Motor Knowledge and Action Understanding:

A Developmental Perspective

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The prediction of where and how people are going to move has obvious relevance for social interaction. As adults, we are extremely adept at predicting at least some of these behaviors automatically in real-time. If, for example, we observe someone reaching in the direction of a half-filled glass on a table, we can predict with relative certainty that the reaching action is directed toward the glass. Often, we can also predict if the actor intends to drink from the glass or intends to remove the glass depending on the state of the actor as well as the context surrounding the action.

How do we detect the goals, intentions, and states of others so rapidly with little if any awareness of these implicit inferences? According to a growing number of social neuroscientists, there are specialized mechanisms in the brain for understanding actions and responding to them. Evidence from neuroimaging studies and neuropsychological studies of normal and brain damaged patients offer considerable support for this claim (Decety & Sommerville, 2004; Frith & Frith, 2006; Grèzes, Frith, & Passingham, 2004; Pelphrey, Morris, McCarthy, 2005; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004). The availability of specialized processes suggests that the brain may be intrinsically prepared for this information and, thus, that action understanding should be evident early in development.

Indeed, even neonates show evidence of responding to human behaviors, such as speech, gaze, and touch (Lacerda, von Hofsten, & Heimann, 2001; von Hofsten, 2003). It is not entirely clear, however, that these responses are contingent on perceived *actions* as opposed to *movements*. In order to avoid unnecessary confusion, it behooves us to begin by distinguishing between movements and actions. Human actions are comprised of a broad range of limb, head, and facial movements, but not all body movements are actions. We reserve this latter description for goal-directed movements. These are movements that are planned relative to an intrinsic or extrinsic goal prior to their execution. For example, a prototypical goal-directed action might involve extending an arm to grasp a ball resting on a table. By contrast, waving an arm and accidentally hitting a ball does not represent an action. Recent findings suggest that infants understand the goal-directed nature of actions by the second half of the first year and perhaps even earlier (e.g., Csibra, Gergely, Biro, Koos, & Brockbank, 1999; Kiraly, Jovanovic, Prinz, Aschersleben, & Gergely, 2003; Luo & Baillargeon, 2002; Woodward, 1998; 1999; Woodward & Sommerville, 2000).

Two Modes for Understanding Actions

What are the mechanisms that underlie action understanding? By action understanding, we mean the capacity to achieve an internal description or representation of a perceived action and to use it to organize and predict appropriate future behavior. Recent neurophysiologically motivated theories (Jeannerod, 1997, 2001; Rizzolatti, Fogassi, & Gallese, 2001) suggest that there are two mechanisms that might explain how action understanding occurs. The more conventional mechanism involves some form of visual analysis followed by categorization and inference. This type of analysis can be thought of as progressing through stages of processing comparable to those proposed by Marr (1982). These processes are mediated via the ventral visual pathway of the brain and are independent of the motor system. For example, when we observe a hand grasping a glass, the visual system parses this scene into an object (i.e., the glass) and a moving hand that eventually contacts and grasps the glass. This visual input is recognized and associated with other information about the glass and the actor in order to understand the observed action.

Whereas this first mechanism applies to all visual information, the second mechanism is unique to the processing of actions (and, perhaps, object affordances) and has been referred to as a *direct matching* or *observation-execution matching* system (Rizzolatti et al., 2001). With this mechanism, visual representations of observed actions are mapped directly onto our motor representation of the same action; an action is understood when its observation leads to simulation (i.e., representing the responses of others by covertly generating similar subthreshold 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 the observer's motor areas (Blakemore & Decety, 2001; Iacoboni, Molnar-Szakacs, Gallese, Buccino, Mazziotta, & Rizzolatti, 2005; Rizzolatti et al., 2001). It is the 'motor knowledge' of the observer that is used to understand the observed goal-directed action via covert imitation. For this reason, knowledge of the action will depend in part on the observer's specific motor experience with the same action (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Longo, Kosobud, & Bertenthal, 2006).

In contrast to the first visual mechanism, the flow of information between perception and action by direct matching enables more than an appreciation of the surface properties of the perceived actions. Simulation 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. This implies that the observer is able to *covertly imitate* as well as *predict* the outcome of an observed action.

Simulation of Actions. Although this latter hypothesis for explaining how we understand actions dates back to the ideomotor theory of James (1890) and Greenwald (1970), direct 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 (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Thus, these neurons provide a common internal representation for executing and observing goal-directed action. More recently, mirror neurons were also observed in the inferior parietal lobule which shares direct connections with the premotor cortex (Fogassi et al., 2005).

This latter finding is important for explaining how visually perceived face and body movements are represented by mirror neurons in the premotor cortex. These movements are coded by the superior temporal sulcus, which does not project directly to the mirror neurons in the ventral premotor cortex. Instead, the superior temporal sulcus projects to the inferior parietal lobule which is connected to the ventral premotor cortex (Rizzolatti & Craighero, 2004). Thus, mirror neurons are innervated by a fronto-parietal circuit in the motor system that also receives visual inputs from the superior temporal sulcus. Human neuroimaging and transcranial magnetic stimulation studies have shown activation of a homologous fronto-parietial circuit during both the observation as well as the imitation of actions (Brass, Zysset, & von Cramon, 2001; Buccino, Binkofski, Fink, Fogassi, Gallese, 2001; Decety, Chaminade, Grèzes, & Meltzoff, 2002; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Grèzes, Armony, Rowe, & Passingham, 2003; Iacoboni, Woods, Brass, Bekkering, Mazziotta, & Rizzolatti, 1999; Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003; for a review, see Rizzolatti & Craighero, 2004).

This neurophysiological evidence is complemented by recent behavioral evidence showing that the observation of actions facilitates or primes responses involving similar actions. For example, visuomotor priming is observed when grasping a bar in a horizontal or vertical orientation is preceded by a picture of a hand or the observation of an action congruent with the required response (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002; Edwards, Humphreys, & Castiello, 2003; Vogt, Taylor, & Hopkins, 2003). Similarly, response facilitation is observed when the task involves responding to a tapping or lifting finger or an opening or closing hand that is preceded by a congruent (e.g., index finger responds to observation of tapping index finger) as opposed to incongruent stimulus (e.g., index finger responds to observation of tapping middle finger) (Bertenthal, Longo, & Kosobud, 2006; Brass, Bekkering & Prinz, 2001; Brass, Bekkering, Wohlschlager, & Prinz, 2000; Heyes, Bird, Johnson, & Haggard, 2005; Longo et al., 2006).

Prediction of the Effects of Actions. While the preceding evidence suggests that action observation is accompanied by covert imitation of the observed action, additional evidence suggests that action observation also leads to the prediction of the effects or outcome of the action. In a study by Kandel, Orliaguet, and Viviani (2000), participants were shown a point-light tracing of the first letter of a two letter sequence handwritten in cursive, and they were able to predict the second letter from the observation of the preceding movements. Neuroimaging evidence revealed that a fronto-parietal circuit (associated with the human mirror system) was activated when predicting the next letter from a point-light tracing, but this same circuit was not activated when predicting the terminus of a point-light tracing of a spring-driven ball after it bounced (Chaminade, Meary, Orliaguet, & Decety, 2001). The finding that the fronto-parietal circuit was only activated when predicting the outcome of a human action and not when predicting the outcome of a mechanical event is consistent with other research suggesting that the mirror system is restricted to biological movements (e.g., Kilner, Paulignan, & Blakemore, 2003; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004).

This last finding implies that the direct matching system is sensitive to the perceived similarity between observed and executed responses, and thus, observers should show an improved ability to predict the effects or outcome of an action based on their own as opposed to others' movements because the match between the observed and executed actions should be greatest when the same person is responsible for both (e.g., Knoblich, 2002; Knoblich, Elsner, Aschersleben, & Metzinger, 2003). A few recent studies manipulating the 'authorship' of the movements find that predictability is indeed greater when predicting the outcomes of self-produced as opposed to other produced movements (Beadsworth & Buckner, 1981; Flach, Knoblich, & Prinz, 2003; Knoblich & Flach, 2001; Repp & Knoblich, 2004).

Why should covert imitation or simulation of movements contribute to predicting their effects? The answer is related to the inertial lags and neural conduction delays that accompany limb movements in the human body. As a consequence of these delays, it is insufficient for movements to be guided by sensory feedback, because such movements would be performed in a jerky and staccato fashion as opposed to being smooth and fluid

(Wolpert, Doya, & Kawato, 2003). Thus, the execution of most movements requires prospective control or planning. Based on computational studies, it has been proposed that this planning or control involves an internal model, dubbed *forward model*, which predicts the sensory consequences of a motor command (Jordan, 1995; Kawato, Furawaka, & Suzuki, 1987; Miall & Wolpert, 1996; Wolpert & Flanagan, 2001). Presumably, the simulation of a goal-directed action includes the activation of these forward models enabling prediction as well as covert imitation of the behavior. As motor behaviors are practiced and learned, these forward models become better specified and enable more precise prediction of the ensuing motor commands. According to Wolpert et al. (2003), similar forward models could be used to predict social behaviors, such as facial expression, gaze direction, or posture.

Perception of the Structure of Human Movements. One additional source of evidence suggesting that an observation-execution matching system is functional in human observers derives from their showing greater sensitivity to biological motions that are consistent as opposed to inconsistent with the causal structure of an action. A common technique for studying the perception of human movements involves the depiction of these movements with point-light displays. These displays are created by filming a person in the dark with small lights attached to his or her major joints and head. (An example of 6 sequential frames from a point-light display is presented in Figure 1.) It is also possible to synthesize these nested pendular motions, which is the technique that we have used in much of our previous research (see Bertenthal, 1993, for a review). Johansson (1973) was the first to systematically study the perception of these displays,. He reported that adult observers perceive the human form and identify different actions (e.g., push-ups, jumping jacks, etc.) in displays lasting less than 200 ms, corresponding to about five frames of a film sequence. This finding is very impressive because these displays are devoid of all featural information, such as clothing, skin, hair, etc. It thus appears that recognition of actions can result exclusively from the extraction of a unique structure from motion-carried information.

In spite of these impressive findings, the recognition of upside down biological motion displays as depicting a person or the person's direction of gait is significantly impaired (Bertenthal & Pinto, 1994; Pavlova & Sokolov, 2000; Sumi, 1984; Verfaillie, 1993). If recognition was based only on the perception of structure from motion, then the orientation of the human form should not matter. It thus appears that some additional processes involving the causal structure of human movement contribute to the perception of biological motions.

For similar reasons, point-light trajectories obeying the kinematics of human movement are perceived as moving at a uniform speed, even though the variations in speed can exceed 200%. By contrast, observers are much more sensitive to speed differences in point-light trajectories that do not conform to the kinematics of human movements (Viviani, Baud-Bovy, & Redolfi, 1997; Viviani & Mounoud, 1990; Viviani & Stucchi, 1992). These latter findings thus suggest that curvilinear movements are not perceived in terms of the actual changes that occur in velocity, but rather in terms of the biological movements that appear smooth and uniform when executed by one or more articulators of the human body.

