Published in final edited form as:
Dev Psychobiol. 2019 April ; 61(3): 390–401. doi:10.1002/dev.21779.

The role of the motor system in action understanding and communication: Evidence from human infants and non-human primates

Virginia C. Salo[1], **Pier F. Ferrari**[2], and **Nathan A. Fox**[1]

[1]University of Maryland, College Park, USA

[2]CNRS/Université Claude Bernard Lyon, France

Abstract

There is growing evidence that activation of the motor system during observation of actions, a phenomenon first observed in non-human primates, underlies action understanding and even communication. This review 1) examines the evidence on motor system activity as an underlying neural correlate of action understanding, 2) reviews the theoretical and empirical work linking action understanding and the development of communication, with a specific focus on the role that gestures play as an intermediary, and 3) discusses the research on and existing opportunities for understanding the link between the motor system and communication in both humans and non-human primates, through the lens of action perception. Bringing together findings and perspectives from developmental social cognition in both humans and non-human primates and applying recent neuroscientific perspectives will help to elucidate the processes underlying the ability to understand and communicate with others.

Keywords

Mirroring; communication; human infants; primates; rhesus macaques; gesture; language

Over the past few decades, a neural phenomenon, known as the mirror neuron system (MNS), in which action and perception are integrally linked has been gaining traction as a hypothesized neural correlate for action understanding. More recently, the MNS has also been implicated in the phylogenetic and ontogenetic development of manual and oral communication systems. In this paper, we examine whether the existing literature supports these claims, and look specifically at a theory suggesting that gestures serve as an intermediary developmental step between actions and language. There is a large and still growing body of work utilizing observational and behavioral methods to support this theory. However, as we will discuss, research directly examining the link between the motor system and communication through the lens of action perception that utilize neurophysiological measures in both humans and non-human primates is still limited.

Address for contact: Virginia C. Salo, Department of Human Development and Quantitative Methodology, 3304 Benjamin Building, University of Maryland, College Park, MD 20742 (vcsalo@umd.edu).

The mirror neuron system

In the 1990s, a group of specialized neurons were discovered in the brain of macaques that were active both when the monkeys performed simple object-directed actions and when they observed conspecifics or humans performing those same actions (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). These neurons, which came to be known as mirror neurons, were found via single-cell recording in the ventral premotor cortex and subsequently in the inferior parietal lobe (Fogassi et al. 2005), providing evidence for a shared neural circuitry in the sensorimotor brain regions for both execution and observation of actions (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Rizzolatti, Fogassi, & Gallese, 2001). This resonant activation of the motor system during action observation has been hypothesized as a neural correlate not only for action recognition, but also for the understanding of the goals and intentions that drive actions (Fogassi et al., 2005; Rizzolatti & Sinigaglia, 2010; Southgate, 2013; although see Steinhorst & Funke, 2014).

Using a variety of neuroimaging techniques, including functional neuroimaging (fMRI: see Caspers, Zilles, Laird, & Eickhoff, 2010 for a review), transcranial magnetic stimulation (TMS: e.g., Cattaneo, Sandrini, & Schwarzbach, 2010; Stadler et al., 2012), EEG (see Fox et al., 2016 for a review) and even single-cell recording, under rare occasions (e.g., Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010), researchers have found evidence for a similar action-perception matching mechanism in humans.

Although most of the information obtained on the mirror neuron system has been possible through neuroimaging or TMS studies, one method of measuring activity of the MNS which is of particular interest is the EEG mu rhythm because it has been utilized with humans across the lifespan, starting from early infancy, and with non-human primates. The mu rhythm, first documented by Berger in 1929 (Berger, 1929), reflects oscillatory activity within the alpha band (~8–13 Hz in adults, ~6–9 Hz in infants) and exhibits changes in amplitude reflecting activation of the sensorimotor system (Neuper & Pfurtscheller, 2001; Pineda, 2005). Specifically, the amplitude of the signal decreases as compared to baseline activity, with peak suppression over sensorimotor areas (Kuhlman, 1978). This suppression of activity is likely due to an increase in desynchronized neuronal activity associated with the processing of motoric information (Pfurtscheller & Lopes da Silva, 1999). Mu rhythm desynchronization has been reported during both execution and observation of actions (see Fox et al., 2016 for a review), and source localization analyses have suggested that the source of the mu rhythm signal is indeed from within the inferior parietal lobe, dorsal premotor cortex, and primary somatosensory cortex (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011; Thorpe, Cannon, & Fox, 2016).

Importantly, as mentioned above, the EEG mu rhythm has proven to be a useful tool for measuring sensorimotor activity across a wide range of ages. Methodologically, EEG is an easier neuroimaging technique with infants as compared to other more invasive and taxing methods, such as fMRI, because it allows assessing more movement-related brain activity (such as gestures or facial expressions) of the participant and for the child and parent to remain together during testing, among other reasons. Further, having a consistent measure of sensorimotor activity from infancy through adulthood is key to understanding the functional significance throughout development. The mu rhythm in infants oscillates at a lower frequency than in adults (~6 to 9 Hz), which is a typical trend in infant compared to adult EEG (Marshall, Bar-Haim, & Fox, 2002). However, the regional specificity of the mu rhythm in infants overlaps with that of adults (Marshall, Young, & Meltzoff, 2011; Thorpe et al., 2016). The greatest desynchronization of the mu rhythm during execution of actions is seen over central scalp locations, while during action observation the activity is a bit more dispersed over frontal, central, and parietal scalp locations. Over the past decade or so there has been an uptick in developmental research utilizing mu rhythm desynchronization (see Cuevas, Cannon, Yoo, & Fox, 2014; Marshall & Meltzoff, 2011 for reviews). Work with non-human primates has also provided evidence that the EEG mu rhythm is a valid measure of the MNS across species (Bimbi et al., 2018; Coudé et al., 2014; Vanderwert et al., 2015).

Mirroring and action understanding

Interest in this pattern of resonant activity of the motor system during action observation is in the functional significance of such activity. In particular, one critical question is what such a mechanism might indicate in terms of our understanding of others' actions (Rizzolatti & Fabbri-Destro, 2008). There is a growing body of empirical evidence that activity of the motor system is related to our understanding of others' actions in both humans and non-human primates. For example, blocking activation of the premotor cortex (via TMS) in human adults during action observation disrupted the participants' ability to discriminate functional differences in observed hand motions (Cattaneo et al., 2010), and the ability to infer or predict the outcome of a partially occluded action (Stadler et al., 2012). Also utilizing TMS, Michael and colleagues (2014) found evidence for somatotopic specificity in the link between the premotor cortex and action understanding, such that stimulation over the hand and lip areas disrupted recognition of hand and mouth movements, respectively. A meta-analysis of studies using lesion-symptom mapping found that damage to premotor, parietal and temporal regions was consistently associated with deficits in action perception and understanding (Urgesi. Candidi, & Avenanti, 2014). Systematic reviews of studies that have compared object-directed versus non-object-directed actions using fMRI, have found a more consistent pattern of activation during observation of actions that are object-directed (Caspers et al., 2010; Morin & Grèzes, 2008; Van Overwalle & Baetens, 2009). These findings suggest that an individual's motor system is recruited both in predicting the outcomes of others' actions and in interpreting the goals and intentions driving actions.

