fig. 6). These infants were also tested for their likelihood of reaching ipsilaterally vs. contralaterally, and as expected the results revealed that contralateral reaching increased with age. More importantly, the likelihood of contralateral reaching covaried with the likelihood of contralateral goal prediction, even after partialling out the effects of age and ipsilateral reaching. As such, these results provide further evidence that motor experience and the development of an observation-execution matching system are related although determining whether this is a reciprocal relation or specifically a function of motor experience mediating the mapping between action observation and execution remains to be determined.

Observation-Execution Matching of Non-human Actions

Thus far the evidence shows that action observation is linked to action understanding at the level of both movements as well as goals. One unresolved issue in the literature is whether the process responsible for mapping the observation and execution of actions is limited to human actions or whether it generalizes to non-human and mechanical actions. Most of the evidence with adults suggests that the observation of robotic or mechanical actions results in less activation of the motor system, and thus at the very least a diminished neural as well as behavioral response. This result is typically interpreted as supporting the hypothesis that an observation-execution matching system is limited to actions within the motor repertoire of the observer, or that the observer codes the action at the level of its intention which cannot be attributed to a non-human agent.

According to either of these interpretations, infants should be unlikely to automatically activate a motor response when observing a non-human agent, such as a mechanical claw. Much of the evidence appears consistent with this claim, but the reason may have more to do with the unfamiliarity of the stimulus than with it being a nonhuman agent. In one series of experiments, researchers tested 9-month-old infants again in the observational version of the A-not-B search paradigm, but this time they observed only a pair of mechanical claws hiding and finding the toy (see Fig. 7). Consistent with previous findings, infants did not produce the search error when tested with the claws, but these results were “turned on their head” when infants were given 2 min to observe an experimenter demonstrating how the claws functioned prior to testing. Thus, it is currently difficult to disambiguate the root cause for infants diminished action understanding when observing non-human actions because these actions are almost invariably less familiar.
One final point about these findings should not go unnoticed. Even though infants did not actively manipulate the claws, they appeared to learn from observing the experimenter operate the claws. We suspect that at least in this situation infants' observational learning benefited from the experimenter not performing the same identical action repeatedly, but rather varying both the location of the toy as well as the hand used to retrieve it. Variation and selection from multiple examples is a well-established mechanism for facilitating learning. This variation is often overlooked when comparing active and passive experience, but infants' actions are not yet well coordinated and thus virtually any action will vary in one or more details each time it is executed. Accordingly, infants are assured to receive some variable experience when performing actions themselves, but this will be less likely when modeled by an adult unless the variation is intentional. This variation that accompanies infants' active learning during training studies could be an important factor in explaining why action understanding improves more following active as opposed to passive learning.

It is very likely that some version of a direct matching system is functional from birth. Newborn infants imitate oro-facial gestures (mouth opening and tongue protrusion), even though they've never seen their own face. The origins and developmental trajectory of this behavior are consistent with an observation–execution matching system. It is well established that fetuses perform mouth opening and closing and tongue protrusion while in utero. Thus, these gestures are already part of the neonate's behavioral repertoire at birth. The evidence also suggests that neonates are more likely to match the modeled gesture after it has been presented for some period of time (~40 s), rather than immediately. This finding is consistent with a motor simulation explanation in which activation would be expected to build up gradually as the gesture is observed, as opposed to an explanation predicting an immediate response because of the availability of higher-level processes from birth. Finally, the empirical evidence suggests that the likelihood of automatic imitation increases until around 2 months of age, and then declines and virtually disappears by 5 months of age. It is during this same window of time that neonatal reflexes are gradually inhibited, suggesting that similar cortical inhibitory processes may serve to suppress neonatal imitation.

As the spontaneous elicitation of these overt facial gestures becomes gradually inhibited with age, they do not disappear entirely. Instead they become subject to volitional control such that the infant determines when and how they are elicited—imitation is no longer automatic, and the observation of a facial gesture will not necessarily lead to its execution by the infant. Thus, rather than reflecting a precocial social ability of the infant as suggested by some theorists, neonatal imitation may reflect a striking inability of the infant to inhibit activation of the motor system by direct matching mechanisms. Similar compulsive imitation is observed in adults after lesions of areas of the frontal lobe involved in inhibitory control, and even in healthy adults when attention is diverted.

Although overt imitation of facial gestures ceases with the development of inhibition, covert imitation continues and provides some knowledge about these gestures when observed in others. Very recent evidence suggests that this same developmental process is played out at different ages for many other important behaviors (e.g., gaze cueing, visually directed reaching and grasping, vocalizations of sounds). As these behaviors are practiced, the infant develops greater control of their execution, as well as knowledge of their effects or outcomes. The development of these motor schemas enables infants to covertly simulate and predict the effects of similar actions performed by others. This reliance on the developing control of self-produced actions explains why action understanding continues to develop with motor experience.
Infants engage in goal-directed and exploratory behaviors from birth, and their actions become better coordinated as the perceptual information becomes more differentiated and mapped to more specific response synergies. In turn, the development of new and more complex responses requires greater perceptual specificity and greater prospective control. This mutuality and reciprocity between perception and action demands that the development of new behaviors is dynamic and multidetermined. In contrast to earlier views of behavioral development reflecting patterns of stability interrupted briefly by transitions to new behaviors, the development of perception and action show significant periods of variability in real and developmental time. This variability introduces new movement patterns or actions for achieving specific goals and also offers greater flexibility in adapting actions to task demands.

**Supplementary data**

Supplementary data related to this article can be found online at http://dx.doi.org/10.1016/B978-0-12-809324-5.05862-4.

Relevant Website

http://www.indiana.edu/~dcnlab/index.html – IU Developmental Cognitive Neuroscience Lab (last accessed 08.08.16.).