Although the preceding evidence is consistent with motor knowledge contributing to action understanding, it is difficult to rule out perceptual learning as the principal reason for observers showing differential sensitivity to familiar and unfamiliar biological motions. Indeed, this same confound is present when interpreting much of the previously reviewed evidence suggesting that motor knowledge contributes to the prediction of human actions. This confound also adds to the challenge of testing whether motor knowledge contributes to infants' understanding of others' actions, which is why it is necessary to consider the contributions of visual attention and experience when studying the functionality of the observation-execution matching system during infancy.

Developmental Evidence for an Observation-Execution Matching System

For those unfamiliar with the preceding evidence for an observation-execution matching system, it will be useful to recap how a direct matching system contributes to action understanding. The traditional view is that others' actions are understood via the same perceptual and conceptual processes as are all other visual events. If, however, the perception of actions also activates the motor system (i.e., direct matching), then the specific motor knowledge associated with the perceived actions will contribute to understanding others' actions. The specific mechanism for this understanding is covert imitation or simulation of the observed action. Although the motor response is not overtly executed, the planning for specific movements (i.e., means) as well as the effects or perceptual consequences (i.e., the goal) are automatically activated in the motor cortex. This activation imparts to the observer embodied knowledge of the perceived action (i.e., motor knowledge) without the need to rely on visual experience or logical inferences based on the perceived information. The implication is that we can then understand others' actions, such as lifting a cup, playing the piano, or displaying a disposition, such as displeasure, based on the internalized motor programs available to us for performing the same actions.

In the remainder of this chapter, we will review a series of experiments designed to investigate whether motor knowledge contributes to action understanding by infants. Although it is certainly possible for infants to achieve this understanding from visual experience alone, there exists a developmental advantage for direct matching, because such a mechanism does not necessitate specific conceptual or symbolic knowledge of actions, which demand the development of higher-level cognitive processes. Thus, the functioning of this system may offer an explanation for the precocious development of young infants' understanding of actions, and social development more generally (Tomasello, 1999).

The evidence is divided into three sections. First, we will review a series of experiments showing that infants demonstrate perseverative search errors following observation of someone else's actions. This evidence will be used to support the claim that an observation execution matching system is functional in infants and that action observation elicits covert imitation. Second, we will review recent experiments showing that infants visually orient in response to deictic gestures, and that this response is specifically a function of motor knowledge enabling prediction of the effect of an observed action. Finally, we will review evidence showing that infants perceive biological motions depicting familiar but not unfamiliar actions, and that the development of this perceptual skill is at least correlated with the development of their motor skills.

Perseverative Errors in Searching for Hidden Objects

The Piagetian A-not-B error, observed in 8- to 12-month-old infants, is among the most consistently replicable findings in developmental psychology. In this task, infants first search correctly for an object they see hidden in one location (A) on one or more trials, but then continue to search at the A location after the object has been hidden in a new location (B). A number of researchers attribute this search error to the formation of a prepotent response. For example, Smith, Thelen, and colleagues (Smith, Thelen, Titzer, & McLin, 1999; Thelen, Schoner, Scheier, & Smith, 2001) claim that the error arises from the task dynamics of reaching, which causes the motor memory of one reach to persist and influence subsequent reaches. Diamond (1985) argues that one cause of the error is the inability to inhibit a previously rewarded motor response. Zelazo and colleagues (Marcovitch, & Zelazo, 1999; Zelazo, Reznick, & Spinazzola, 1998) account for perseverative responses in young children in terms of the relative dominance of a response-based system "activated by motor experience" over a conscious representational system (Marcovitch & Zelazo, 1999, p. 1308). In each of these accounts, a history of reaches to the A location is a crucial aspect of the perseverative response.

If an observation-execution matching system is functional in young infants, then simply observing someone else reach to the same location repeatedly may be sufficient for eliciting this error. This prediction follows from the claim that observing an action will lead to covert imitation of that same action, and thus will be functionally similar to executing the action oneself. We (Longo & Bertenthal, 2006) tested this prediction by administering the standard A-not-B hiding task to a sample of 9-month-old infants. Twenty 9-month-old infants were tested with the canonical reaching task, and twenty were tested in a condition in which they watched an experimenter reach, but did not reach themselves.

Infants were seated on their mother's lap in front of a table covered with black felt and allowed to play with a toy (a rattle or a plastic Big-Bird) for several seconds. Four pretraining trials were administered using procedures similar to those used by Smith et al. (1999). On the first pretraining trial, the toy was placed on top of a covered well. On the second trial, the toy was placed in the well but with one end sticking out of the well. On the third trial, the toy was placed completely in the well but left uncovered. On the final trial, the toy was placed completely in the well and covered.

The experimental trials used a two-well apparatus and consisted of three A trials and one B trial (see Figure 2). Infants in the *reaching* condition were allowed to search on all trials. Infants in the *looking* condition were only allowed to search on the B trial and observed the experimenter recover the object on the A trials. On each trial, the toy was waved and the infant's name was called to attract his or her attention. The experimenter removed the lid with one hand and placed the toy in the well with the other hand. The location (right or left) of the A trials and experimenter's arm (right or left; coded as which arm the experimenter used to hide the toy) were counterbalanced between infants. Thus, the experimenter's reaches were ipsilateral half of the time (right-handed reach to the location on the right or left-handed reach to location on the left) and contralateral half of the time (right-handed reach to the location on the left or left-handed reach to the location on the right).

For A trials in the reaching condition, the apparatus was slid forward to within the baby's reach following a three second delay. If, after ten seconds, the infant had not retrieved the toy from the A location, the experimenter uncovered the well and encouraged the infant to retrieve the toy. For A trials in the looking condition, the experimenter did not slide the apparatus toward the infants and recovered the toy following a three second delay. The experimenter used the same arm to retrieve the toy as was used to hide the toy. On B trials, in both conditions, the experimenter hid the toy (using the same hand as on the A trials) and then the apparatus was moved to within the infant's reach following a three second delay. The dependent measure was whether the infant searched for the hidden toy at the correct B location or reverted to search at the A location where the toy had been previously found.

The results revealed that infants in the Reaching condition were significantly more likely to make an error on B trials (15 of 20) than on any of the A trials, the canonical A-not-B error. Infants also made significantly more errors on looking B trials (12 of 20) than infants in the reaching condition made on A trials (see Figure 3). These results demonstrate that overt reaching to the A location by the infant is not necessary to elicit the A-not-B error. During training, infants in the looking condition had reached four times to a central location using the single-well apparatus, but had *never* reached to the A location. Still, they were found to "perseverate" on their very first reach using the two-well apparatus. The likelihood of making an error did not differ between the two B conditions.

In sum, these data suggest that looking A trials influenced performance on the B trials. Nonetheless, in order to establish that these responses are truly *perseverative*, as opposed to simply random, it is necessary to demonstrate errors on significantly more than 50% of the trials. Binomial tests revealed greater than chance perseveration on reaching, but not on looking B trials. Thus, these data are consistent with findings from previous studies showing that infants perseverate after reaching A trials, but the evidence of perseveration following looking A trials was somewhat equivocal.

In the second experiment, we sought to provide more definitive evidence for perseverative search in the looking condition. Marcovitch, Zelazo, and Schmuckler (2002) found that the likelihood of a perseverative search error increased as the number of A trials increased, at least between the range of one to six. If the A-not-B error is indeed a function of similar mechanisms inducing perseverative search in both the reaching and looking conditions, then we would expect search errors in the looking condition to be more robust as the number of A trials increases. Thus, in order to increase the likelihood of finding perseveration at greater than chance levels, the following experiment included six looking A trials instead of three.

Thirty 9-month-old infants were tested following the procedures described for the first experiment, except that all infants were tested in the looking condition and there were six instead of three A trials. The results from this experiment revealed that 70% (21 of 30) of the infants made the A-not-B error, significantly more than half of the sample. This finding suggests that observation of a reaching action is sufficient to elicit perseverative search. As such, these findings are consistent with infants covertly imitating the observed action of searching for the toy in the covered well. Can these results be explained by other mechanisms?

Some researchers suggest that the crucial factor leading to search errors at the B location is not a history of reaching to the A location, but rather a history of visually attending to or planning to reach to the A location (e.g., Diedrich, Highlands, Spahr, Thelen, & Smith, 2001; Munakata, 1997; Ruffman & Langman, 2002). In the current experiments, greater attention to one location than the other will likely covary with the history of simulated reaching to that location, and thus it is difficult to disambiguate these two interpretations. Although this attentional confound is often a problem when testing the contribution of motor knowledge to performance, converging analyses assessing infants own reaching behavior were helpful in showing that an attentional interpretation was not sufficient for explaining their search errors.

It is well documented in the literature that infants show an ipsilateral bias in their reaching. Bruner (1969), for example, referred to the apparent inability of young infants to reach across the body midline as the "mysterious midline barrier," arguing that contralateral reaches do not occur before 7 months of age. Contralateral reaching becomes more frequent with age both on reaching tasks during infancy (van Hof, van der Kamp, & Savelsbergh, 2002) and in 'hand, eye, and ear' tasks in later childhood (Bekkering, Wohlschläger, & Gattis, 2000; Schofield, 1976; Wapner & Cirillo, 1968). Nevertheless, a clear preference for ipsilateral reaches is consistently observed in early development.

In Experiment 1, infants showed an ipsilateral bias in their reaching. On looking B trials, 90% (18 of 20) of the infants made ipsilateral reaches, which was significantly more than would be expected by chance. Similar ipsilateral biases were observed on the three reaching A trials (81.7%), and the reaching B trials (73.7%, 14 of 19 one-handed reaches). Intriguingly, infants' simulation of the experimenter's actions mirrored their motor bias, as infants in the looking condition were significantly more likely to reach to location A than to location B when the experimenter had reached ipsilaterally (8 of 10), rather than contralaterally (4 of 10) (see Figure 4). This result suggests that infants' responses following observation of the experimenter's reaches were not random, at least for ipsilateral reaches. In Experiment 2, an ipsilateral bias in infants' reaching was again observed, with 85% (23 of 27) of one-handed reaches scored as ipsilateral, Furthermore, this ipsilateral bias was again mirrored by infants' representation of the experimenter's reaching. Perseveration was observed more often than predicted by chance when the experimenter had reached ipsilaterally on the A trials (13 of 15 infants made the error), but not when the experimenter had reached contralaterally (8 of 15 made the error). This difference between conditions was significant (see Figure 4).

It is very possible that the infants' ipsilateral bias may have influenced their likelihood of covertly imitating the experimenter. A number of recent studies suggest that simulation by the mirror system is significantly stronger when observed actions are within the motor repertoire of the observer (e.g., Calvo-Merino et al., 2005; Longo et al., 2006). If an observer does not possess the motor skill to precisely and reliably perform an action, then he or she cannot simulate it with the same level of specificity as a skilled performer. Since infants have difficulty reaching contralaterally, simulation of observed contralateral reaches should be weaker than that for ipsilateral reaches, or perhaps absent entirely. Thus, if an observation-execution matching mechanism is operative, then infants should perseverate more often following observation of ipsi- rather than contralateral reaches to the A location by the experimenter, as we found.

Although the preceding findings are not meant to discount the relative contributions of attention to response perseveration, at the very least the current evidence appears to challenge the sufficiency of an attentional explanation focused on spatial coding of the hidden object. In particular, it is not at all apparent how such an account would explain why infants showed greater perseveration after observing the experimenter reach ipsilaterally than contralaterally. Other potential explanations involving, for example, object representations (e.g., Munakata, 1998), have similar difficulty accounting for this effect. By contrast, a direct matching interpretation accounts for this effect in terms of infants' own difficulties with contralateral reaching, which should lead to weaker or absent motor simulation following observed contralateral, compared with ipsilateral reaches, and consequently less perseveration.