The use of the mu rhythm as measured via EEG has fostered an increase of attention and research on the development of the link between mirroring and action understanding. The youngest infants included in a published observation of mu rhythm desynchronization were 4-month-olds (Virji-Babul, Rose, Moiseeva, & Makan, 2012), and the findings from this study suggest that the infant mu rhythm is initially sensitive to all coherent motion, not necessarily human actions or actions with which they have experience. The infants ranged from 4- to 11-months old and included only 14 total infants, thus results should be interpreted cautiously. However, such a finding fits with behavioral data suggesting that younger infants will attribute goals to both human and nonhuman agents (Luo & Baillargeon, 2007), while older infants only do so for human and human-like agents

(Johnson, 2003; Meltzoff, 1995), but not inanimate objects. Thus, interpreted in light of the behavioral findings, this early pattern of non-discriminant mu rhythm desynchronization might suggest that young infants are recruiting their motor system in trying to decipher the meaning or purpose behind all motion as they learn to discriminate that which is similar to their own developing motor repertoire and that which is not. A similar developmental trajectory has been observed in studies of mu rhythm desynchronization in response to goal-directed versus non-goal directed actions. 8- to 9-month-olds exhibit greater mu desynchronization during observation of a goal-directed action as compared to during observation of a non-goal directed action (Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; Southgate, Johnson, Karoui, & Csibra, 2010), as do older children (Lepage & Théoret, 2006) and adults (e.g., Muthukumaraswamy, Johnson, & McNair, 2004; Nyström, 2008). However, six-month-olds do not exhibit such a difference (Nyström, 2008). Thus, sensorimotor activity seems to be correlated with infants' developing understanding of the actions they observe.

In a series of studies with 9-month-olds, Southgate and colleagues found evidence that mu rhythm desynchronization is a reflection of action and goal prediction (Southgate et al., 2010; Southgate, Johnson, Osborne, & Csibra, 2009). Infants' mu rhythm desynchronization was measured during both execution and observation of grasping actions (Southgate et al., 2009). As expected, the researchers found overlap between the two conditions. What was of most interest was the time-course of activation during the observation trials. Specifically, they observed two periods of desynchronization: one that occurred during observation of the reaching/grasping action, and one that occurred just prior to the start of the action. This first period of suppression might suggest that the motor system was active even prior to an observed action and that it is involved not only in prediction of goals, but also in prediction of the actions performed to reach those goals. This predictive desynchronization was compared across trials and the researchers found that it was only significant after the first three trials, suggesting that once the infants learned that they could expect an action, the motor system came on board to facilitate prediction of that action. In a second study, also with 9-month-olds, infants were shown grasping actions either without an object or with the end of the action being hidden behind an occluder (Southgate et al., 2010). The purpose of these conditions was to compare motor system activity when a goal could (occluder condition) or could not (no object condition) be inferred. Indeed, they found significant mu rhythm desynchronization during action observation in the occluder condition, but not in the no object condition, suggesting that motor system activity is involved in the inference of goals.

More recently, researchers have begun to examine how individual differences in activation of the motor system in infants during observation of actions might predict behavioral evidence of their action understanding. For example, Filippi and colleagues (2016) found that the strength of mu rhythm desynchronization during observation of grasping actions in 7-month-olds was related to the infants' propensity to imitate the goal of the observed actor by subsequently selecting the same toy that the actor had grasped. A very recent, unpublished infant study provides further evidence. Yoo, Thorpe, and Fox (2016) found that mu rhythm desynchronization during observation of grasping actions predicted infants' ability to learn a novel means-end motor task (retrieving a toy with a cane) whereas it did not predict their learning in a visual pattern task, further suggesting the motor system activity is indeed related to action processing *and* goal interpretation.

The link between mirroring activity and action understanding is not limited to humans. Using single-cell recording in the ventral premotor cortex of monkeys, Coudé and colleagues (2016) found evidence that activity of mirror neurons can be modulated by the presence of a social or pedagogical cue, specifically the direction of eye gaze that accompanies an action. There is also a subset of monkey mirror neurons that become active during the final part of an observed action even when the end of the action is hidden (Umiltà et al., 2001). Thus, these mirror neurons in the monkey seem to be involved or recruited when the monkey is inferring the goal or outcome of an action.

How does mirroring support understanding? There are a number of hypotheses for how such a mechanism might work. Rizzolatti and colleagues have proposed, and we have reviewed evidence above, that internal representation of perceived actions is supported through activation of a one-to-one overlapping system with one's own actions (Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001). More specifically, according to this direct-matching hypothesis it is through a simulation process with resonant activation of the motor system in which the visual description of an action is mapped on to the corresponding motor representation. Such motor activation indicates that an observed action is described into a motor format, which belongs to the observer's motor repertoire. However, according to some researchers, goal ascription is too complex for a simple mapping system such as motor resonance (e.g., Hickok, 2009). Paulus (2012) has proposed applying the ideomotor theory to explain how motor system activation can lead to action understanding. Based on this account, repeated co-occurrence of an action and its effect creates a bidirectional link between the activation of one's motor system and a representation of the effect. When subsequently observing another person perform the same or a similar action, one's motor program for that action is engaged which in turn activates the effect representation. The effect representation then facilitates anticipatory behaviors relevant to that effect, for example directing visual attention toward the target object of an action (2012). Thus, according to this theory, resonant motor activity during observation of actions supports goal interpretation through facilitating an expectation of the outcome. In an even more conservative interpretation, Heyes (2010, 2013) has contended that such a matching system is simply the result of associative learning. Specifically, that contingency and contiguity of action-perception experiences create and shape the function of the motor system during action observation. Alternative accounts (Ferrari, Tramacere, Simpson, & Iriki, 2013; Murray et al. 2016) have emphasized the role of associative learning while also expanding on it, showing, for example, that during development infants can build visuomotor connections through contingencies. However, these cannot be done without strong predispositions and neural prewiring, which prepare the infant brain to capitalize on relatively few opportunities to create new associations in the course of everyday life. In addition to this, Iacoboni and Wilson (2006) propose that several systems are likely interacting to support action understanding, a theory for which there is growing evidence that will be discussed briefly later on. A key difference between these various theories seems to be how encompassing one's definition of action understanding may be, and many researchers have specifically argued for the need to empirically tease apart 'action understanding' from other coincidental processes such as perception and mentalizing (Gallese, Gernsbacher, Heyes, Hickok, & Iacoboni, 2011). However, what these different theories share is the notion that activity of the motor system is in some way, either directly or more indirectly, related to our understanding of others' actions.

Action understanding and communication

Research into what supports the ability to understand actions receives a great deal of attention because action understanding is seen as a critical foundation for the development of social cognitive advances such as Theory of Mind, empathy, cooperation, and other important uniquely human cognitive skills, such as language. Critically, gestures have been cited as an important intermediary in the link between action understanding and language (Capirci, Contaldo, Caselli, & Volterra, 2005), such that infants are able to extend their understanding of actions to communicative gestures, which in turn supports their understanding of spoken language. Specifically, gestures support a transition from an earlier ability for interpreting concrete actions with visible consequences, to the more difficult process of interpreting spoken words which are completely abstract, often arbitrary, and have no visible consequence in the physical world. As described by Woodward (2004), "In the infant's world, words are actions, and infants most likely draw on their understanding of action in making sense of words from the very beginning (p. 150)." That is, action, gesture, and language are proposed to be overlapping cognitive systems, and the ability to communicate through language builds, both ontogenetically and phylogenetically, from the ability to understand the intentions and goals driving one's own and others' actions (Corballis, 2012).

