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11 Developmental Perspectives on Action Science: Lessons from Infant Imitation and Cognitive Neuroscience

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Introduction

Before Silicon Valley became known for computers and Stanford University, the region spawned innovations in action science. In 1882 the politician Leland Stanford asked the photographer Eadweard Muybridge to investigate a puzzle in biomechanics: do all four hooves of a galloping horse leave the ground at the same time? Muybridge's photographs showed that galloping horses were momentarily airborne, settling the dispute about "unsupported transit."

Muybridge was obsessed with action. In *Descriptive Zoopraxography, or The Science of Animal Locomotion* (1893), Muybridge developed technology that was the forerunner of today's motion pictures. In *The Human Figure in Motion* (1901), he provided a "dictionary of human action." The history of developmental psychology and action science might have been different if Muybridge had turned his genius to documenting action learning and development.

Thirty years after Muybridge, Jean Piaget began his classic studies of action from a developmental perspective. Piaget's theory of cognitive development was built on two pillars: the action assumption and the invisibility assumption. The action assumption holds that all knowledge is rooted in action, and the two are inseparable in infancy: to know an object is to use it, and the acquisition of new knowledge requires motor exploration. Preverbal infants are confined to "knowing how," not "knowing that." The corollary, the invisibility assumption, proposes that when young infants lose sensory and motor contact with an object, the object ceases to exist for them (the Piagetian problem of "object permanence").

Modern developmental scientists have reexamined Piaget's theory of infant action and cognition. Using the technology spawned by Muybridge (digital video-recordings), there is now an emerging developmental science of action. This field examines many of the phenomena highlighted by Piaget: reaching and grasping, play, and imitation. Although contemporary developmental science shares Piaget's conviction that action is central to infancy, the prevailing ideas are no longer strictly Piagetian. Nowhere is this more evident than in the topic of the imitation of action.

Piaget defined imitation in a commonsense way: one person reproducing the acts of another. A problem, however, is that such duplication may occur by chance. We adopt a more technical definition following Meltzoff (2005): "Imitation occurs when three conditions are met: (a) the observer produces behavior similar to that of the model, (b) the perception of an act causes the observer's response, and (c) the equivalence between the acts of self and other plays a role in generating the response." Equivalence need not be registered at a conscious level, but if it is not used at any level in the system (neurally, cognitively, computationally), it is judicious to describe the behavioral correspondence using some other term than "imitation."

This chapter provides a developmental perspective on action representation, using imitation as a focal point. The study of imitation is a burgeoning area and has attracted interest from diverse interdisciplinary fields including developmental science, experimental psychology, cognitive neuroscience, robotics, evolutionary biology, and the philosophy of action (e.g., Dautenhahn & Nehaniv, 2002; Hurley & Chater, 2005; Meltzoff & Prinz, 2002; Meltzoff, Kuhl, Movellan & Sejnowski, 2009). The study of imitation helps to elucidate the psychological and neural mechanisms connecting action perception and production and sheds light on the social-cognitive functions and consequences of such connectivity.

We consider seven interrelated themes. First, we analyze Piaget's view of action development with respect to imitation. Second, we review discoveries about neonatal imitation and deferred imitation (imitation from memory). The theory is developed that humans, starting from infancy, have a "supramodal representation" of human action that undergirds imitation. Third, we show that children's imitation is not rote but flexible and selective in surprising ways. Fourth, we discuss young children's ability to reenact inferred goals, rules, and strategies underlying visible behavior. Fifth, we review studies demonstrating that action imitation is not an uncontrollable impulse but can be regulated by top-down control. Sixth, we highlight that young children are emotionally engaged by being imitated. The mechanisms involved in imitation are bidirectional, supporting both the generation of imitative action and the recognition of being imitated by others, with deep consequences for social development. Finally, we consider imitation from a neuroscience viewpoint. There is interest in how to connect behavioral imitation to the work on neural mirroring systems. We examine potential links and also discuss pitfalls in overinterpretations. The most relevant neuroscience work in infants derives from newly emerging studies using the electroencephalogram (EEG), with a focus on developmental aspects of the mu rhythm, and we analyze these studies.

Piaget's Stages of Imitation as Windows into Action Development

Piaget's (1962) theory postulates six stages of action imitation between 0 and 24 months of age, which can be grouped into three broader levels.

At level 1 (0–12 months, encompassing stages 1–3) infants are thought to be restricted to imitating simple vocal and manual maneuvers such as hand opening or finger movements. The key to such imitation, according to Piaget, is that infants can perceive both the adult's model and their own responses through the same perceptual modality. For example, manual imitation can be guided visually through within-modality pattern matching. The adult's acts can be compared directly or "assimilated" to the infant's.