The final experiment in this series was designed to probe whether a simulative response to an observed action is initiated only when the action is performed by a human agent or also when it is performed by a robot or some other mechanical agent. As previously discussed, research with adults reveals that the execution of an action is often facilitated when observing that same action, and impaired when observing a different action (Brass et al., 2001; Bertenthal et al., 2006). It appears, however, that this conclusion applies only when observing actions performed by human agents. For example, Kilner et al. (2003) instructed participants to make vertical or horizontal arm movements while observing either a human or a robot making the same or the opposite arm movements. The results showed that observation of incongruent arm movements interfered significantly with the performance by the observer, but this effect was limited to observation of the human agent. When observing the robot, there was no evidence of an interference effect on the performance of the observer.

In order to test this same question with infants, we modified the testing situation so that the human experimenter would be hidden behind a curtain, but would be able to manipulate the covers and the toy with two large mechanical claws that were held vertically in front of the curtain. Thus, the infant was only able to observe the mechanical claws, and even the experimenter's hands that gripped the mechanical claws were not visible (see Figure 5). A total of 30 infants were tested, and the procedure was similar to that used in the preceding experiment. After the training trials, there were six A trials followed by one B trial. From the infants' perspective, the hiding and finding of the toy was identical to the previous two experiments, except that the experimenter was not visible and two mechanical claws appeared in her place. Unlike the results from the previous experiments, the perseverative error was made by only 40% (12 of 30) of the infants, which was significantly less than occurred in the previous two experiments. Moreover, the likelihood of the error was essentially the same for ipsilateral and contralateral searches by the claw. Thus, the substitution of a mechanical agent for a human agent reduced the frequency of the perseverative error.

Our interpretation for this finding is that infants' tendency to simulate observed actions is less likely when the action is not performed by a human. We realize, however, that the mechanical agent is less familiar than the human agent, and thus familiarity, per se, may be responsible for these differences in the likelihood of a perseverative search error. In future research, we plan to manipulate whether the mechanical claw is observed as an independent agent or as a tool used by the human agent. If perseverative performance is greater when the mechanical claw is perceived as a tool, the importance of familiarity for explaining perseverative performance will be diminished, because familiarity will remain constant in both the tool and agent conditions.

Although support for this prediction awaits an empirical test, a recent study by Hofer, Hauf, and Aschersleben (2005) suggests that infants distinguish between tools and mechanical agents. In this experiment, 9-month-old infants did not interpret an action performed by a mechanical claw as goal-directed but did interpret the action as goal-directed when the mechanical claw was perceived as a tool. Presumably the tool is interpreted as goal-directed at an earlier age than the mechanical agent because infants perceive it as an extension of the human arm, and thus are better able to simulate and understand its effects.

Until recently, this finding may have seemed at odds with the evidence for mirror neurons in the monkey's brain. When these neurons were first discovered, it was reported that they discharge to goal-directed actions performed by conspecifics or humans, but not to actions performed by tools, such as a pair of pliers (Rizzolatti et al., 2001). Recently, however, Ferrari, Rozzi, and Fogassi (2005) reported identifying a population of neurons in the monkey's ventral premotor cortex that specifically discharges to goal-directed actions executed by tools. Taken together, this evidence suggests that an action performed by a tool perceived as an extension of a human agent will be more likely to induce motor simulation than an action performed by the same tool perceived as a mechanical agent.

Visual Orienting in Response to Deictic Gestures

Joint attention to objects and events in the world is a necessary prerequisite for sharing experiences with others and negotiating shared meanings. As Baldwin (1995, p. 132) puts it: "joint attention simply means the simultaneous engagement of two or more individuals in mental focus on one and the same external thing." A critical component in establishing joint attention involves following the direction of someone else's gaze or pointing gesture (Deak, Flom, & Pick, 2000). Both of these behaviors require that the deictic gesture is interpreted not as the goal, itself, but rather as the means to the goal. When responding to a redirection of gaze or to the appearance of a pointing gesture, the observer does not fixate on the eyes or the hand but rather focuses on the referent of these gestures (Woodward & Guarjardo, 2002). In this case the behavior is communicative and the goal is some distal object or event ("there's something over there"). Thus, it is necessary for the observer to *predict* the referent or the goal of the action from observing its execution by someone else.

Until recently, the empirical evidence suggested that infants were unable to follow the direction of a gaze or a point until approximately 9 to 12 months of age (e.g., Corkum & Moore, 1998; Leung & Rheingold, 1981; Scaife & Bruner, 1975). If, however, these behaviors are mediated by an observation-execution matching system, then gaze-following should precede following a pointing gesture because control of eye movements and saccadic localization appear at birth or soon thereafter (von Hofsten, 2003), whereas the extension of the arm and index finger to form a pointing gesture does not appear until approximately 9 months of age (Butterworth, 2003). Indeed, it should be possible to show evidence of gaze-following long before 9 months of age.

This prediction has now been validated. Hood, Willen, and Driver (1998) adapted a method popularized by Posner (1978; 1980) for studying spatial orienting. In a prototypical study, adult subjects are instructed to detect visual targets, which may appear on either side of a fixation point. Their attention can be cued to one side or the other before the target appears (e.g., by a brief but uninformative flash on that side). The consistent finding from this paradigm is that target detection is more rapid on the cued side, because attention is oriented in that direction. It is relevant to note that the attentional cueing preceding the orienting response is covert and does not involve an overt eye movement. As such, this attentional cueing is consistent with a simulation of an eye movement that enables prediction before the visual target appears.

Hood et al. tested 4-month-old infants to determine if they would shift their visual attention in the direction toward which an adult's eyes turn. The direction of perceived gaze was manipulated in a digitized adult face. After infants oriented to blinking eyes focused straight ahead, the eyes shifted to the right or to the left. A key innovation of this paradigm was that the central face disappeared after the eyes were averted to avoid difficulties with infants disengaging their fixation of the face. An attentional shift was measured by the latency and direction of infants' orienting to peripheral probes presented after the face disappeared. Infants oriented faster and made fewer errors when presented with a probe congruent with the direction of gaze than when presented with an incongruent probe.

These findings suggest that young infants interpret the direction of gaze as a cue to shift attention in a specified direction. It is significant to note that the attentional cue was not in the location of the probe, but simply pointed to that location. Thus, faster responding to the spatially congruent cue required that infants understand at some level the meaning of the change in gaze direction in order to predict the future location of the probe. More recent research reveals that gaze following was restricted to a face in which infants observed a dynamic shift in gaze direction (Farroni, Johnson, Brockbank, & Simion, 2000). When the averted gaze was presented statically, there was no evidence of infants following the gaze shift. Intriguingly, a new report by Farroni and colleagues (Farroni, Massaccesi, Pividori, & Johnson, 2004) suggests that these findings are replicable with newborn infants.

With Katharina Rohlfing, we sought to extend this paradigm to study whether infants younger than 9 months of age would also reorient their attention in response to the direction that another person is pointing with their hand. Interestingly, Amano, Kezuka and Yamamoto (2004) conducted an observational study showing that 4-month-old infants responded differently to the pointing done by an experimenter and their mothers. In order to redirect attention, infants more often needed the combination of eye gaze and pointing while interacting with the experimenter than while interacting with their mothers. When interacting with their mothers, infants were able to follow the pointing gesture alone while the mothers maintained eye contact. One interpretation for these findings is that infants are more familiar with their mothers' gestures and thus are more likely to correctly interpret them. A different interpretation is that infants are more likely to follow the pointing gesture of their mothers because their mother's face is more familiar and thus it is easier for them to disengage from the face. By adapting the same paradigm used by Hood et al. (1998) to study gaze-following, we were able to eliminate some of the possible confounds present in previous studies of pointing because infants did not have to disengage from a central stimulus of a face.

Infants between 4.5- and 6.5-months-old were tested. They were shown a series of computerized stimuli on a projection screen while sitting on their parents' laps. Each trial consisted of the following sequence of events (see Figure 6):

1. The hand appeared on the screen with fingers oriented upward. The fingers waved up and down and were accompanied by a voice saying “look baby, look!” to recruit the baby’s attention. This segment was played until the infant fixated the hand.
2. Once the finger waving ended, the hand was seen transforming into a canonical pointing gesture that moved a short distance in the direction of the pointing finger. This segment lasted 1000 ms.
3. After the hand disappeared, a digitized picture of a toy appeared randomly on the left or right side of the screen. On half of the trials, this probe was congruent with the direction of the point and on the other half of the trials it was incongruent with the pointing direction. The probe remained visible for 3 sec and was accompanied by a voice saying “wow!” Two different toys (a clown and an Ernie puppet) were presented in a randomized order.

Based on the videotapes of the infants’ behavior, we measured the response time to shift attention in the direction of the peripheral probe. The probe that appeared in the direction cued by the pointing finger is referred to as the *congruent* probe, and the probe that appeared in the opposite direction is referred to as the *incongruent* probe. A total of 20 infants completed an average of 26 trials (*SD* = 6.2, range: 10–32). As can be seen in Figure 7 (Dynamic condition), infants oriented toward the congruent probe significantly faster than they did toward the incongruent probe. These results suggest that infants as young as 4.5 months of age respond to a dynamic pointing gesture by shifting their visual attention to a shared referent.

The second experiment tested whether the movement of the pointing finger was necessary to elicit the shift in attention or whether a static pointing gesture would be sufficient. A new sample of 14 infants between 4.5 to 6.5 months of age was tested with the same procedure, except that the pointing finger remained stationary when it appeared on the screen for 1000 ms. Infants completed an average of 22 trials (*SD* = 7.7, range: 10–32). Unlike the responses to the dynamic pointing finger, infants showed no difference in responding to the congruent and incongruent probe (see Figure 7, Static condition).

It thus appears that observation of an action and not just the final state is necessary for young infants to follow a point, analogous to the findings of infants following eye gaze (Farroni et al., 2000). Two possible interpretations for these results are that the movement associated with the gesture increased the salience of the stimulus, or increased the likelihood of visual tracking in the direction of the moving finger. Either of these two possibilities would bias infants to shift their attention in the direction of the pointing gesture.

If the results were exclusively a function of following the principal direction of the moving finger, then we would expect a reversal in the reaction time results when the finger moved backwards rather than forwards. The next experiment tested this interpretation. A total of 25 infants between 4.5 and 6.5 months of age were tested in two conditions. In the *forward* condition, the direction of the pointing finger and the movement of the finger were compatible, whereas in the *backward* condition, the direction of the pointing finger and the movement of the finger were incompatible. Half of the trials in each condition involved a congruent probe and half of the trials involved an incongruent probe.

Infants completed an average of 25 trials (*SD* = 5.68, range: 14-31). In the forward condition, infants showed the same advantage for responding to the congruent vs. incongruent probe that they showed in the first experiment (see Figure 8). In the backward condition, infants were expected to show the opposite pattern of responses if they were responding only to the direction of movement and not to the direction of the pointing finger. As can be observed in Figure 8, this pattern of results was not obtained – infants responded just as fast to the congruent as to the incongruent probe. These results thus suggest that infants as young as 4.5 months of age do not respond to a shared referent simply by following the direction of movement irrespective of the direction of the point.