Evolutionary arguments for how gestures may have served as a stepping stone between action and language have been put forth by several researchers (Arbib, 2005, 2012; Corballis, 2012; Hewes, 1973; Rizzolatti & Arbib, 1998; Fogassi and Ferrari 2007; Tomasello, 2008), who all propose a similar phylogenetic trajectory such that: our prehistoric (and prelingual) ancestors learned that they could direct others' attention through their physical movements (e.g., motioning toward a perceived object of threat), and in turn that others could direct their attention similarly (Tomasello, 2008). These physical movements gradually became more refined and specific and became used not only for directing attention but also to convey specific information. These actions, or what we would now refer to as communicative gestures, became the first medium for a human communication system, what Arbib refers to as a "proto-sign" (Arbib, 2005). As the use of gestures to communicate expanded and became ritualized, these gestures also became paired with vocalizations which exponentiated the number and specificity of ideas one could convey. Just as with gestures, vocalizations became increasingly fine-tuned and eventually became representations and means for communication all on their own.

It should be noted that there are limitations to this theory of the evolution of language. The transition from a manual to vocal communication system is a primary sticking point (MacNeilage, 1998). Indeed, many argue for alternative theories of language evolution in which gestures have little to no formative role (e.g., Aboitiz, García, Bosman, & Brunetti, 2006; Falk, 2004; Hillert, 2014). Alternatively, Kendon (2011, 2017) argues for the co-evolution of speech and gestures.

A similar trajectory to that outlined above linking action understanding, gestures, and language can also be observed ontogenetically. Through a process of sensorimotor exploration, the infants' intentional actions on the environment first become meaningful to her as she uncovers a sense of her own agency (Foglia & Wilson, 2013; Piaget, 1952). Soon after, infants are able to recognize others' behavior as 'commensurate' with their own actions, and this you-to-me matching allows the infant to use their own behavior and experiences as a basis for interpreting the behavior of others (Meltzoff, 2007). Understanding actions and responding accordingly relies on the infant's ability to represent her own as well as her partner's goal-related intentional behavior (Tomasello, Carpenter, Call, Behne, & Moll, 2005). When an infant is presented with an action, correct interpretation is based on an understanding of that action in terms of the outcomes it is designed to achieve (Tomasello, Kruger, & Ratner, 1993). Once an infant understands that the people around her are acting with intention, just as she can and does, every action becomes instilled with meaning and discovering that meaning becomes her task. This is crucial in learning language because to learn the meaning of a communicative symbol (i.e., a gesture or a word) one must understand the purpose for which it was used.

Using a range of behaviors to operationalize action understanding in infancy (including, but not limited to, gaze-following, point-following, predictive eye movements, and imitation), researchers have found repeated evidence that early action understanding predicts language development. Gaze following measured at the end of the first year predicts both vocabulary size and rate of growth in vocabulary over the first two years of life (Brooks & Meltzoff, 2008; Tenenbaum, Sobel, Sheinkopf, Malle, & Morgan, 2015). The ability to imitate the goals of actions in the second year of life predicts language production skills at 3 years (Charman et al., 2000) and can even predict whether an infant exhibits later language delays (Zambrana, Ystrom, Schjølberg, & Pons, 2013). Engaging in joint attention, which involves sharing attention with a partner to a third entity, such as when an infant is attending simultaneously to both a parent and a toy (Seibert, Hogan, & Mundy, 1982; Tomasello & Farrar, 1986), involves much of the behaviors used to measure infants' action understanding listed above and has been implicated as a manifestation of infants' intention understanding (Salo, Rowe, & Reeb-Sutherland, 2018). In line with this interpretation, there is a bounty of evidence linking infants' ability to initiate and respond to bids for joint attention with concurrent and later language abilities (Bates, Benigni, Bretherton, Camaioni, & Volterra, 1979; Camaioni, Castelli, Longobardi, & Volterra, 1991; Desrochers, Morissette, & Ricard, 1995; Markus, Mundy, Morales, Delgado, & Yale, 2000; Morales et al., 2000; Morales, Mundy, & Rojas, 1998; Mundy & Gomes, 1998).

As alluded to above, gestures are thought to serve as an important intermediary between actions and language for infants (Capirci et al., 2005). According to this 'gesture as intermediary' hypothesis, infants extend their understanding of actions to communicative gestures, which in turn supports their understanding of spoken language. That is, the same process for understanding the referential, intentional, and goal-directed nature of actions is applied to understanding gestures and eventually to word learning (Woodward, 2004).

Gestures are pivotal in this developmental trajectory because they support a transition from the earlier ability for interpreting concrete object-directed actions, whose consequences are often visible making inferences about the underlying intentions more accessible, to the more difficult process of interpreting spoken words which are completely abstract, often arbitrary, and have no visible consequence in the physical world. Gestures share important aspects with both actions and words. Gestures are actions in that they involve movement of the body, and there is evidence that producing both actions and gestures support learning (Kontra, Goldin-Meadow, & Beilock, 2012; Wakefield. Novack, Congdon, Franconeri, & Goldin-Meadow, 2018). Further, experience producing actions is linked with one’s understanding of those same actions as goal-directed (Sommerville & Woodward, 2005), and similarly experience producing gestures is linked with infants’ understanding of gestures. As an example, by 12 months, infants exhibit an understanding of the relational aspect of pointing gestures (Woodward & Guajardo, 2002). That is, they understand that a point is associated with a specific referent. It is during this time that infants also begin to produce their own points (Carpenter et al., 1998), and critically, the ability to make the association between point and referent depends on the infants’ own experience producing points. That is, infants are more likely to understand pointing gestures as relational if they already produce object-directed points (Brune & Woodward, 2007).

A critical aspect that gestures share with spoken words is that they are also representational. This concept is nicely defined by Novack & Goldin-Meadow:

> When we say that gestures are representational actions, we mean that they are meaningful substitutions and analogical stand-ins for ideas, objects, actions, relations, etc.
>
> (2017, p. 1).

Just as with actions, we interpret gestures in terms of the goal or intention driving one to produce them. However, the intended consequence of a gesture is to represent something that both the producer and observer of the gesture will understand, that is the intention is communicative. Thus, both gestures and words, or language more broadly, serve a communicative function. Through the use of gestures the infant attains a manner in which to communicate about objects in her world in a modality that is available to her, actions of the hand, before she is able to express herself via speech (Capirci, Iverson, Pizzuto, & Volterra, 1996; Goldin-Meadow & Butcher, 2003; McNeill, Duncan, Cole, Gallagher, & Bertenthal, 2008; Volterra, Caselli, Capirci, & Pizzuto, 2005). Once an infant understands the goal-directedness of actions, she can extend that property to more abstract gestures, and in turn to words.