At level 2 (12–18 months, encompassing stages 4–5) infants go beyond within-modality comparisons. The landmark development in level 2 is the imitation of facial gestures at approximately one year. Although the infant can see an adult's face, he cannot see his own. Piaget referred to facial imitation as "invisible imitation" and regarded it as a sophisticated achievement drawing on cognitive resources that are not available to younger infants.

At level 3 (18–24 months, encompassing stage 6) infants first become capable of "deferred imitation," that is, imitation from memory. According to Piaget, deferred imitation emerges synchronously with other complex cognitive abilities such as symbolic play, insightful problem solving, and high-level object permanence.

Theoretical Challenge Posed by Facial Imitation: Implications for Action Science

Piaget's theory of cognitive development dominated developmental science for 50 years. Research using experimental methods has emerged to test his predictions, which were based on case studies of his own three children. This newer research does not support the stagelike emergence of action imitation that Piaget envisioned.

A significant piece of evidence against Piaget's stage-developmental model comes from studies with human neonates. Meltzoff and Moore

(1977) reported that 12- to 21-day-old infants were able to imitate facial gestures such as tongue protrusion. Although the results first came as a surprise, the findings have now been replicated in more than two dozen experiments (Meltzoff & Moore, 1997). Researchers are now exploring the psychological and neural mechanisms underlying this behavior and the functions that imitation serves.

Ruling Out Alternative Explanations for Neonatal Imitation

Crucial controls were included in the tests of early facial imitation to exclude low-level explanations. One concern is that infants might be more aroused when they see an adult act, and therefore increase their general activity, including their facial movements. The specificity of the responses rules out this explanation. Infants respond differentially when the same face, at the same distance, moving at the same rate, performs two closely matched gestures (e.g., tongue protrusion versus lip protrusion). Moreover, studies since 1977 have shown that infants differently imitate two different types of tongue protrusion—ordinary tongue protrusion versus tongue protrusion to the side (Meltzoff & Moore, 1994, 1997). An arousal interpretation cannot account for such response specificity. Nor can arousal account for the range of gestures that have been documented, including lip, tongue, head, and manual actions (see Meltzoff & Moore, 1997, for a review).

What about associative learning? Might infants learn to associate the oral movements they see with their own oral movements through experience with feeding or parental imitation of the children's own behavior? Piaget carefully analyzed associationism as an account of imitation and identified several logical and empirical shortcomings of this view.[1] As a more direct test, Meltzoff and Moore conducted two studies using newborns who were still in the hospital after birth. One study found imitation of mouth opening and tongue protrusion (Meltzoff & Moore, 1983); the other found imitation of head movements (Meltzoff & Moore, 1989). The mean age of the participants in these studies was 36 hours old; the youngest was only 42 minutes old. This renders associative learning induced by adult imitation of the child an unlikely basis. Of course, associative learning may occur in older infants, but it is not a necessary precursor for imitation to occur in the first place.

Temporal Flexibility and Response Correction: Evidence for a Closed-Loop System

If arousal and learned associations cannot account for the early matching responses, what other explanatory mechanisms can we turn to, and what are the implications for action science? One possibility is rooted in Gibson's theory of perceptual-motor resonance. Gibson (1966, 1979) developed the notion of resonance, drawing on the analogy of two tuning forks. Meltzoff and Moore (1977) wondered whether neonatal imitation might be explained by such Gibsonian resonance. This led to an experiment in which neonates had a pacifier in their mouths while observing an adult's action. After the infant observed the adult action, the adult stopped gesturing, assumed a passive face, and only then removed the pacifier. Despite having direct resonance blocked by the pacifier—even engaging in alternative activity (sucking)—infants imitated (Meltzoff & Moore, 1977, experiment 2). Subsequent studies also reported temporal gaps between the stimulus and the response (Fontaine, 1984; Heimann, Nelson & Schaller, 1989; Heimann & Schaller, 1985; Legerstee, 1991; Meltzoff & Moore, 1994). Matching through perceptual resonance probably occurs in infants and adults, but neither is restricted to it.

Beyond the raw existence of early imitation, the most important discovery for action science concerns the organization of the response. Empirical evidence from several independent laboratories shows that the infants' first imitative responses are not complete reproductions of the adult's (Abravanel & Sigafoos, 1984; Heimann, Nelson & Schaller, 1989; Meltzoff & Moore, 1977, 1983). A microanalysis of the response reveals that infants gradually correct their imitative attempts over time in a sequence of ordered steps (Meltzoff & Moore, 1994). Our interpretation is that infant imitation is organized by the goal of matching the adult's target, which is compatible with other findings of primitive goal-directedness in the actions of infants (Butterworth & Hopkins, 1988; von Hofsten, 2007).