A third possibility for why infants were able to follow the direction of a dynamic point is that the perceived point is mapped onto infants' own motor representations for pointing. This hypothesis is supported by at least two sources of evidence. In the case of pointing, the goal of the observed action is to reorient the attention of another person so that an object becomes the shared focus of attention (Woodward & Guajardo, 2002). Research with adults reveals that action simulation facilitates the ability of observers to predict the effect of an action (e.g., Chaminade, Meary, Orliaguet, & Decety, 2001; Knoblich, & Flach, 2001; Louis-Dam, Orliaguet, & Coello, 1999; Orliaguet, Kandel, & Boe, 1997). In addition, recent research suggests that slightly older infants, 6 to 12 months of age, also understand the goals or effects of an action (e.g., Gergely et al., 2003; Luo & Baillargeon, 2006; Woodward, 1998).

If visual attention is the principal factor responsible for the preceding results, then it should not matter whether the action is carried out by a human or a mechanical agent as long as both agents are equally salient. If, however, the preceding results are a function of action simulation, then the distinction between a human and a mechanical agent should make a difference. Recall that simulation depends on the perceived similarity between the observed action and the specific motor responses available to the observer.

In the last experiment, we put this hypothesis to the test by repeating the previous experiment with a stick moving to the left or to the right in place of a human hand. The stick initially appeared to be pointing toward the infant and waved up and down in a manner similar to the fingers waving up and down. After the infant fixated the stick, it was rotated so that it pointed toward the left or the right side of the screen, and then moved a short distance either in the direction it was pointing or in the opposite direction. This movement lasted 1000 ms. Similar to the previous experiments, the stick then disappeared and was replaced by a toy probe that appeared on the left or right side of the screen.

A new sample of 18 infants between 4.5 and 6.5 months of age was tested. Infants completed an average of 21.7 trials (SD = 5.3, range: 12-30). In both the forward and backward conditions, infants did not show a significant response time advantage to either the congruent direction of pointing or the congruent direction of movement (i.e., forward movement: congruent condition or backward movement: incongruent condition) (see Figure 9). It is possible that this result is attributable to the decreased familiarity or salience of the stick, because, on average, response times were higher. However, this factor, by itself, is unlikely sufficient to explain the null results, because the critical finding is not the absolute difference in response times, but rather the relative difference in response times. Accordingly, we conclude that infants, like adults, are more likely to predict the effect of an action when it is performed by a human effector, such as a hand, as opposed to a mechanical effector with little resemblance to the morphology or movements of the human action.

In sum, these results on following the direction of a point suggest that infants as young as 4.5 months of age are capable of shifting their attention in response to this action as long as the action is performed by a human agent. This finding thus appears consistent with infants predicting the goal of the deictic gesture, but there is a problem with attributing this prediction to simulating the observed action. A number of studies agree that canonical pointing emerges on average at 11 months of age, although some babies as young as 8.5 months of age have been observed to point (Butterworth & Morissette, 1996). If action simulation requires that the observed action is already in the motor repertoire of the observer, then the interpretation of simulation as the basis for predicting the referent cannot be correct.

There is, however, another way to interpret the basis for simulation which is more compatible with the current findings. Infants as young as 4.5 months of age are not able to differentiate their hand and fingers so that only the index finger is extended in the direction of the arm, but it is entirely possible that the extension of the arm and hand is sometimes performed for the same purpose as a pointing gesture at an older age. Consistent with this hypothesis, Leung and Rheingold (1981) directly compared 10.5- to 16.5-month-old infants' arm extensions with open or closed hands and arm extensions with index finger extended toward objects located at a distance from where they were sitting. The authors report that at the younger ages the majority of responses were reaches rather than pointing gestures to the distal objects. Although reaches are typically associated with an instrumental response, they were interpreted in this context as serving a social communicative function because they accompanied looking at and vocalizing to the mother.

The preceding evidence thus suggests that two actions executed by infants can share the same goal even though the means for achieving that goal differ. Interestingly, most of the evidence for an observation-execution matching system is based on shared goals and not shared means to achieve these goals. Consider, for example, the previously discussed neurophysiological findings on mirror neurons. It was shown that these neurons discharge when observing or executing the same goal-directed action regardless of whether or not the specific movements matched (Rizzolatti et al., 1996). Likewise, behavioral research with human adults shows that response priming following observation of an action depends primarily on the observation of the goal and not the specific means to the goal. For example, Longo et al. (2006) tested human adults in a choice reaction time task involving imitation of an index or middle finger tapping downwards. The results showed equivalent levels of response priming following the observation of a biomechanically possible or impossible finger tapping movement. In this example, the movements were different, but the goal of tapping downwards was the same in both conditions.

If the movements associated with the observation of a goal-directed action need not be identical in order to simulate an observed action, then it may be sufficient that the two representations share some similar features. Indeed, this is the basis for the Theory of Event Coding as presented by Hommel, Müsseler, Aschersleben, and Prinz (2001). It is well established that infants are capable of predictive reaching for moving objects by

4.5 months of age (Bertenthal & von Hofsten, 1998; Rose & Bertenthal, 1995). The motor representation for predictive reaching may be sufficient to make contact with the goal of specifying a distal referent for young infants to index and predict the goal of the point. Clearly, more research is needed to fully evaluate this hypothesis, but the possibility that a common code underlies the observation and execution of a manual gesture for specifying a distal referent by 4.5 months of age is certainly consistent with the available evidence.

Perception of Point-Light Displays of Biological Motion

The first step in understanding human actions is to perceptually organize the constituent movements in a manner consistent with the causal structure of the action. We have relied on moving point-light displays depicting biological motions to study this question, because observers are then forced to perceptually organize the stimuli in terms of the movements of the limbs without any contextual cues specified by featural information. In spite of the apparent ambiguity in these displays, adult observers are quite adept at extracting a coherent and unique structure from the moving point-lights (Bertenthal & Pinto, 1994; Cutting, Moore, & Morrison, 1988; Johansson, 1973; Proffitt, Bertenthal, & Roberts, 1984).

This conclusion is true even when the stimulus displays are masked by a large number of additional point lights that share the same absolute motion vectors with the point-lights comprising the biological motion display. In one experiment (Bertenthal & Pinto, 1994) observers were instructed to judge whether the biological motion display depicted a person walking to the right or to the left. The target was comprised of 11 point-lights that moved in a manner consistent with the spatiotemporal patterning of a person walking, but was masked by an additional 66 moving point-lights that preserved the absolute motions and temporal phase relations of the stimulus display (see Figure 10). In spite of the similarity between the point-lights comprising the target and those comprising the distracters, adult observers displayed very high recognition rates for judging the correct direction of the gait. This judgment could not be attributed to the perception of individual point-lights, because recognition performance declined to chance levels when the stimuli were rotated 180 deg. If performance was based on the movements of individual point-lights, then the orientation of the display should not have mattered. Apparently, observers were detecting an orientation specific spatiotemporal structure of the moving point-lights because it matched their internal representation which was limited by ecological constraints to a person walking upright.

This orientation specificity appears to be the norm with regard to the perception of biological motions (e.g., Pavlova & Sokolov, 2000; Sumi, 1984). One intriguing interpretation for this repeated finding is that motor experience contributes to the perception of biological motions. Of course, this finding is also consistent with visual experience contributing to the perception of biological motions in a point-light display. Although there is still insufficient evidence to reach any firm conclusions, some recent experiments by Shiffrar and colleagues (Jacobs, Pinto, Shiffrar, 2005; Loula, Prasad, Harber, & Shiffrar, 2005; Shiffrar & Pinto, 2002; Stevens, Fonlupt, Shiffrar, & Decety, 2000) have suggested that motor experience provides a unique contribution to the perception of biological motions by adults. In the remainder of this section, we will explore whether the same conclusion holds for infants' perception of biological motions.

In a series of studies begun in the 1980s, my colleagues and I (Bertenthal, Proffitt, & Cutting, 1984; Bertenthal, Proffitt, & Kramer, 1987a; Bertenthal, Proffitt, Kramer, & Spetner, 1987b; Bertenthal, Proffitt, Spetner, & Thomas, 1985; Pinto & Bertenthal, 1992) showed that infants are sensitive to the spatial and temporal structure in biological motion displays. For example, 3- and 5-month-old infants are able to discriminate a canonical point-light walker display from one in which the spatial arrangement of the point-lights is scrambled or the temporal phase relations of the point lights are perturbed (Bertenthal et al., 1987a; Bertenthal et al., 1987b). Similar to adults, infants show an orientation specific response by 5 months of age (Bertenthal, 1993; Pinto & Bertenthal, 1993; Pinto, Shrager, & Bertenthal, 1994). At 3 months of age, infants discriminate a canonical from a perturbed point-light walker display when the displays are presented upright or upside down (Pinto et al., 1994). By 5 months of age, infants only discriminate these displays when they are presented upright (Pinto et al., 1994). Our interpretation for this developmental shift is that infants are responding to local configural differences at 3 months of age, but they are responding to global configural differences at 5 months of age (Bertenthal, 1993). In essence, the local configural differences can be detected independent of orientation.

Converging evidence for this interpretation comes from two experiments showing that infants do not discriminate point-light walker displays requiring a global percept until 5 months of age. In the first of these experiments (Pinto, 1997), 3- and 5-month-old infants were tested for discrimination of two point-light walker displays with a habituation paradigm. In this paradigm, infants are presented with one of the two stimulus displays for a series of trials until their visual attention to the stimulus declines significantly, and then they are presented with a novel stimulus display for two trials. Increased visual attention to the novel display is interpreted as discrimination.

Infants were presented with a point-light walker display translating across the screen during the habituation phase of the experiment. Following habituation, infants were shown a translating point-light walker display in which the point-lights corresponding to the upper portion of the body were spatially shifted relative to the point-lights corresponding to the lower portion of the body. According to adult observers, this spatial displacement resulted in the perception of two point-light walkers in which one appeared to have its legs occluded and the other appeared to have its torso, arms, and head occluded. If infants did not perceive a point-light walker display as a global percept, then they would be less likely to detect this perturbation because both the spatially aligned and shifted displays would be perceived as a number of sub-groupings of point lights. If, however, infants did perceive the habituation stimulus display as a unitary object, then the spatially shifted translating walker would be discriminated from the preceding translating point-light walker. The results revealed that 3-month-old infants did not discriminate these two displays, but 5-month-old infants did.

In the second study, Amy Booth, Jeannine Pinto, and I conducted two experiments testing 3- and 5-month-old infants’ sensitivity to the symmetrical patterning of human gait (Booth, Pinto, & Bertenthal, 2001). In this case, sensitivity to the patterning of the limbs implies that discrimination between displays could not occur on the basis of the perceived structure of any individual limb. If infants were primarily sensitive to this patterning, then we predicted that they would not discriminate between a point-light display depicting a person walking and a person running because both displays share the same symmetrical gait pattern (even though they differ on many additional dimensions). By contrast, infants should discriminate between two displays in which the symmetrical phase relations of the limbs were perturbed.