There is a large and growing body of evidence for this link between actions and gestures and between gestures and language. Woodward and Guajardo (2002) found that infant’s understand the object-directedness of concrete actions (i.e., reaching and grasping) a few months earlier than gestures (i.e., pointing). A series of studies by Goldin-Meadow and colleagues (Novack et al., 2015; Wakefield, Novack, & Goldin-Meadow, 2018) shows that, while children understand that gestures convey information from an early age, the ability to interpret and learn from gestures develops throughout childhood. Further, evidence for this link can be found in the work of Volterra and colleagues (see Volterra, Capirci, Caselli, Rinaldi, & Sparaci, 2017 for a review). For example, in one study the researchers observed the action, gesture, and language production of three infants from 10- to 23-months (Capirci et al., 2005). The infants produced specific actions with objects (e.g., bringing an empty spoon to their mouth or pushing a toy car) prior to their use of pantomimic gestures (e.g., bringing an empty hand to their mouth or making a pushing motion) or words (e.g., "eat" or "vroom vroom") to indicate those same objects or actions. Lastly, there are a number of studies showing that gesture precedes and predicts language development (e.g., Kuhn, Willoughby, Wilbourn, Vernon-Feagans, & Blair, 2014; Ozcaliskan & Goldin-Meadow, 2005; Rowe & Goldin-Meadow, 2009a; Rowe & Goldin-Meadow, 2009b; Rowe, Ozcaliskan, & Goldin-Meadow, 2008; also see Goldin-Meadow & Alibali, 2013 for a review). However, what is particularly needed in this area are thorough investigations of the neural correlates for this developmental trajectory, specifically to determine if the motor system is functionally involved in the transition from action to gesture and language.

Mirroring and communication

The mirror system hypothesis for the evolution of language, first proposed by Rizzolatti and Arbib (1998) and since refined and expanded upon by Arbib (2005, 2012, 2015, 2017) and others (Fogassi and Ferrari, 2007), posits that the MNS lays the foundation for this link between actions, action understanding, gestures, and language. That is, insofar as the ability to represent and interpret others' actions supports the understanding of communicative gestures and spoken language, the MNS may serve as one means for that representation – a direct link between actor and observer or communicator and receiver (Rizzolatti & Arbib, 1998). Although the research is limited, there is evidence in adults for motor system activity during observation of communicative gestures. In a behavioral study, Ping, Goldin-Meadow & Beilock (2014) showed that busying one's own motor system can impede understanding of gestures. Using fMRI, Montgomery, Isenberg, & Haxby (2007) examined the potential overlap between observation and execution of what they termed non-object directed communicative gestures (e.g., fingers curled into the palm and thumb pointing up for "thumbs up" or pointer finger meeting the thumb to create circle and other fingers extended for "ok"), as compared to mimed non-communicative object-directed actions (e.g., striking a match or flipping on a light switch; mimed because the objects were not actually present). They found similar activation in the primary and premotor cortices, inferior parietal lobe, and the superior temporal sulcus during both observation and execution across the two types of actions/gestures. Schippers and colleagues (2009) had participants take part in a modified game of charades while monitoring their mirror system activity using fMRI. They found activation of the motor cortex during both production and "decoding" of the charades actions. In a follow up analysis, the researchers found that the activation in the observer's brain even followed a similar temporal trajectory as that of the charade producer (Schippers, Roebroeck, Renken, Nanetti, & Keysers, 2010).

A few studies utilizing the EEG mu rhythm desynchronization have also found evidence for activation of the sensorimotor regions during observation of gestures (Avanzini et al., 2012, Quandt, Marshall, Shipley, Beilock, & Goldin-Meadow, 2012; Streltsova, Berchio, Gallese, & Umiltà, 2010). For example, Stretslova and colleagues (2010) observed significant desynchronization when participants were watching meaningless hand movements (e.g., moving the thumb in and out of an open palm), communicative gestures (e.g., thumbs up), and grasping that was either social (grasping a ball in someone's hand) or non-social (grasping a ball on a table).

The body of research examining a link between the motor system and processing of spoken language is also limited and has mostly focused on processing of action related words or phrases (see Fischer & Zwaan, 2008 for a review). Using behavioral measures of motor activity (e.g., grip force and posture changes), listening to action-related verbs in sentences induces motor activity (da Silva, Labrecque, Caromano, Higgins, & Frak, 2018; Shiller et al., 2013), however this may be modulated by semantic context (Aravena et al., 2012). Studies using fMRI, TMS, MEG, and the EEG mu rhythm have found activation of the motor system when adults process (hear or read) verbs or phrases about actions (Di Cesare, Errante, Marchi, & Cuccio, 2017; Egorova, Shtyrov, & Pulvermüller, 2016; Hauk, Johnsurde, & Pulvermüller, 2004; Moreno et al., 2015; Moreno, de Vega, & León, 2013) or while decoding degraded speech sounds (d'Ausilio et al. 2012).) Indeed, there is evidence that the motor system is functionally linked to representing action related language (Vukovic, Feurra, Shpektor, Myachykov, & Shtyrov, 2017), and some studies have also found left-hemisphere specifiticy for the action-language link (e.g., Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005). Other TMS studies show motor areas are involved during the hearing of speech sounds or phonemes with no clear meaning, thus suggesting a phonological resonance within the motor cortex (d'Ausilio et al. 2009; Roy, Craighero, Fabri-Destro, & Fadiga, 2008; Fadiga et al. 2002).

Taken as a whole, these findings are promising in terms of identifying a link between the resonant motor system activity and language, but more research is clearly needed, and furthermore what is severely lacking is a developmental perspective. One study conducted with 14-month-olds reported EEG mu rhythm desynchronization in the infants during dyadic interactions as compared to non-dyadic interactions (Reid, Striano, & Iacoboni, 2011). Antogini and Daum (2017) have found evidence for sensorimotor activity in toddlers while listening to verbs and action phrases. However, the question remains unanswered whether the activation of the motor system might play a formative or foundational role in the development of communicative skills.

There is a body of work that has examined the connection between development of children's motor abilities such as sitting, crawling, and walking and communicative development (see Iverson, 2010 for a review). While a comprehensive look at this topic is beyond the scope of the current review, the connection to be made is this: in light of the proposed link between the neural motor system and the development of communication and language, it seems logical that behavioral advances in motor skill, also reflecting activation of the neural motor system would in turn be supportive of or at least related to the development of language. A common driving theory for the link between motor and language development is that certain motoric achievements such as reaching/grasping, sitting, crawling, and walking open up new opportunities for interacting with the environment and increase language learning opportunities. While this is likely the case, we would argue that there is also a deeper, systemic connection between these developmental processes and that they are, as we see evidence for here, neurally linked. Further insights may be provided through investigations of the atypical motor and language development in individuals with Autism Spectrum Disorder (ASD), and many researchers in this area have begun to examine ASD as a unique test case for the action-perception integration and its functional role in communication (see Moseley & Pulvermüller, 2018 for a review).

In considering the link between the motor system and language, the fact that speech production itself involves action of the mouth, tongue, and larynx should rightfully be considered. Indeed, in adults, the same areas which are recruited in producing certain types of sounds (sounds involving movement of the lips versus the tongue for example) also become active when listening to those same sounds (Pulvermuller et al., 2006). Similarly, studies measuring the motor evoked potential of the tongue and mouth muscles, found differential motor activity depending on whether the participants listened to words that recruited the tongue and mouth muscles to varying degrees (Fadiga et al., 2002; Watkins, Strafella, & Paus, 2003). Interestingly, in the study by Fadiga and colleageus (2002), the effect was greater for words than for non-words, which the authors suggest may be indicative of inferring meaning or simply due to the familiarity of the words.

From mirror neurons in monkeys to human language: beyond the motor cortex.