A Psychological Mechanism for Imitation: AIM Hypothesis and Body Babbling

Meltzoff and Moore (1977, 1997) proposed that imitation is based on active intermodal mapping (AIM). The core idea is that infant imitation is rooted in infants' capacity to register equivalences between the bodily transformations performed by others and the body transformations the infants feel themselves make. In this account, facial imitation involves cross-modal equivalences. The infants' own facial gestures are invisible to them, but they are not unperceived: infants monitor their unseen motor acts through proprioception. Meltzoff and Moore postulated that infants link perception and production through a "supramodal" coding of human acts. This may explain why infants can correct their imitative movements and imitate from memory: infants store a representation of the adult's act and recursively compare their own imitative efforts against this stored representation. That is what we mean when we say that early imitation involves an "active" component (AIM) and is goal directed.

Body Babbling and Self-Experience

We argue that infants' own motor experience plays a role in early facial imitation. Films of fetal behavior reveal repeated lip, tongue, and hand movements *in utero* (e.g., de Vries, Visser & Prechtl, 1985; Zoia et al., 2007). This self-generated activity continues after birth. Meltzoff and Moore (1997) characterized these movements as "body babbling" and proposed that such motor activity plays a role in action imitation, analogous to the role that vocal babbling plays in speech production (Kuhl & Meltzoff, 1982, 1996).

Tongues move in certain ways, and these ways are very different from the action patterns of hinged joints such as in fingers and elbows. Based on self-experience with the felt movements of one's own body, the kinetic signatures of another person's tongue protrusion and withdrawal (or mouth opening and closing, or finger flexing) could be recognized as cross-modally equivalent to those produced by oneself. A more detailed computational model specifying the "metric of equivalence" that infants use to achieve facial imitation is described elsewhere (Meltzoff & Moore, 1997). This model provides our explanation of what is sometimes referred to as the "correspondence problem" (how the imitator matches perception and production).

Characterizing the Supramodal Action System: Differentiating My Acts from Yours

The ideas about a supramodal representation of human action can be developed further, and a critical point concerns the differentiation between actions performed by the self and observed in others. One possibility might be that the supramodal system is simply a translation device for turning visual perceptions into motor output: a perception-production transducer. There are three reasons to think that we need a more differentiated notion than this, both in adults and in preverbal infants.

First, the observed actions can be remembered and imitated at a later time (the temporal gap studies). These findings suggest that there is a stored representation of the observed act, which allows infants (and adults) to imitate after a temporal delay and after performing intervening motor activity. Second, the imitative acts are corrected to achieve a more faithful match, and this correction can occur after the demonstration of the target act has stopped and is no longer visible. Thus information from one's acts must be available for comparison to the stored representation of the target act. Third, infants show interest in being imitated themselves, and they recognize when their facial and manual behavior is being copied. Such recognition implies that infants store a representation of their own bodily actions (even if those actions are invisible to them).

Taken together, these three facts suggest a differentiation in the supramodal system. The representation derived from observing the other person's actions is separable from the representation of one's own bodily actions. Successful imitation involves comparing the two. Theories that suppose no distinction—a merging or lack of differentiation between the actions of self and other—cannot easily account for these facts (for further analysis of the mechanism of imitation, see Meltzoff & Moore, 1997, pp. 185–187).

Learning and Memory for Actions on Objects: Instrumental Imitation

Over and above the imitation of gestures, human beings imitate acts they see others perform on objects. Before language becomes available to the child, imitation is a chief mechanism by which they learn about tool use and acquire causal knowledge about how novel objects and machines work. This "instrumental imitation" continues to play such a role in adults: how to tie a knot, build a fire, or use a lever is more efficiently learned through studying others' behavior than via an instruction manual or a linguistic narrative.

In imitation involving objects, immediate responding is often not possible. There may be only one object, and the child may not have access to it during the time that the expert is demonstrating what to do. Children often watch adults' object manipulations and imitate at a later time when granted access to the object or tool. Such "deferred imitation" goes beyond immediate perception-production coupling and constitutes an important aspect of human learning. From the point of view of action science, deferred imitation also provides a way of exploring the memory and representation of action.

In using deferred imitation to investigate memory for actions, it is crucial to distinguish between (a) forming a representation of an act from observation alone, and (b) retaining one's own already executed behavior (or motor habit) over time. At stake is whether an action has to have been initially executed to be retained over long intervals.