A habituation paradigm was again used to test infants' discrimination of the point-light displays. In Experiment 1 infants were presented with a point-light display depicting a person running and a second display depicting a person walking (see Figure 11). Unlike previous experiments in which the stimulus displays were synthesized with a computational algorithm, the stimulus displays in this study were created with a motion analysis system that tracked and stored the three-dimensional coordinates of discrete markers on the major joints of a person walking or running on a treadmill. Infants' discrimination performance revealed that 3-month-old infants discriminated the walker and the runner, whereas 5-month-old infants did not (see Figure 12a). These results are consistent with the possibility that 3-month-old infants were responsive to the differences in the speed and joint angles of the two displays, but that 5-month-old infants were more sensitive to the symmetrical patterning of both displays and therefore were less attentive to lower-level differences.

In order to confirm this interpretation, a second experiment was conducted to assess whether 3- and 5-month-old infants were sensitive to differences in the symmetrical patterning of gait. Infants were tested for discrimination of a canonical point-light walker and a point-light runner in which the point-lights corresponding to the right leg and the left arm were temporally phase shifted by 90^o. The effect of this manipulation was to create a display in which one pair of diagonally opposite limbs reversed direction at 90^o and 270^o of the gait cycle, whereas the other pair of limbs reversed direction at 0° and 180° of the gait cycle (see Figure 13). The results from this experiment revealed that both 3- and 5-month-old infants discriminated the two point-light displays (see Figure 12b). Presumably, the younger infants discriminated these displays for the same reason that they discriminated the two displays in the first experiment, although strictly speaking we cannot rule out the possibility that they also detected the change in the symmetrical patterning of the displays. By contrast, the older infants had not discriminated the two displays in the first experiment, and thus their discrimination performance can only be explained in terms of detecting the changes in the gait pattern.

Taken together, the results from these last two experiments are illuminating for a number of reasons. First, they confirm that by 5 months of age, infants respond perceptually to the global structure of a moving point-light display. Second, the results from the second study suggest that infants by 5 months of age are sensitive to a fairly subtle higher-level property of the displays – symmetrical patterning of the gait pattern. One interpretation for these findings is that the visual system becomes more spatially integrative with development and also becomes more sensitive to the temporal properties of moving point-light displays. A second interpretation is that infants' sensitivity to a point-light walker display as a unitary object or as a hierarchical nesting of pendular motions with dynamic symmetry is specifically related to this stimulus depicting a familiar event. We have previously argued that the orientation specificity of our findings suggests that visual experience is an important factor in the perceptual organization of these displays (Bertenthal, 1993). The third and final interpretation is that a globally coherent and hierarchically nested moving object with bilateral symmetry corresponds to an internal representation that is relevant not only to the perception of human gait, but to the production of this behavior as well.

Previous research reveals that infants capable of stepping on a split treadmill are biased to maintain a 180 deg phase relation between their two legs even when both sides of the treadmill are moving at different speeds (Thelen, Ulrich, & Niles, 1987). In a longitudinal investigation of this phenomenon, Thelen and Ulrich (1991) report that infants' performance shows rapid improvement between 3 and 6 months of age (see Figure 14). Interestingly, this is the same period of development during which infants show increased perceptual sensitivity to the global coherence of biological motions, especially as defined by bilateral symmetry or 0˚ and 180˚ phase modes. This correspondence in age gives further credence to the suggestion of a shared representation between the perception and production of biological motions. As previously discussed by Bertenthal and Pinto (1993), the perception and production of human movements share similar processing constraints relating to the phase relations of the limb movements; thus the development of one skill should facilitate the development of the other skill and vice versa.

The evidence for a shared representation is also supported by the results from a neuroimaging study conducted by Grèzes, Fonlupt, Bertenthal, Delon-Martin, Segebarth, & Decety (2001) showing that perception of point-light walker displays by adults activates an area in the occipital-temporal junction as well as an area in the intraparietal sulcus. Whereas the former cortical area is associated with the perception of objects, the latter area is part of the neural circuit involved in the planning and execution of actions. Converging evidence supporting this finding has also been reported by Saygin, Wilson, Hagler, Bates, & Sereno (2004). It is thus possible that the perception of these point-light displays by infants also activates the motor system which confers via simulation an appreciation of the differences between a canonical and an unnatural gait pattern.

One final source of evidence to support this conjecture comes from an experiment testing infants' discrimination of a canonical point-light cat and a phase-shifted point-light cat (Bertenthal, 1993). Similar to the findings on discrimination of inverted point-light displays, 3-month-old infants discriminated these two point-light cat displays, but neither 5- nor 8-month-old infants discriminated these displays. Presumably, 3-month-old infants discriminated these displays based on local differences that were not specific to the identity of the stimulus. Although it is reasonable to suggest that older infants did not discriminate these displays at a global level because they lacked sufficient visual experience, correlative evidence is inconsistent with this hypothesis (Pinto et al., 1996). When infants were divided into two groups based on whether one or more cats or dogs lived in their home, the results revealed absolutely no difference in discrimination performance as a function of whether or not infants had daily visual experience with a cat or dog. Thus, it appears that infants' insensitivity to the spatiotemporal perturbations in these displays may have not been attributable to their limited visual experience, but rather to their limited motor knowledge of quadrupedal gait. Interestingly, infants begin crawling on hands-and-knees between 7 and 9 months of age, which suggests that crawling experience as opposed to visual experience may have been a better predictor of their discrimination performance.

Conclusions

The findings summarized in this chapter provide some of the first evidence to suggest that an observation-execution matching system is functional during infancy and contributes to action understanding through: (1) online simulation of observed actions, (2) prediction of the effects of observed actions, and (3) perceptual organization of component movements comprising an action. In order to avoid any confusion, we want to emphasize that suggesting a possible contribution of the motor system for the perception and understanding of actions is not meant to exclude the very important contributions of more traditional mechanisms (e.g., visual attention and visual experience) for understanding actions. Furthermore, the evidence presented is by no means definitive, but it is buttressed by recent neurophysiological, neuroimaging, and behavioral findings suggesting a shared representation for the observation and execution of actions by primates and human adults (e.g., Bertenthal et al., 2006; Decety & Grèzes, 1999; Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004).

The specialized circuitry and automatic activation following observation of an action suggest that the neural mechanisms mediating these functions may be part of the intrinsic organization of the brain. Indeed, this hypothesis is supported by evidence showing neonatal imitation (Meltzoff and Moore, 1994). The best known example of imitation in young infants is the evidence for oro-facial gestures (mouth opening and tongue protrusion) by infants who have never seen their own face (Meltzoff & Moore, 1977). Unlike true imitation (cf. Tomasello & Call, 1997), only actions already in the motor repertoire can be facilitated. Still, visual information about the perceived action must somehow be mapped onto the infants' own motor representations (Meltzoff &

Moore, 1994). In essence, this is the function of an observation-execution matching system.

Corollary evidence on the prenatal and early postnatal development of these oro-facial gestures is consistent with this conjecture. It is well established that fetuses perform mouth opening and closing and tongue protrusion while in utero (Prechtl, 1986). 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's been presented for some period of time (~40 s), rather than immediately (Anisfeld, 1991). This finding is consistent with a motor priming explanation in which activation would be expected to build up gradually as the gesture is modeled, as opposed to an explanation claiming the availability of higher-level processes from birth (cf. Meltzoff and Moore, 1994). 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 (Fontaine, 1984; Maratos, 1982). It is during this same window of time, approximately 2 and 6 months of age, that neonatal reflexes are gradually inhibited (McGraw, 1943), 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 lead to its execution by the infant. Thus, rather than reflecting a precocial social ability of the infant as suggested by Meltzoff and Moore (1994), neonatal imitation may reflect a striking *in*ability of the infant to inhibit activation of the motor system by direct matching mechanisms. (See Nakagawa, Sukigara, and Benga (2003) for some preliminary evidence supporting this interpretation.) Similar compulsive imitation is observed in adults after lesions of areas of the frontal lobe involved in inhibitory control (Lhermitte, Pillon, & Serdaru, 1986), and even in healthy adults when attention is diverted (Stengel, 1947).

Although overt imitation of facial gestures ceases with the development of inhibition, covert imitation continues and provides specific knowledge about these gestures when observed in others. We suggest that this same developmental process is played out at different ages for many other important behaviors (e.g., direction of gaze, 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 throughout the lifespan.

Finally, the findings reviewed in this chapter are relevant to the current debate in the literature regarding the development of action understanding. The early development of representing actions as goal-directed has been studied from two different theoretical perspectives: (1) action understanding is reciprocally coupled to the capacity to *produce* goal-directed actions (Hofer, Hauf, & Aschersleben, 2005; Longo & Bertenthal, 2006; Sommerville, Woodward, & Needham, 2005), or (2) recognizing, interpreting, and predicting goal directed actions is an *innately based, abstract, and domain-specific* representational system, specialized for identifying intentional agents and/or for representing and interpreting actions as goal-directed (e.g., Baron-Cohen, 1994; Csibra & Gergely, 1998; Gergely et al., 1995; Premack, 1990). The first perspective is consonant with the views discussed in this chapter. The second perspective suggests that infants are innately sensitive to *abstract behavioral cues* (such as self-propulsion, direction of movement or eye gaze) that indicate agency, intentionality, or goal-directedness, irrespective of previous experience with the types of agents or actions that exhibit these cues. Infants are presumed sensitive to unfamiliar actions of humans or unfamiliar agents with no human features from very early in development as long as the actions are consistent with one or more of the proposed abstract cues.

Although the findings presented here cannot resolve this controversy, at the very least they cast doubt on the assertion that understanding goal-directed actions is based on an abstract representation that is independent of whether the agents are human or mechanical. In both object search and follow the point studies, infants showed different levels of responding to human and mechanical agents. Moreover, the evidence reviewed on infants' sensitivities to biological motions suggests that the perceived structure of a point-light display is significantly greater when the display depicts a human action as opposed to a familiar or unfamiliar quadrupedal action. As we and our colleagues continue to investigate the evidence for common coding of observed and executed actions by infants, we hope to develop a more finely nuanced theory that will reveal what specific knowledge about actions is innate and what knowledge develops with age and experience.

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Figure Captions

Figure 1. Six sequentially sampled frames from a moving point-light display depicting a person walking.

Figure 2. Infant searching for toy in one of the two hiding wells. (from Longo & Bertenthal, 2006)

Figure 3. Percentage of infants searching incorrectly on first, second, and third reaching A trials, searching B trial, and looking B trial. (from Longo & Bertenthal, 2006)

Figure 4. Percentage of infants searching incorrectly following observation of ipsi- and contralateral reaches by the experimenter in the looking condition of Experiments 1 and 2. (from Longo & Bertenthal, 2006)

Figure 5. Infant observing the toy being hidden by two mechanical claws.

Figure 6. Stimulus sequence for each trial. 1. Fingers wave up and down. 2. Index finger points toward left or right side of screen. 3. Probe appears on left or right side. (This sequence corresponds to an incongruent trial.)

Figure 7. Mean response times for infants to orient toward the congruent and incongruent probes. In the dynamic condition, infants were shown a pointing finger that moved a short distance in the same direction that the finger was pointing. In the static condition, infants were shown a pointing finger that didn't move.

Figure 8. Mean response times for infants to orient toward the congruent and incongruent probes. In the *forward* condition the finger moved in the same direction it was pointing. In the *backward* condition the finger moved in the opposite direction that it was pointing.