Thus far, we have reviewed evidence that the motor system – specifically, the mirroring mechanism of the motor system – is recruited in the process of action understanding, that action understanding supports language development, and that gestures may serve as a stepping stone from understanding actions to communicating through spoken language. We have also reviewed a body of literature suggesting that the mirroring mechanism is involved in language and gesture processing in humans. But what, if any, is the role of mirroring in monkeys' communication? In the early studies on mirror neurons, it has been observed that a relatively minor percentage of mouth mirror neurons respond to facial gestures, such as lip smacking, a typical affiliative gesture of macaques (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003). There is also evidence for mirroring activity in newborn monkeys when they observe communicative facial gestures (Ferrari et al., 2012). And, as noted earlier, monkey mirror neurons are modulated by eye gaze (Coudé et al., 2016), a key feature in communicative contexts across species. In the last decade there have been a number of studies demonstrating that macaques can learn to partially control vocalization, with a very limited number of utterances (Coudé et al., 2011; Hage & Nieder, 2013). In addition, following such training to vocalize, researchers found neurons activating specifically for vocalizations in the ventral premotor cortex and ventrolateral prefrontal cortex, even though no mirror activity was detected. According to Fogassi and Ferrari (2007), in the monkey ventral premotor cortex and adjacent regions there are neurophysiological properties for the control of manual and facial gestures, the control of the larynx, and the possibility to learn new sounds through cortical control, which have been exploited in the course of primate evolution for the emergence of complex forms of communications. However, monkeys do not use or learn a formal language despite the fact that their vocal tract could potentially produce most of the human sounds (Fitch, de Boer, Mathur, & Ghazanfar, 2016). If both human and non-human primates have a MNS that functions similarly and that seems to have a functional role in language processing in humans, what accounts for this difference?

More recent research approaches the MNS as just that, a system or network that extends beyond the motor cortex and involves interactions with other brain regions, particularly those known to be involved in higher-order social cognitive processes. For example, Cavallo and colleagues (2015) found significant connectivity between typical mirroring areas of the brain (inferior frontal gyrus and premotor cortex) and the anterior rostralmedial prefrontal cortex, an area involved in inferring mental states. A meta-analysis of fMRI studies found evidence for activation of not only mirroring areas of the brain (anterior intraparietal sulcus and the premotor cortex), but also mentalizing areas (temporo-parietal junction, medial prefrontal cortex, and the precuneus) depending on the type of goal-related inferences being made during observation of actions (Van Overwalle & Baetans, 2009). It has also been suggested that the MNS is supplemented by advanced planning capacities, suggesting connectivity with the prefrontal cortex (Bridgeman, 2005). Thus, one possible difference between the human and monkey mirroring systems that may also result in the differences in communicative skills is the connectivity between different neural systems.

Conclusions and Future Directions

In this review we examined the literature linking the motor system, and specifically the mirroring mechanism, with action understanding and communicative skills in both humans and non-human primates. However, there are still important questions left unanswered and key areas left unexplored to determine the extent to which the mirroring mechanism does (or did) indeed functionally support the development of language both ontogenetically and phylogenetically. While there is evidence for motor activity during language processing, this body of work is limited in two key ways. First, the language stimuli used is almost entirely action-related. To understand the extent of this link between action and language, we must understand whether and/or how the motor system is involved in processing a wider range of linguistic stimuli. Second, there is a dearth of work with developmental populations looking at motor system activity during language or gesture processing. While neuroimaging methods are more difficult to use reliably with infants and children, the EEG mu rhythm may prove particularly fruitful in addressing this gap. Research with infants and children can also prove to be a useful comparison for findings with non-human primates, as has been done in the large body of evolutionary anthropological work comparing human infants' and non-human primates' non-verbal communication (e.g., Tomasello, 2007).

In sum, bringing together findings and perspectives from developmental social cognition in both humans and non-human primates and applying recent neuroscientific perspectives will help to elucidate the processes underlying the ability to understand and communicate with others and the functional role that the motor system may play. Taking a longitudinal, developmental approach will help to unveil the role of the MNS as gesture and spoken language skills emerge in infancy and toddlerhood. Comparing the functional networks involving the MNS across human and non-human primates may provide insight into the species-specific differences in how this system functions.

References

Aboitiz F, García RR, Bosman C, & Brunetti E (2006). Cortical memory mechanisms and language origins. Brain and Language, 98(1), 40–56. 10.1016/J.BANDL.2006.01.006 [PubMed: 16481035]

Antognini K, & Daum MM (2017). Toddlers show sensorimotor activity during auditory verb processing. Neuropsychologia. 10.1016/j.neuropsychologia.2017.07.022

Aravena P, Delevoye-Turrell Y, Deprez V, Cheylus A, Paulignan Y, Frak V, & Nazir T (2012). Grip force reveals the context sensitivity of language-induced motor activity during "action words" processing: Evidence from sentential negation. PLoS ONE, 7(12), e50287 10.1371/journal.pone.0050287 [PubMed: 23227164]

Arbib MA (2005). From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. Behavioral and Brain Sciences, 28(2), 105–124. 10.1017/S0140525X05000038 [PubMed: 16201457]

Arbib MA (2012). How the brain got language: The mirror system hypothesis. New York: Oxford University Press.

Arbib MA (2016). Towards a computational comparative neuroprimatology: Framing the language-ready brain. Physics of Life Reviews, 16(September), 1–54. 10.1016/j.plrev.2015.09.003 [PubMed: 26482863]

Arbib MA (2017). Toward the language-ready brain: Biological evolution and primate comparisons. Psychonomic Bulletin & Review, 24(1), 142–150. 10.3758/s13423-016-1098-2 [PubMed: 27368635]

Arnstein D, Cui F, Keysers C, Maurits NM, & Gazzola V (2011). mu-suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. Journal of Neuroscience, 31(40), 14243–14249. 10.1523/JNEUROSCI.0963-11.2011 [PubMed: 21976509]

Avanzini P, Fabbri-Destro M, Dalla Volta R, Daprati E, Rizzolatti G, & Cantalupo G (2012). The dynamics of sensorimotor cortical oscillations during the observation of hand movements: An EEG study. PLoS ONE, 7(5), e37534 10.1371/journal.pone.0037534 [PubMed: 22624046]

Bates E, Benigni L, Bretherton I, Camaioni L, & Volterra V (1979). The emergence of symbols: Cognition and communication in infancy. New York: Academic Press.

Berger H (1929). Über das elektrenkephalogramm des menschen. Arch Psyiat Nervenkr, 87, 527–570.