This distinction has been addressed using the "observation only" design in deferred imitation (Meltzoff, 1995b). In this design, children are shown target acts on objects but are not allowed to touch or handle the objects. After a delay, children are allowed to manipulate the objects for the first time. Control groups are used to evaluate the spontaneous manipulations of children at this age. Infants in the second year succeed in imitating after delays as long as four months using the observation-only procedure (Meltzoff, 1995b). Deferred imitation of actions on objects has been documented in infants as young as 6 to 12 months (Barr, Dowden & Hayne, 1996; Klein & Meltzoff, 1999; Meltzoff, 1988b), which runs against the Piagetian stage-developmental model.

Importantly, infants can also perform deferred imitation of completely novel acts on objects. In one experiment, Meltzoff (1988a) discovered that infants would imitate a novel act such as leaning forward to touch a box with their forehead so as to turn on a light. The experiment was set up so that the infants carefully observed the novel act without distractions. After a one-week delay, infants were presented again with the box, and the results showed successful imitation of the head-touch act. These results are based on imitation, because the object's properties alone did not elicit the response in control infants (who were given the box but did not see the relevant action demonstration). Such deferred imitation using the observation-only design established that infants can generate a novel act based on a stored memory of a perceptually absent act they saw in the past.

The organization of the deferred response illuminates issues about action representation. The deferred-imitation response is not a trial-and-error process in which children run through a variety of acts, eventually recognizing the one that was used with a particular object. The target act is essentially the *first* act that infants do with the object after the delay (Meltzoff, 1988a). Infants rarely confused which act to perform on an object despite having seen a series of different acts on a variety of objects. This accuracy suggests an object-organized representational system. Infants do not represent the observed actions alone; the stored representation includes the object together with the act performed on it.

Outcomes, Hierarchies, Causal Results, and Overimitation

As we have seen, young children imitate actions without objects, such as facial gestures, and they also imitate object manipulations that are more instrumental in nature. This has led researchers to compare the two. Several studies have shown that young children are more likely to imitate behaviors that cause salient physical outcomes than behaviors that do not (e.g., body movements alone) (Brugger, Lariviere, Mumme & Bushnell, 2007; Hauf, Elsner & Aschersleben, 2004). Young children also take into account the adult's success in attaining a goal in determining whether and what to imitate (Meltzoff, 2007b; Nielsen, 2006; Schulz, Hooppell & Jenkins, 2008; Want & Harris, 2001; Williamson & Meltzoff, 2011; Williamson, Meltzoff & Markman, 2008).

Bekkering, Wohlschläger, and Gattis (2000) noted that children selectively imitate different aspects of what they see, and proposed that this may be due to their representing actions in terms of a hierarchy of goals. When presented actions to imitate, three- and five-year-olds reproduce those that are highest in the hierarchy. In one study, children saw an adult reach either cross-laterally (across the body) or ipsilaterally (with the arm on the same side of the body). When the adult's reach was directed at a spot on the table (Wohlschläger, Gattis & Bekkering, 2003) or at the adult's own ear (Gleissner, Meltzoff & Bekkering, 2000), children disregarded the manner of reach used and simply reached for the appropriate spot. However, when there was no obvious goal (e.g., when the same hand movement was made but there was no spot), children were more likely to reproduce the exact type of reach with high fidelity. Thus children vary what aspect of the display they imitate depending on what they identify to be the purpose of the behavior (see also Carpenter, Call & Tomasello, 2005; Loucks & Metzoff, in press).

Williamson & Markman (2006) tested a similar idea. Three-year-olds saw an adult place an object using unusual means (e.g., turning a cup over and rotating it in a two-handed grip). When there was no contextual support for this placement, children reproduced the adult's actions with great fidelity; when a context provided the reason for the placement (e.g., the cup was a nose in a face configuration), children imitated the placement but often ignored the precise movements and manner by which the adult put the object there.

Children seem to use a trade-off between reenacting the goal versus the particular actions the adult uses. If children lack a clear understanding of an overall goal or how to achieve it, it is often beneficial for children to imitate the bodily actions in more precise detail. If you imitate the details of the act with fidelity, then the outcome often comes for free—so when in doubt, imitate what the expert is doing and precisely how he or she does it.

This may partially explain a phenomenon that has been termed "over-imitation," the reproduction of actions that are not needed (from the adult's viewpoint) to reach an outcome (e.g., Horner & Whiten, 2005;

Lyons, Young & Keil, 2007; McGuigan, Whiten, Flynn & Horner, 2007; Nielsen & Tomaselli, 2010). In most studies reporting this effect, children reproduce acts that are salient and obviously purposeful by the adult (even if they are causally unnecessary), such as repeatedly banging a handle within a box. Children in these studies may be have doubts about what actions are causally necessary to achieve the demonstrated outcome.