Figure 9. Stick experiment. Mean response times for infants to orient toward the congruent and incongruent probes. In the *forward* condition the finger moved in the same direction it was pointing. In the *backward* condition the finger moved in the opposite direction that it was pointing.

Figure 10. Left panel depicts point-light walker display appearing to walk to the right. (Outline of human form is drawn for illustrative purposes only.) Right panel depicts point-light walker display masked by moving point-lights preserving the absolute motions and temporal phase relations of the target stimulus. (from Bertenthal & Pinto, 1994)

Figure 11. Four frames of the walker (in gray) superimposed over the runner (in black). Point-lights are connected for ease of comparison. (from Booth et. al., 2001)

Figure 12. (a) Top panel; Walker vs. Runner. Mean looking times on the last three habituation trials and on the two test trials as a function of age. The stimuli included a point-light walker and a point-light runner, each of which served as the habituation stimulus for half of the infants. (b) Bottom panel; Walker vs. Phase-Shifted Runner. Mean looking times on the last three habituation trials and on the two test trials as a function of age. The stimuli included a point-light walker and a phase-shifted point-light runner, each of which served as the habituation stimulus for half of the infants. (from Booth et. al., 2001)

Figure 13. Four frames of the walker (in gray) superimposed over the phase-shifted runner (in black). Point-lights are connected for ease of comparison. (from Booth et. al., 2001)

Figure 14. Mean number of alternating steps by trial and age, pooled across all infants. Trials 1 and 9 are baseline trials. (from Thelen & Ulrich, 1991).

Figure 1

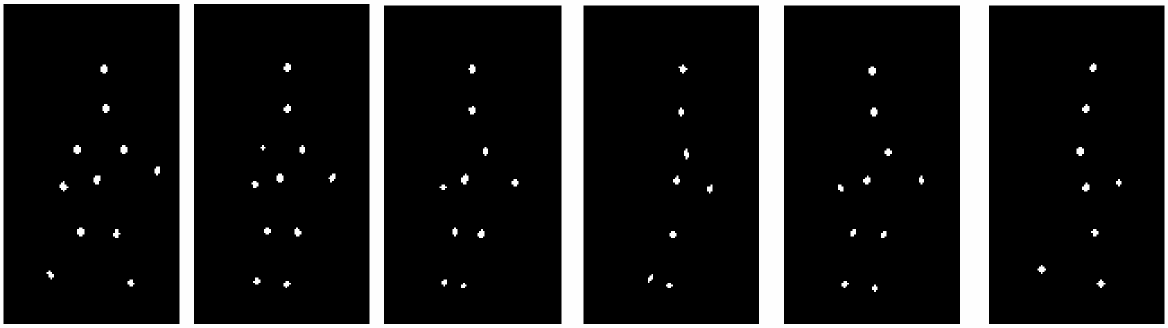


Figure 2

Figure 3

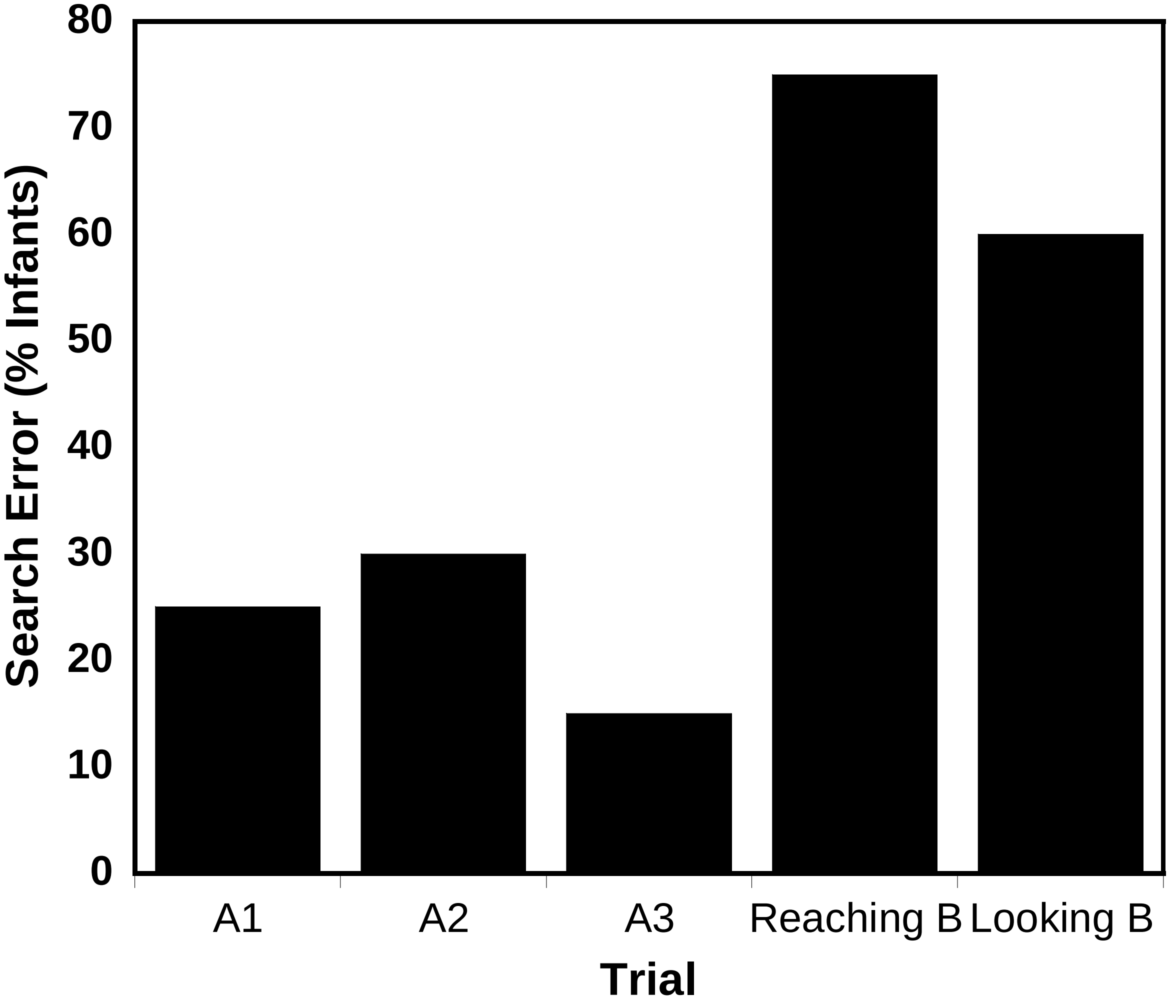

80
70
60
50
40
30
20
10
0
Search Error (% Infants)
A1
A2
A3
Reaching B
Looking B
Trial

Figure 4

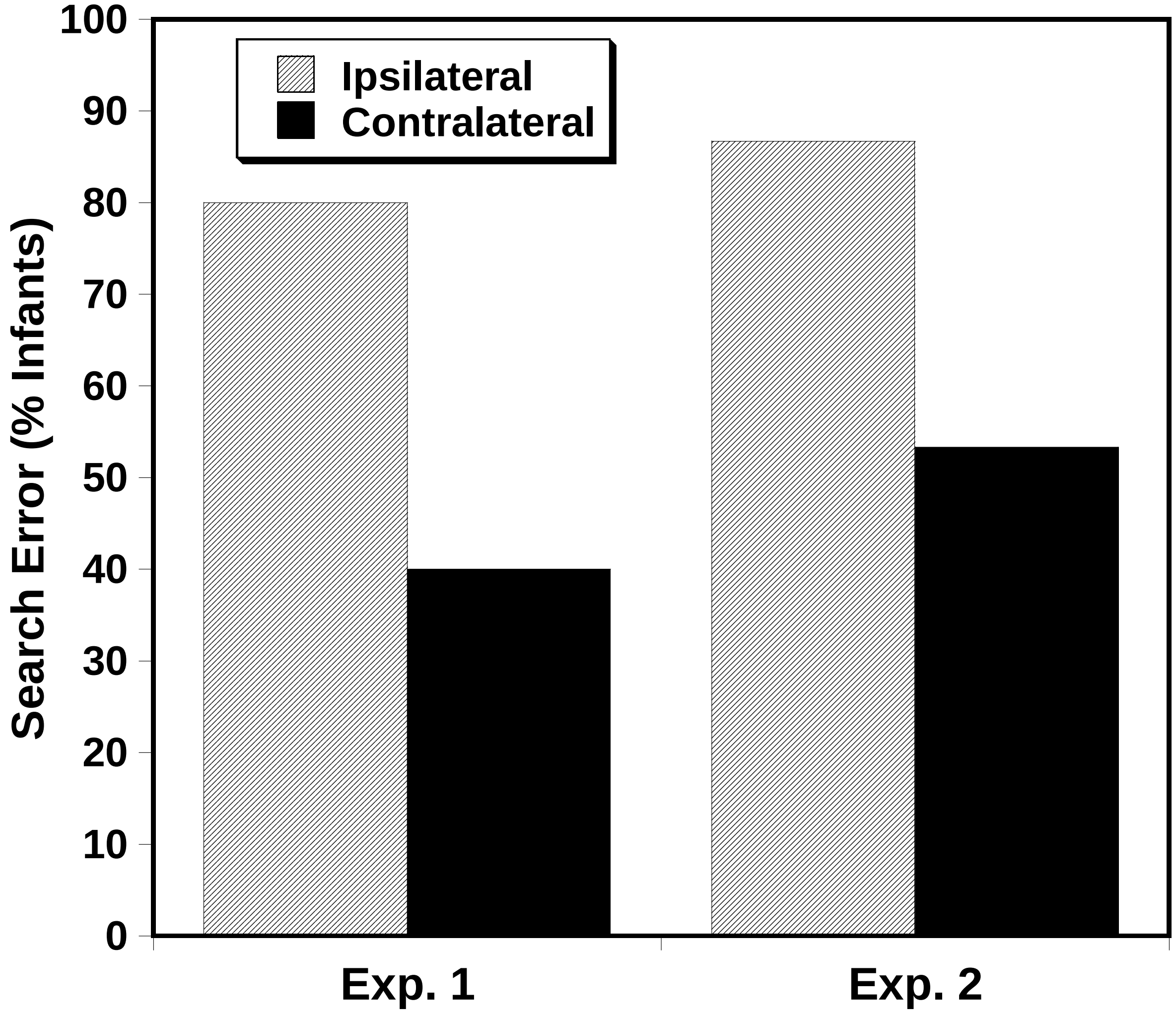
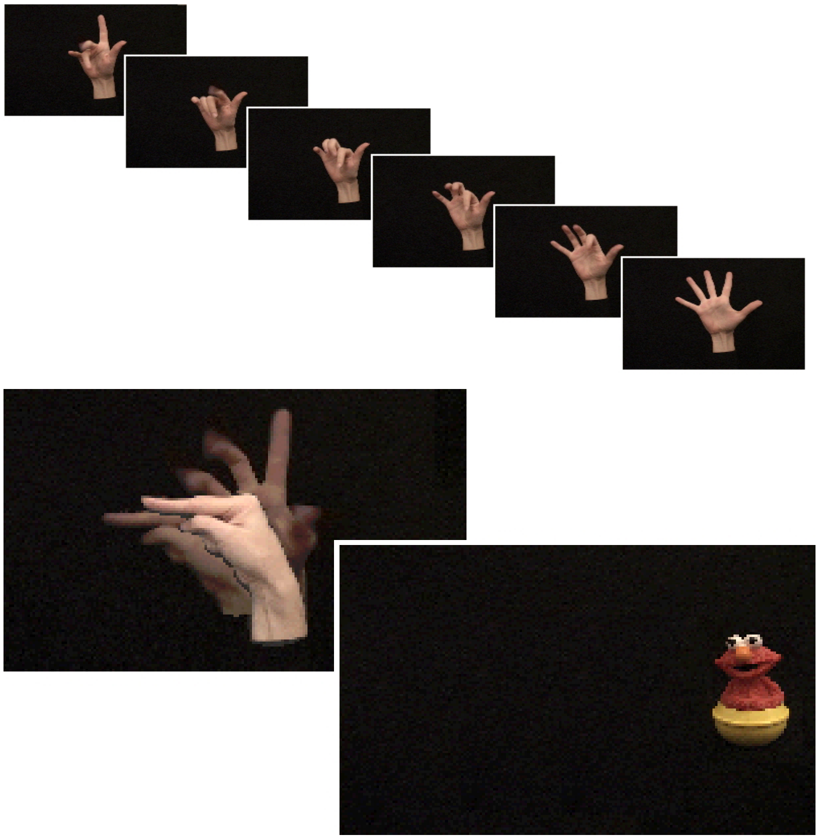