Bimbi M, Festante F, Coudé G, Vanderwert RE, Fox NA, & Ferrari PF (2018). Simultaneous scalp recorded EEG and local field potentials from monkey ventral premotor cortex during action observation and execution reveals the contribution of mirror and motor neurons to the mu-rhythm. NeuroImage, 175, 22–31. 10.1016/j.neuroimage.2018.03.037 [PubMed: 29571717]

Bridgeman B (2005). Action planning supplements mirror systems in language evolution. Behavioral and Brain Sciences, 28(2), 129–130. 10.1017/S0140525X0526003X

Brooks R, & Meltzoff AN (2008). Infant gaze following and pointing predict accelerated vocabulary growth through two years of age: A longitudinal, growth curve modeling study. Journal of Child Language, 35, 207–220. 10.1017/S030500090700829X [PubMed: 18300435]

Brune CW, & Woodward AL (2007). Social cognition and social responsiveness in 10-month-old infants. Journal of Cognition and Development, 8(2), 133–158. 10.1080/15248370701202331

Camaioni L, Castelli MC, Longobardi E, & Volterra V (1991). A parent report instrument for early language assessment. First Language, 11(33), 345–358. 10.1177/014272379101103303

Capirci O, Contaldo A, Caselli MC, & Volterra V (2005). From action to language through gesture: A longitudinal perspective. Gesture, 5(2005), 155–177. 10.1075/gest.5.1.12cap

Capirci O, Iverson JM, Pizzuto E, & Volterra V (1996). Gestures and words during the transition to two-word speech. Journal of Child Language, 23(3), 645–673. 10.1017/S0305000900008989

Carpenter M, Nagell K, & Tomasello M (1998). Social cognition, joint attention, and communicative competence from 9 to 15 months of age. Monographs of the Society for Research in Child Development, 63(4).

Caspers S, Zilles K, Laird AR, & Eickhoff SB (2010). ALE meta-analysis of action observation and imitation in the human brain. NeuroImage, 50(3), 1148–67. 10.1016/j.neuroimage.2009.12.112 [PubMed: 20056149]

Cattaneo L, Sandrini M, & Schwarzbach J (2010). State-dependent TMS reveals a hierarchical representation of observed acts in the temporal, parietal, and premotor cortices. Cerebral Cortex, 20(9), 2252–2258. 10.1093/cercor/bhp291 [PubMed: 20051360]

Cavallo A, Lungu O, Becchio C, Ansuini C, Rustichini A, & Fadiga L (2015). When gaze opens the channel for communication: Integrative role of IFG and MPFC. NeuroImage, 119, 63–69. 10.1016/j.neuroimage.2015.06.025 [PubMed: 26080312]

Charman T, Baron-Cohen S, Swettenham J, Baird G, Cox A, & Drew A (2000). Testing joint attention, imitation, and play as infancy precursors to language and theory of mind. Cognitive Development, 15(4), 481–498. 10.1016/S0885-2014(01)00037-5

Corballis MC (2012). How language evolved from manual gestures. Gesture, 12(2), 200–226. 10.1075/gest.12.2.04cor

Coudé G, Ferrari PF, Rodà F, Maranesi M, Borelli E, Veroni V, … Fogassi L (2011). Neurons controlling voluntary vocalization in the macaque ventral premotor cortex. PLoS ONE, 6(11), e26822 10.1371/journal.pone.0026822 [PubMed: 22073201]

Coudé G, Festante F, Cilia A, Loiacono V, Bimbi M, Fogassi L, & Ferrari PF (2016). Mirror neurons of ventral premotor cortex are modulated by social cues provided by others' gaze. Journal of Neuroscience, 36(11), 3145–56. 10.1523/JNEUROSCI.3220-15.2016 [PubMed: 26985026]

Coudé G, Vanderwert RE, Thorpe S, Festante F, Bimbi M, Fox NA, & Ferrari PF (2014). Frequency and topography in monkey electroencephalogram during action observation: possible neural correlates of the mirror neuron system. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 369(1644), 20130415 10.1098/rstb.2013.0415 [PubMed: 24778383]

Cuevas K, Cannon EN, Yoo KH, & Fox NA (2014). The infant EEG mu rhythm: Methodological considerations and best practices. Developmental Review, 34(1), 26–43. 10.1016/j.dr.2013.12.001 [PubMed: 24563573]

D 'Ausilio A, Bufalari I, Salmas P, & Fadiga L (2012). The role of the motor system in discriminating normal and degraded speech sounds. Cortex, 48, 882–887. 10.1016/j.cortex.2011.05.017 [PubMed: 21676385]

D'Ausilio A, Pulvermüller F, Salmas P, Bufalari I, Begliomini C, & Fadiga L (2009). The motor somatotopy of speech perception. Current Biology, 19(5), 381–385. 10.1016/j.cub.2009.01.017 [PubMed: 19217297]

da Silva RL, Labrecque D, Caromano FA, Higgins J, & Frak V (2018). Manual action verbs modulate the grip force of each hand in unimanual or symmetrical bimanual tasks. PLOS ONE, 13(2), e0192320 10.1371/journal.pone.0192320 [PubMed: 29401468]

Desrochers S, Morissette P, & Ricard M (1995). Two perspectives on pointing in infancy In Moore C & Dunham PJ (Eds.), Joint attention: Its origins and role in development (pp. 85–101). Hillsdale, NJ: Lawrence Erlbaum Associates.

Di Cesare G, Errante A, Marchi M, & Cuccio V (2017). Language for action: Motor resonance during the processing of human and robotic voices. Brain and Cognition, 118, 118–127. 10.1016/j.bandc.2017.08.001 [PubMed: 28829994]

di Pellegrino G, Fadiga L, Fogassi L, Gallese V, & Rizzolatti G (1992). Understanding motor events: a neurophysiological study. Experimental Brain Research, 91(1), 176–180. 10.1007/BF00230027 [PubMed: 1301372]

Egorova N, Shtyrov Y, & Pulvermüller F (2016). Brain basis of communicative actions in language. NeuroImage, 125, 857–867. 10.1016/j.neuroimage.2015.10.055 [PubMed: 26505303]

Fadiga L, Craighero L, Buccino G, & Rizzolatti G (2002). Speech listening specifically modulates the excitability of tongue muscles: a TMS study. European Journal of Neuroscience, 15(2), 399–402. 10.1046/j.0953-816x.2001.01874.x [PubMed: 11849307]

Falk D (2004). Prelinguistic evolution in early hominins: Whence motherese? Behavioral and Brain Sciences, 27(4), 491–503. 10.1017/S0140525X04000111 [PubMed: 15773427]

Ferrari PF, Gallese V, Rizzolatti G, & Fogassi L (2003). Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. European Journal of Neuroscience, 17(8), 1703–1714. 10.1046/j.1460-9568.2003.02601.x [PubMed: 12752388]

Ferrari PF, Tramacere A, Simpson EA, & Iriki A (2013). Mirror neurons through the lens of epigenetics. Trends in Cognitive Sciences, 17(9), 450–457. 10.1016/J.TICS.2013.07.003 [PubMed: 23953747]

Ferrari PF, Vanderwert RE, Paukner A, Bower S, Suomi SJ, & Fox NA (2012). Distinct EEG amplitude suppression to facial gestures as evidence for a mirror mechanism in newborn monkeys. Journal of Cognitive Neuroscience, 24(5), 1165–1172. 10.1162/jocn_a_00198 [PubMed: 22288390]

Filippi C, Cannon EN, Fox NA, Thorpe SG, Ferrari PF, & Woodward AL (2016). Motor system activation predicts goal imitation in 7-month-old infants. Psychological Science. 10.1177/0956797616632231

Fischer MH, & Zwaan RA (2008). Embodied language: A review of the role of the motor system in language comprehension. Quarterly Journal of Experimental Psychology, 61(6), 825–850. 10.1080/17470210701623605

Fitch WT, de Boer B, Mathur N, & Ghazanfar AA (2016). Monkey vocal tracts are speech-ready. Science Advances, 2(12), e1600723–e1600723. 10.1126/sciadv.1600723 [PubMed: 27957536]