It would be a mistake, we think, to infer from these studies that young children's imitation is always compulsive, rote, or slavish. Evidence suggests that children and adults are flexible and selective imitators who weigh information about the observed outcomes and their understanding of how to achieve them. If children understand how to use an object to reach a desired outcome (e.g., how to use object x to push object y to achieve z), they may choose to reach the same outcome (achieve z) using actions that are easier for them. If, however, they do not understand how to achieve the demonstrated outcome, or if they construe matching the adult's intentional behaviors as a goal in itself, children imitate the precise bodily actions they see with greater fidelity.

Action Interpretation and Inference: Abstracting beyond the Surface Actions

For adults, actions are not processed solely in terms of surface characteristics. Human acts also carry information about something deeper. The envelope of human actions, even the unsuccessful attempts, sometimes reveals information about the actor, including goals and intentions. Several lines of research have begun to explore young children's ability to decode human actions in this way.

Inferred Goals

Human beings are imperfect—we sometimes act in ways we do not intend. We slip; we make mistakes. These mishaps carry information about the actor and his or her goals. The behavioral reenactment procedure was designed to provide a nonverbal technique for exploring goal understanding in preverbal infants (Meltzoff, 1995a). The experimental procedure involves showing infants an unsuccessful act. For example, the adult accidentally overshoots his target, or he tries to pull apart a dumbbell-shaped toy, but his hand slips off the ends and he is unsuccessful. Thus the goal state is not achieved. The experimental question is whether children read through the literal body movements to the underlying goal of the act.

Results show that 18-month-old infants understand the goals the adult is striving to attain, even if these goals are not reached (Meltzoff, 1995a).

Infants who saw unsuccessful attempts at performing an act, and infants who saw the full act, both produced the successful goal-directed target acts at a significantly higher rate than controls (who saw the adult manipulate the object in other ways). Evidently toddlers can extract goals from the envelope of actions that unfold, even without seeing them achieved (see also Bellagamba & Tomasello, 1999; Nielsen, 2009). This interpretation is also supported by infant studies using looking-time methods (e.g., Brandone & Wellman, 2009; Gergely, 2011; Woodward, 1998) and other imitation tasks (Carpenter, Akhtar & Tomasello, 1998; Tomasello & Barton, 1994).

Abstracting Rules and Strategies from Others' Behaviors

Another inference that adults make from seeing actions concerns the rules or strategies that govern the person's behavior. We might not imitate the precise details of another's actions but instead extract and adopt the rules they follow. One important activity used in everyday life and scientific endeavors involves the categorization of objects. People often embody categorization through a set of particular actions, sorting behavior, by which they separate objects into distinct piles according to their properties.

Work by Williamson, Jaswal, and Meltzoff (2010) investigated whether 36-month-olds could learn different categorization strategies by watching the sorting behavior of another person. Children watched an adult sort objects. In one study, the adult sorted according to a visible property (color rather than shape). In a second study, she sorted by an invisible property (sounds made when shaken). In control groups, the experimenter presented a presorted array. Children who saw the adult sorting action sorted the objects (by color or sound) significantly more often than did the controls.

This illustrates the power of imitation. Children can abstract from actions the underlying rules and strategies that generated them, and then can adopt those same rules to generate their own behavior. Based on these inferences, children begin to act like the others in their culture, for example, categorizing an array of objects along the same properties as done by an expert or acting in accord with the roles and cultural norms specified by society.

Top-Down Control of Imitation

Children do not imitate compulsively or blindly; imitation has its reasons. Recent laboratory work has uncovered several top-down influences on imitation.

Social Communication, Naive Pedagogy, and Emotions

Older theories supposed that imitation was automatic, compulsory, and not subject to voluntary choice and control. Increasing evidence indicates, however, that even preverbal children regulate their imitation. In the simplest example, infants are more likely to imitate the actions of a model who engages them socially (Brugger, Lariviere, Mumme & Bushnell, 2007; Nielsen, 2006). Other studies suggest that the "mere belief" that a social agent caused an outcome yields an increase in infants' tendency to imitate it (Meltzoff, 2007b, experiment 3; see also Bonawitz et al., 2010; Meltzoff, Waismeyer & Gopnik, 2012; Thompson & Russell, 2004).

Csibra and Gergely (2006; Gergely, 2011) have suggested that multiple cues, including eye contact and "motherese" intonational patterns, set up an expectation of a pedagogical exchange. Such social cues may draw attention to the relevant aspect of the adult's demonstration and mark it as significant, thus changing the likelihood that it will be chosen for imitation (cf. Gergely, Bekkering & Király, 2002; Paulus, Hunnius, Vissers & Bekkering, 2011; Zmyj, Daum, Prinz & Aschersleben, 2007).