100
90
80
70
60
50
40
30
20
10
0
Search Error (% Infants)
Ipsilateral
Contralateral
Exp. 1
Exp. 2

Figure 5

Figure 6



1. Finger waving

2. Finger pointing
(1000 ms)

3. Probe appears

Figure 7

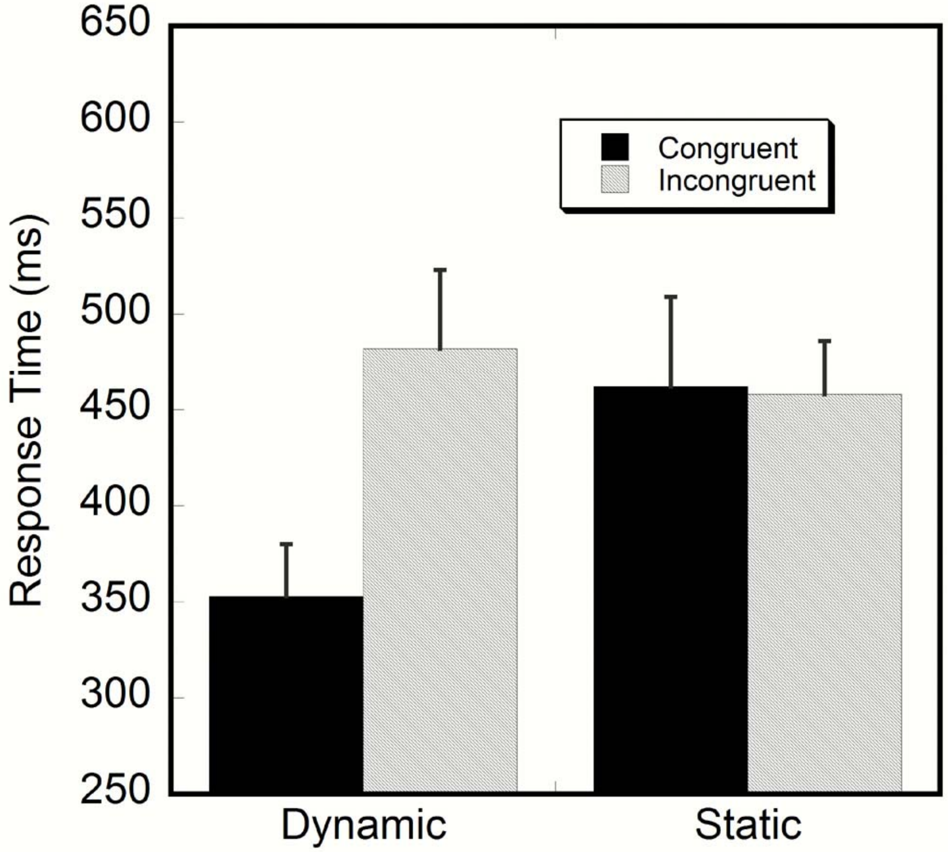

650
600
550
500
450
400
350
300
250
Response Time (ms)
Congruent
Incongruent
Dynamic
Static

Figure 8

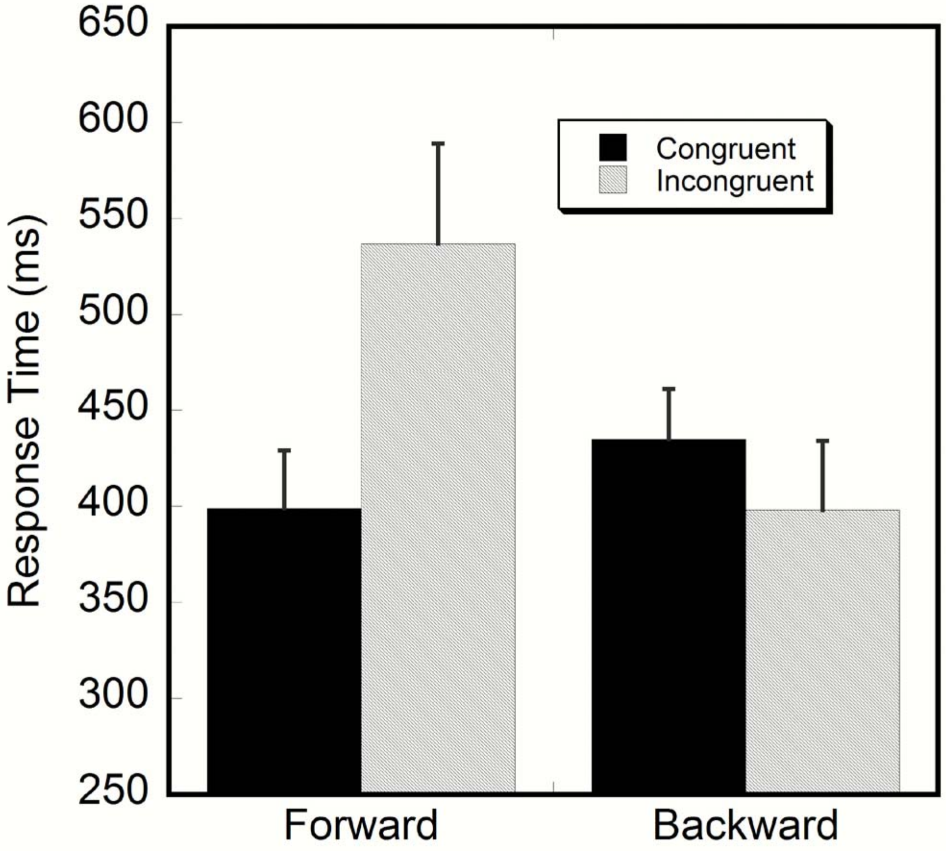

650
600
550
500
450
400
350
300
250
Response Time (ms)
Congruent
Incongruent
Forward
Backward

Figure 9

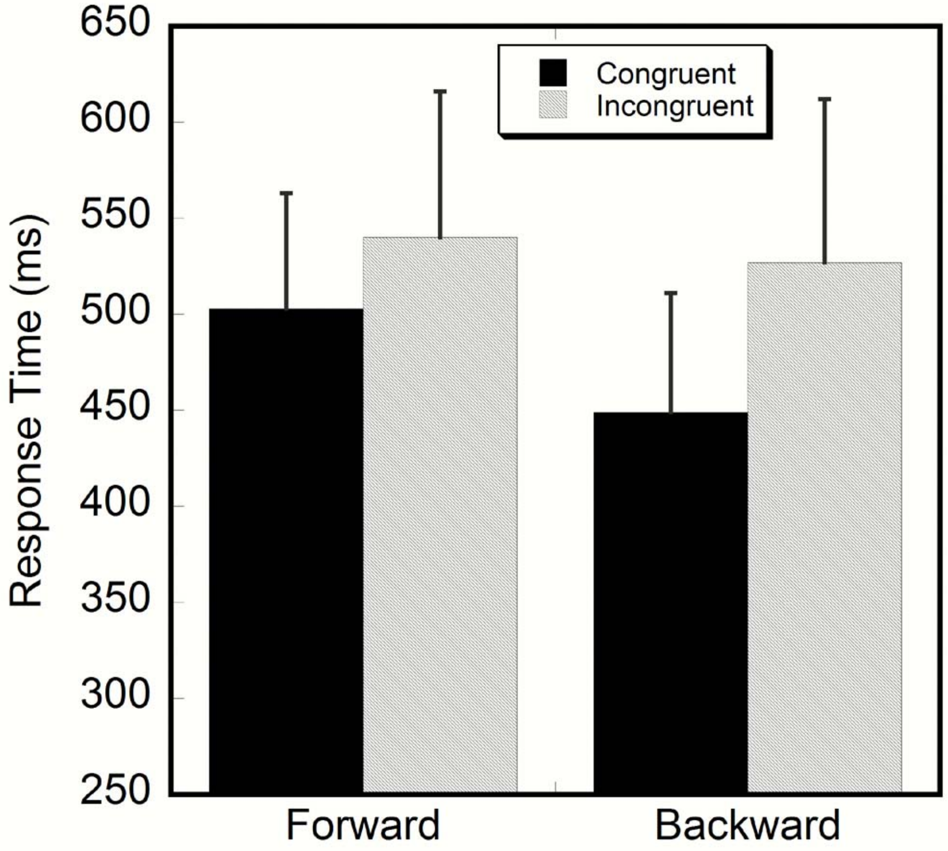

650
600
550
500
450
400
350
300
250
Response Time (ms)
Congruent
Incongruent
Forward
Backward