Fogassi L, & Ferrari PF (2007). Mirror neurons and the evolution of embodied language. Current Directions in Psychological Science, 16(3), 136–141. 10.1111/j.1467-8721.2007.00491.x

Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, & Rizzolatti G (2005). Parietal lobe: From action organization to intention understanding. Science (New York, N.Y.), 308(5722), 662–7. 10.1126/science.1106138

Foglia L, & Wilson RA (2013). Embodied cognition. Wiley Interdisciplinary Reviews: Cognitive Science, 4(3), 319–325. 10.1002/wcs.1226 [PubMed: 26304209]

Fox NA, Bakermans-Kranenburg MJ, Yoo KH, Bowman LC, Cannon EN, Vanderwert RE, … van IJzendoorn MH (2016). Assessing human mirror activity with EEG mu rhythm: A meta-analysis. Psychological Bulletin, 142(3), 291–313. 10.1037/bul0000031 [PubMed: 26689088]

Gallese V, Fadiga L, Fogassi L, & Rizzolatti G (1996). Action recognition in the premotor cortex. Brain, 119(2), 593–609. 10.1093/brain/119.2.593 [PubMed: 8800951]

Gallese V, Gernsbacher MA, Heyes C, Hickok G, & Iacoboni M (2011). Mirror neuron forum. Perspectives on Psychological Science, 6(4), 369–407. 10.1177/1745691611413392 [PubMed: 25520744]

Goldin-Meadow S, & Alibali MW (2013). Gesture's role in speaking, learning, and creating language. Annual Review of Psychology, 64, 257–83. 10.1146/annurev-psych-113011-143802

Goldin-Meadow S, & Butcher C (2003). Pointing toward two-word speech in young children In Kita S (Ed.), Pointing: Where language, culture, and cognition meet (pp. 85–107). Mahwah, NJ: Erlbaum.

Hage SR, & Nieder A (2013). Single neurons in monkey prefrontal cortex encode volitional initiation of vocalizations. Nature Communications, 4, 2409 10.1038/ncomms3409

Hauk O, Johnsrude I, & Pulvermüller F (2004). Somatotopic representation of action words in human motor and premotor cortex. Neuron, 41(2), 301–307. 10.1016/S0896-6273(03)00838-9 [PubMed: 14741110]

Hewes GW (1973). Primate communication and the gestural origin of language. Current Anthropology, 14(1–2), 5–24.

Heyes C (2010). Where do mirror neurons come from? Neuroscience & Biobehavioral Reviews, 34(4), 575–583. 10.1016/j.neubiorev.2009.11.007 [PubMed: 19914284]

Heyes C (2013). A new approach to mirror neurons: Developmental history, system-level theory and intervention experiments. Cortex, 49(10), 2946–2948. 10.1016/j.cortex.2013.07.002 [PubMed: 23962893]

Hickok G (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. Journal of Cognitive Neuroscience, 21(7), 1229–1243. 10.1162/jocn.2009.21189 [PubMed: 19199415]

Hillert D (2014). Protomusic and speech In The Nature of Language (pp. 15–24). New York, NY: Springer New York 10.1007/978-1-4939-0609-3_2

Iacoboni M, & Wilson SM (2006). Beyond a single area: Motor control and language within a neural architecture encompassing Broca's area. Cortex, 42, 503–506. 10.1016/S0010-9452(08)70387-3 [PubMed: 16881259]

Iverson JM (2010). Developing language in a developing body: The relationship between motor development and language development. Journal of Child Language, 37(2), 1–25. 10.1017/S0305000909990432.Developing [PubMed: 19323859]

Johnson SC (2003). Detecting agents. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 358(1431), 549–59. 10.1098/rstb.2002.1237 [PubMed: 12689380]

Kendon A (2011). Vocalisation, speech, gesture, and the language origins debate: An essay review on recent contributions. Gesture. 10.1075/gest.11.3.05ken

Kendon A (2017). Reflections on the “gesture-first” hypothesis of language origins. Psychonomic Bulletin & Review, 24(1), 163–170. [PubMed: 27439503]

Kontra C, Goldin-Meadow S, & Beilock SL (2012). Embodied learning across the life span. Topics in Cognitive Science, 4(4), 731–739. 10.1111/j.1756-8765.2012.01221.x [PubMed: 22961943]

Kuhlman WN (1978). Functional topography of the human mu rhythm. Electroencephalography and Clinical Neurophysiology, 44(1), 83–93. 10.1016/0013-4694(78)90107-4 [PubMed: 74329]

Kuhn LJ, Willoughby MT, Wilbourn MP, Vernon-Feagans L, & Blair CB (2014). Early communicative gestures prospectively predict language development and executive function in early childhood. Child Development, 85(5), 1898–1914. 10.1111/cdev.12249 [PubMed: 24773289]

Lepage J-F, & Théoret H (2006). EEG evidence for the presence of an action observation-execution matching system in children. European Journal of Neuroscience, 23(9), 2505–2510. 10.1111/j.1460-9568.2006.04769.x [PubMed: 16706857]

Luo Y, & Baillargeon R (2007). Do 12.5-month-old infants consider what objects others can see when interpreting their actions? Cognition, 105(3), 489–512. 10.1016/j.cognition.2006.10.007 [PubMed: 17182023]

MacNeilage PF (1998). Evolution of the mechanisms of language output: Comparative neurobiology of vocal and manual communication In Hurford JR, Studdert-Kennedy M, & Knight C (Eds.), Approaches to the evolution of language (pp. 222–241). New York: Cambridge University Press.

Markus J, Mundy P, Morales M, Delgado CEF, & Yale M (2000). Individual differences in infant skills as predictors of child-caregiver joint attention and language. Social Development, 9(3), 302–315. 10.1111/1467-9507.00127

Marshall PJ, Bar-Haim Y, & Fox NA (2002). Development of the EEG from 5 months to 4 years of age. Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology, 113(8), 1199–208. 10.1016/j.cogpsych.2012.08.001 [PubMed: 12139998]

Marshall PJ, & Meltzoff AN (2011). Neural mirroring systems: Exploring the EEG mu rhythm in human infancy. Developmental Cognitive Neuroscience, 1(2), 110–123. 10.1016/j.dcn.2010.09.001 [PubMed: 21528008]

Marshall PJ, Young T, & Meltzoff AN (2011). Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study. Developmental Science, 14(3), 474–80. 10.1111/j.1467-7687.2010.00991.x [PubMed: 21477187]

McNeill D, Duncan S, Cole J, Gallagher S, & Bertenthal B (2008). Growth points from the very beginning. Interaction Studies, 9(1), 117–132. doi: 10.1075/is.9.1.09mcn

Meltzoff AN (1995). Understanding the intentions of others: Re-enactment of intended acts by 18-month-old children. Developmental Psychology, 31(5), 838–850. 10.1037/0012-1649.31.5.838 [PubMed: 25147406]

Meltzoff AN (2007). “Like me”: A foundation for social cognition. Developmental Science, 10(1), 126–134. 10.1111/j.1467-7687.2007.00574.x [PubMed: 17181710]

Michael J, Sandberg K, Skewes J, Wolf T, Blicher J, Overgaard M, & Frith CD (2014). Continuous theta-burst stimulation demonstrates a causal role of premotor homunculus in action understanding. Psychological Science, 25(4), 963–972. 10.1177/0956797613520608 [PubMed: 24549297]