The emotional response that a person gives to an action also serves as a top-down controller of imitation. In one study, an adult performed a seemingly innocent act, and a second adult reacted with negative emotion (saying, "That is so irritating!") as if it were a "forbidden action." The experiment systematically manipulated whether the second adult was looking at the child when the child had a chance to imitate. Children did not imitate the forbidden action if the previously angry adult (now with a neutral face) was watching the child. If the previously angry adult left the room and could no longer visually monitor the child's action, the child would imitate (Repacholi & Meltzoff, 2007; Repacholi, Meltzoff & Olsen, 2008). This documents top-down regulation of imitation based on the expected emotional consequences of performing the action oneself.

Self-Experience

Another line of work shows that children regulate their imitation of actions depending on their own prior action experience. Williamson, Meltzoff, and Markman (2008) tested 36-month-old children to see if they were more likely to imitate another person's actions if the child's own previous experience had revealed that the task was difficult. A surreptitious resistance device made a drawer difficult to open when the child first explored it. Then the adult demonstrated a distinctive technique for opening the drawer (pressing a button on the side of the box). Children were significantly more likely to imitate the adult's distinctive act if the child had a prior difficult experience with the task. These results fit with educational philosophies asserting that self-experience confronting a problem can help the student be more open to instruction (see also Williamson & Meltzoff, 2011).

Being Imitated: Social-Emotional Consequences

Parent-child games are often reciprocal in nature, and mirroring games are a childhood favorite. What makes a child so engaged and joyful at seeing his or her own actions mirrored by an adult? Temporal contingencies are important, but so is the similarity of the *form* of the participants' actions. Research has investigated whether infants simply prefer people who are acting "just *when* they act" (temporal contingency) or whether they also prefer those who are acting "just *like* they act" (structural congruence).

To test this idea, Meltzoff (2007a) had infants sit across a table from two adults. Both adults sat passively until the infant performed one of the target actions on a predetermined list. Then both experimenters began to act in unison, but one of the adults matched the infant, while the other performed a mismatching response. The results showed that the infants looked and smiled more at the matching adult. This shows that infants are sensitive to the matching *form* of the behavior.

From a cognitive viewpoint, these findings are important because they show that the mechanisms underlying imitation are bidirectional. The machinery that takes visual input and generates a matching motor response can also run in reverse and recognize when the self's own actions are being mirrored.

From a social-emotional viewpoint, the findings are important because they show a social function of imitation. This research revealed that infants are visually engaged by, and have strong positive emotions toward, being imitated by someone else: infants smiled more at the imitator. Being imitated provides a nonverbal bond between the two actors, which may increase emotional attachment, prosocial feelings, and a sense of being understood. Adults also have positive reactions to being imitated even when they are unaware of it (Chartrand & Bargh, 1999). A special "psychological jolt" is induced by seeing one's actions mirrored. Researchers have only just begun to perform the relevant neuroscience studies on being imitated by another person. Work in this area has been carried out with adults (Decety, Chaminade, Grèzes & Meltzoff, 2002) and more recently with infants (Saby, Marshall & Meltzoff, 2012). In both cases, specific neural signatures were found for being imitated by another person.

Cognitive Neuroscience and Action Science

A comprehensive, contemporary action science requires an integration of behavioral findings, cognitive theorizing, and neuroscience data. Much of the neuroscientific study of perception-action coordination has been driven by the concept of the mirror neuron system (MNS). This originates in the discovery, using single-cell recording techniques, of neurons in the ventral premotor cortex (F5) of macaque monkeys that respond not only when a monkey carries out a particular action on an object but also when the monkey observes the same action being carried out (di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992; Rizzolatti, Fadiga, Gallese & Fogassi, 1996).

Although a good deal of evidence exists for overlaps in patterns of regional brain activity between action perception and action production in human adults (Caspers, Zilles, Laird & Eickhoff, 2010; Hari & Kujala, 2009), researchers debate the function of this overlap and its relation to the macaque MNS. We do not aim to address these controversies here. Instead we focus on developmental issues, which have sometimes been overlooked. The corpus of behavioral work on infant imitation firmly establishes that young children link action perception and production. We can infer that some (as yet unspecified) neural circuitry supports such observation-execution coordination. A pressing question is how best to characterize the origins and development of these neural processes (Marshall & Meltzoff, 2011).