Figure 10

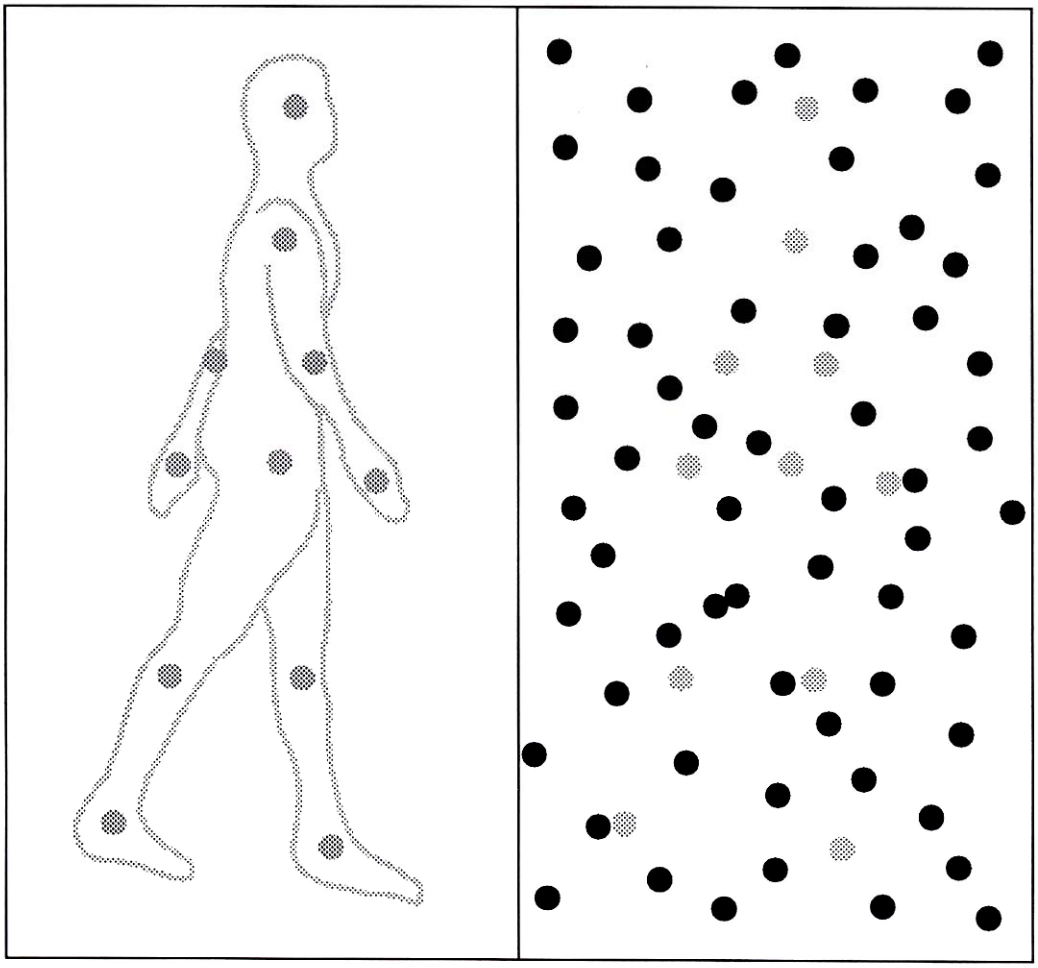


Figure 11

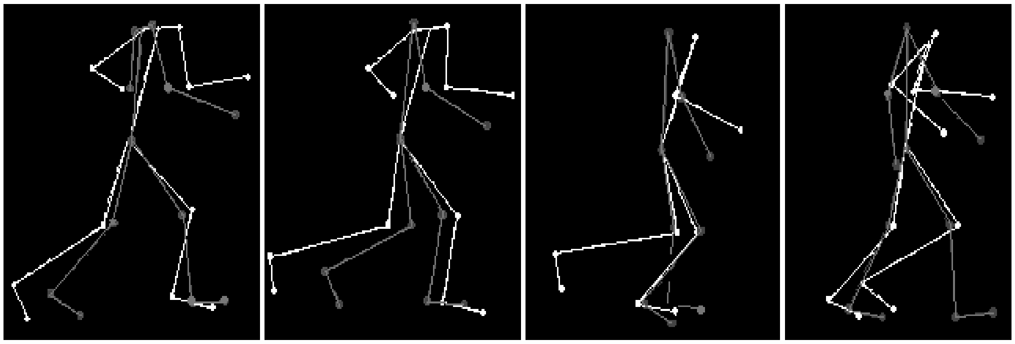


Figure 12a

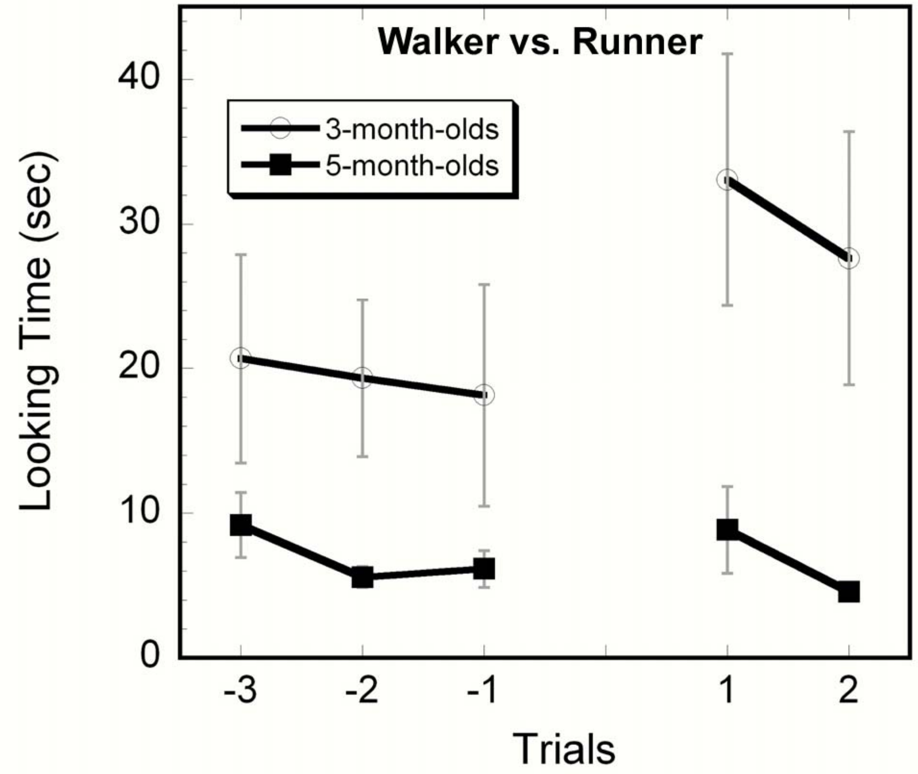

Walker vs. Runner
3-month-olds
5-month-olds
Looking Time (sec)
0
10
20
30
40
-3
-2
-1
1
2
Trials

Figure 12b

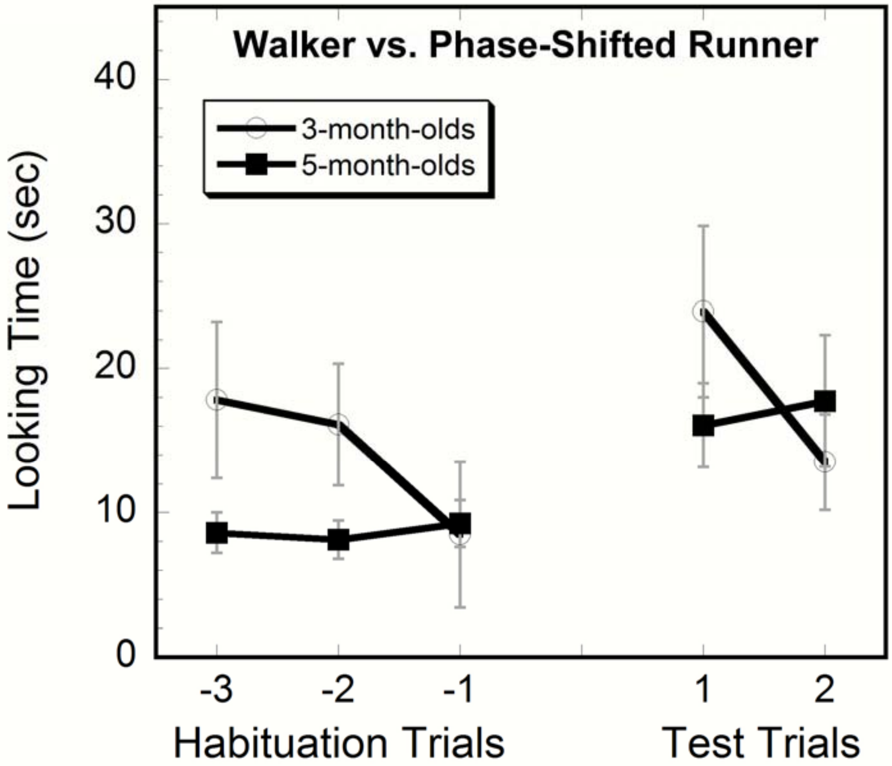

Walker vs. Phase-Shifted Runner
3-month-olds
5-month-olds
Looking Time (sec)
40
30
20
10
0
-3
-2
-1
1
2
Habituation Trials
Test Trials

Figure 13

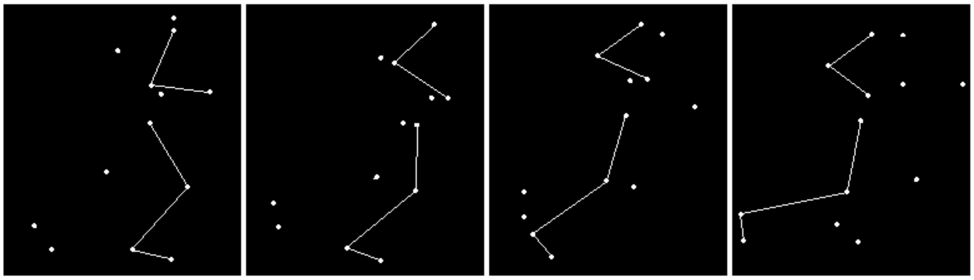
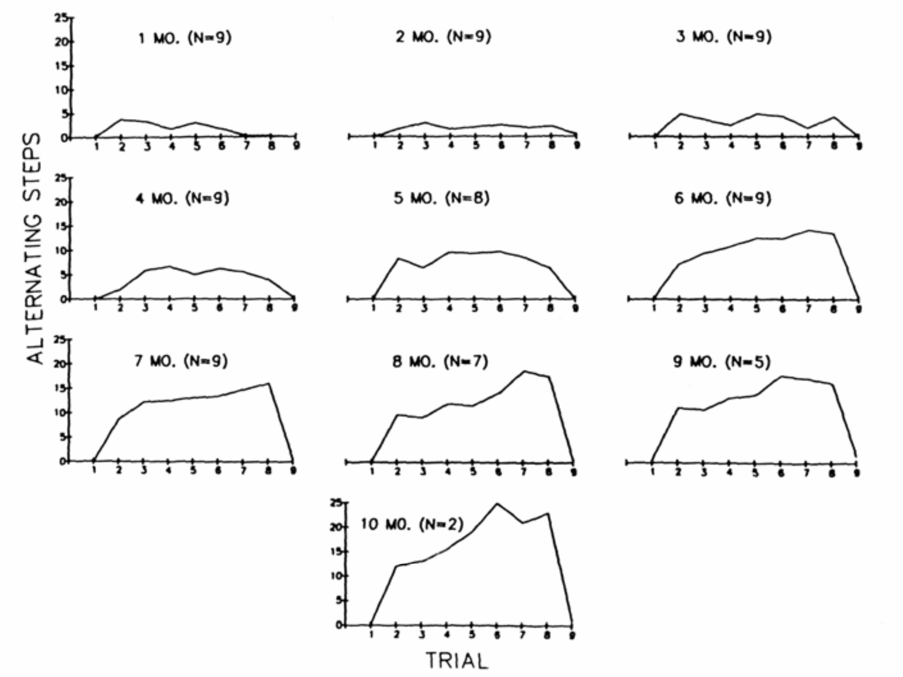


Figure 14


ALTERNATING STEPS
TRIAL
1 MO. (N=9)
2 MO. (N=9)
3 MO. (N=9)
4 MO. (N=9)
5 MO. (N=8)
6 MO. (N=9)
7 MO. (N=9)
8 MO. (N=7)
9 MO. (N=5)
10 MO. (N=2)
0
5
10
15
20
25
1
2
3
4
5
6
7
8
9