EEG as a Tool in Action Science in Adults

The developmental neuroscience work on action processing has mainly employed the electroencephalogram (EEG), with a focus on the sensorimotor mu rhythm. To understand this work, it is first useful to consider results from adult studies. In adults, the mu rhythm occurs in the alpha frequency range (8–13 Hz) and is typically recorded from central electrode sites overlying motor and somatosensory cortices. Early work showed a desynchronization (reduction in amplitude) of the mu rhythm during movement (Gastaut, Dongier & Courtois, 1954), with more recent work examining the specific time course of mu activity during voluntary actions (Pfurtscheller & Lopes da Silva, 1999). Building on recent magnetoencephalography (MEG) findings (Hari et al., 1998), studies with adults have further shown that the mu rhythm is also desynchronized during the observation of others' actions (e.g., Muthukumaraswamy & Johnson, 2004; Streltsova, Berchio, Gallese & Umiltà, 2010). Taken together, these findings raise the suggestion that the mu rhythm may be informative in the study of neural mirroring mechanisms (Pineda, 2005).

Mu Rhythm and Action Processing in Infancy

There is an explosion of interest in elucidating the properties of the mu rhythm in infancy (for a review, see Marshall & Meltzoff, 2011). A number of studies of the infant mu rhythm in relation to action processing have restricted their testing only to action observation conditions, without including action production conditions (Nyström, 2008; Nyström, Ljunghammar, Rosander & von Hofsten, 2011; Reid, Striano & Iacoboni, 2011; van Elk, van Schie, Hunnius, Vesper & Bekkering, 2008). These studies provided useful information, although without an action production condition, the implications for mirroring processes remain limited.

Two teams have used infant EEG to examine perception-production overlaps more directly. Southgate, Johnson, Osborne, and Csibra (2009) examined EEG responses in nine-month-olds who were reaching for and grasping a small toy. Relative to a baseline epoch, there was a significant desynchronization in the alpha frequency range at central-parietal sites during the infants' reaches. Power in a similar frequency range was also found to be reduced relative to baseline when infants viewed a human hand reaching for and grasping an object. In a second study of nine-month-olds, EEG desynchronization was found in response to a reaching hand in a grasping posture even when the outcome of the hand action was not seen (Southgate, Johnson, El Karoui & Csibra, 2010). This finding was seen as reflecting infants' prediction of the motor program that would be needed to achieve the goal of the action, that is, grasping (see also Csibra, 2007).

Marshall, Young, and Meltzoff (2011) used a different interactive task to examine infants' EEG responses during both action perception and action production conditions. Fourteen-month-old infants took turns with an adult executing and observing a discrete goal-directed act, namely, a button press on a custom-made button box (fig. 11.1). EEG reactivity was examined to both perception and production of the button press, relative to baseline epochs preceding each trial. The study predicted reactivity of the infant mu rhythm (6–9 Hz) over central electrode sites (Marshall, Bar-Haim & Fox, 2002), although it also analyzed activity over a range of other scalp regions.

As predicted, infants' own actions on the button box were associated with a significant desynchronization over the central region. A significant desynchronization also occurred in the same frequency range at central

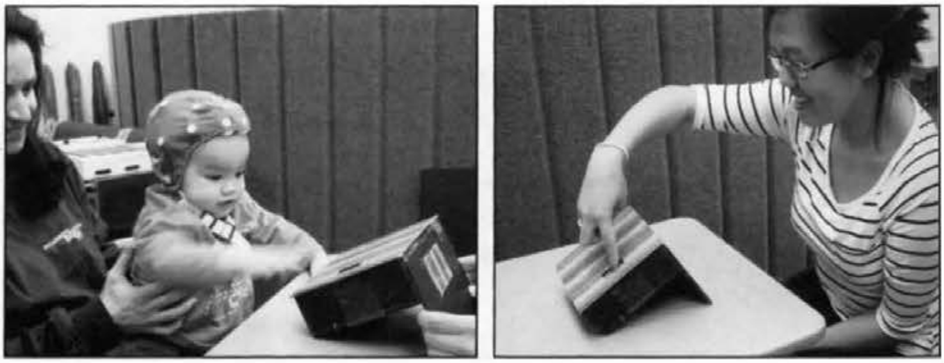

Figure 11.1
Photographs illustrating the execution (*left*) and observation (*right*) conditions in the infant EEG study by Marshall, Young & Meltzoff (2011). Reprinted with permission from Marshall and Meltzoff (2011).

sites when infants simply observed an adult perform the same act. Although the desynchronization during action observation went beyond central sites (to frontal and parietal regions), the desynchronization during action production was more specific to central sites, consistent with work on the adult mu rhythm (Muthukumaraswamy & Johnson, 2004).

Toward a Developmental Neuroscience of Action Processing
The emerging literature on infant EEG suggests that the mu rhythm has utility in the study of the neural processes involved in infants' action processing. It may be tempting to see the infant mu response as a measure of a mirroring mechanism; however, we should be cautious, because research in this area is still at a very early stage. Marshall and Meltzoff (2011) articulated several key questions about the infant mu rhythm that may help to build a firmer foundation for neuroscientific aspects of developmental action science.

One issue concerns the developmental changes that may occur in the mu rhythm (e.g., Berchicci et al., 2011). Another concerns the relative lack of specificity of the EEG response, such that we cannot assume that regional overlaps in desynchronization between conditions necessarily reflect activation of the same underlying neural systems. Infant MEG technologies promise to provide more specific information on regional changes in cortical activity (Imada et al., 2006; Kuhl, 2010).

Another key theoretical issue about mirroring mechanisms is what aspects of perceived actions might be "mirrored" and how such a system can be related to the demonstrated flexibility of human imitation and action understanding. This question is the subject of much debate in the adult literature (Csibra, 2007; Jacob, 2008; Kilner, 2011; Rizzolatti & Sinigaglia, 2010) but has been less considered from a developmental perspective. Part of this debate concerns the degree to which neural mirroring mechanisms are responsive to the goals of observed actions versus the specific means used. For instance, one unaddressed question concerns whether the mu response in infants is equally responsive to observing actions in which different movements are used to achieve the same goal. At the behavioral level, we know from studies of imitation that infants can imitate both the specific means used and the goal achieved, but the relevant studies have not been conducted using neuroscience measures.

A related theoretical issue concerns top-down influences and the degree to which neural mirroring mechanisms are influenced by social, cognitive, and contextual factors. As we have seen, behavioral studies have documented the flexibility and top-down control of imitation in infants and children.

A final, far-reaching theoretical question revolves around the role of self-experience with actions that an individual observes being performed by others. In adults, various methods have been used to explore self-experience, including experimental psychology (Schütz-Bosbach & Prinz, 2007) and neuroscience (e.g., Calvo-Merino, Grèzes, Glaser, Passingham & Haggard, 2006; Marshall, Bouquet, Shipley & Young, 2009). From a developmental perspective, work using behavioral methods has suggested the importance of infants' self-experience with particular behaviors on their subsequent processing of those behaviors by others (e.g., Kuhl & Meltzoff, 1984; Meltzoff & Brooks, 2008; Sommerville, Woodward & Needham, 2005). Developmental neuroscience data are so far sparse on this issue (van Elk et al., 2008; Saby et al., 2012). One important point is that infants are able to imitate novel actions (Meltzoff, 1988a), showing that generative mappings between perception and production go beyond well-practiced motor routines and habitual actions. Integrating the emerging developmental neuroscience work with the flexibility and generative capacity of infant behavioral imitation is a grand challenge that remains to be met.

Conclusion

In this chapter, we used imitation to elucidate ideas about the development of links between action perception and action production. We reviewed the AIM theory of imitation, which holds that humans have a "supramodal representation" of action that undergirds imitation. Discoveries about infant imitation suggest that an intrinsic link between seeing an action and producing it exists before language. Although action imitation is present at birth (the youngest infant was 42 minutes old at the time of test), we argued that such imitation may build on prior self-experience with "body babbling."

We reviewed work establishing that imitation is not an uncontrollable impulse. Children select who, when, and what aspects of the adult's display to imitate; moreover, imitative reactions can be regulated by top-down factors, including children's evaluation of the likely adult emotional reactions to the children repeating the actions. Imitation is both cognitive and social: young children recognize having their actions imitated by others. Experiencing such an interpersonal match promotes feelings of affinity and a sense of emotional connection to others viewed as acting "like me" (Meltzoff, 2007a). Mutual imitation is an important aspect of social-cognitive development.

Finally, we considered infant imitation from the viewpoint of developmental cognitive neuroscience. The field is generating new work on the development of neural mirroring mechanisms, and questions arise about how to connect such neuroscience work to the large body of work on behavioral imitation in infancy. We focused here on infant neuroscience work using EEG, with an emphasis on the mu rhythm. Further careful studies are needed for understanding the bidirectional influences of neural and behavioral development. We know that behavior itself provides experience and input that modulates biological plasticity (Gottlieb, 2007; Marshall, 2009), and we know that behavioral evidence often provides the impetus for neuroscience work. Neither field is primary, nor can it stand alone. We need to embrace these bidirectional influences for the emerging field of developmental action science to prosper.

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Note

1. Piaget's theory does not deny that young infants could be trained to associate their own movements with similar movements of another. Every time a child poked out his tongue, the parent could do so. The acts might become linked. Piaget (1962)

argued that associationism could not provide a comprehensive theory of imitation, because if it was the mechanism, there would be "haphazard" and "spurious" associations. Mismatched stimulus-response action pairings could be as easily formed as matched ones, and imitation as a learning mechanism would never emerge if one's mother (or caretaker or peers) was not a good imitator.

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