Montgomery KJ, Isenberg N, & Haxby JV (2007). Communicative hand gestures and object-directed hand movements activated the mirror neuron system. Social Cognitive and Affective Neuroscience, 2(2), 114–22. 10.1093/scan/nsm004 [PubMed: 18985130]

Morales M, Mundy P, Delgado CEF, Yale M, Messinger D, Neal R, & Schwartz HK (2000). Responding to joint attention across the 6- through 24-month age period and early language acquisition. Journal of Applied Developmental Psychology, 21(3), 283–298. 10.1016/S0193-3973(99)00040-4

Morales M, Mundy P, & Rojas J (1998). Following the direction of gaze and language development in 6-month-olds. Infant Behavior and Development, 21(2), 373–377. 10.1016/S0163-6383(98)90014-5

Moreno I, de Vega M, & León I (2013). Understanding action language modulates oscillatory mu and beta rhythms in the same way as observing actions. Brain and Cognition, 82(3), 236–242. 10.1016/j.bandc.2013.04.010 [PubMed: 23711935]

Moreno I, de Vega M, León I, Bastiaansen M, Glen Lewis A, & Magyari L (2015). Brain dynamics in the comprehension of action-related language. A time-frequency analysis of mu rhythms. NeuroImage, 109, 50–62. 10.1016/j.neuroimage.2015.01.018 [PubMed: 25583610]

Morin O, & Grèzes J (2008). What is “mirror” in the premotor cortex? A review. Neurophysiologie Clinique/Clinical Neurophysiology, 38(3), 189–195. 10.1016/j.neucli.2008.02.005 [PubMed: 18539253]

Moseley RL, & Pulvermüller F (2018). What can autism teach us about the role of sensorimotor systems in higher cognition? New clues from studies on language, action semantics, and abstract emotional concept processing. Cortex, 100, 149–190. 10.1016/J.CORTEX.2017.11.019 [PubMed: 29306521]

Mukamel R, Ekstrom AD, Kaplan J, Iacoboni M, & Fried I (2010). Single-neuron responses in humans during execution and observation of actions. Current Biology, 20(8), 750–756. 10.1016/j.cub.2010.02.045 [PubMed: 20381353]

Mundy P, & Gomes A (1998). Individual differences in joint attention skill development in the second year. Infant Behavior and Development, 21(3), 469–482.

Murray L, De Pascalis L, Bozicevic L, Hawkins L, Sclafani V, & Ferrari PF (2016). The functional architecture of mother-infant communication, and the development of infant social expressiveness in the first two months. Scientific Reports, 6, 39019 10.1038/srep39019 [PubMed: 27966659]

Muthukumaraswamy SD, Johnson BW, & McNair NA (2004). Mu rhythm modulation during observation of an object-directed grasp. Cognitive Brain Research, 19(2), 195–201. 10.1016/j.cogbrainres.2003.12.001 [PubMed: 15019715]

Neuper C, & Pfurtscheller G (2001). Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates. International Journal of Psychophysiology, 43(1), 41–58. 10.1016/S0167-8760(01)00178-7 [PubMed: 11742684]

Novack MA, & Goldin-Meadow S (2017). Gesture as representational action: A paper about function. Psychonomic Bulletin & Review, 24(3), 652–665. 10.3758/s13423-016-1145-z [PubMed: 27604493]

Novack MA, Goldin-Meadow S, & Woodward AL (2015). Learning from gesture: How early does it happen? Cognition, 142, 138–147. 10.1016/j.cognition.2015.05.018 [PubMed: 26036925]

Nyström P (2008). The infant mirror neuron system studied with high density EEG. Social Neuroscience, 3(3–4), 334–347. 10.1080/17470910701563665 [PubMed: 18979389]

Nyström P, Ljunghammar T, Rosander K, & von Hofsten C (2011). Using mu rhythm desynchronization to measure mirror neuron activity in infants. Developmental Science, 14(2), 327–335. 10.1111/j.1467-7687.2010.00979.x [PubMed: 22213903]

Ozçalişkan S, & Goldin-Meadow S (2005). Gesture is at the cutting edge of early language development. Cognition, 96(3), B101–13. 10.1016/j.cognition.2005.01.001 [PubMed: 15996556]

Paulus M (2012). Action mirroring and action understanding: an ideomotor and attentional account. Psychological Research, 76(6), 760–767. 10.1007/s00426-011-0385-9 [PubMed: 22057651]

Pfurtscheller G, & Lopes da Silva FH (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. Clinical Neurophysiology, 110(11), 1842–1857. 10.1016/S1388-2457(99)00141-8 [PubMed: 10576479]

Piaget J (1952). The origins of intelligence in children. New York: Norton.

Pineda J. a. (2005). The functional significance of mu rhythms: translating “seeing” and “hearing” into “doing”. Brain Research. Brain Research Reviews, 50(1), 57–68. 10.1016/j.brainresrev.2005.04.005 [PubMed: 15925412]

Ping RM, Goldin-Meadow S, & Beilock SL (2014). Understanding gesture: Is the listener's motor system involved? Journal of Experimental Psychology, 143(1), 195–204. 10.1037/a0032246 [PubMed: 23565671]

Pulvermüller F, Hauk O, Nikulin VV, & Ilmoniemi RJ (2005). Functional links between motor and language systems. European Journal of Neuroscience, 21(3), 793–797. 10.1111/j.1460-9568.2005.03900.x [PubMed: 15733097]

Pulvermuller F, Huss M, Kherif F, Moscoso del Prado Martin F, Hauk O, & Shtyrov Y (2006). Motor cortex maps articulatory features of speech sounds. Proceedings of the National Academy of Sciences, 103(20), 7865–7870. 10.1073/pnas.0509989103

Quandt LC, Marshall PJ, Shipley TF, Beilock SL, & Goldin-Meadow S (2012). Sensitivity of alpha and beta oscillations to sensorimotor characteristics of action: An EEG study of action production and gesture observation. Neuropsychologia, 50(12), 2745–2751. 10.1016/j.neuropsychologia.2012.08.005.Sensitivity [PubMed: 22910276]

Reid VM, Striano T, & Iacoboni M (2011). Neural correlates of dyadic interaction during infancy. Developmental Cognitive Neuroscience, 1(2), 124–130. 10.1016/j.dcn.2011.01.001 [PubMed: 22436436]

Rizzolatti G, & Arbib MA (1998). Language within our grasp. Trends in Neurosciences, 21(5), 188–194. [PubMed: 9610880]

Rizzolatti G, & Craighero L (2004). The mirror-neuron system. Annual Review of Neuroscience, 27, 169–92. 10.1146/annurev.neuro.27.070203.144230

Rizzolatti G, & Fabbri-Destro M (2008). The mirror system and its role in social cognition. Current Opinion in Neurobiology, 18(2), 179–184. 10.1016/j.conb.2008.08.001 [PubMed: 18706501]

Rizzolatti G, Fadiga L, Gallese V, & Fogassi L (1996). Premotor cortex and the recognition of motor actions. Cognitive Brain Research, 3(2), 131–141. 10.1016/0926-6410(95)00038-0 [PubMed: 8713554]

Rizzolatti G, Fogassi L, & Gallese V (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. Nature Reviews Neuroscience, 2(9), 661–670. 10.1038/35090060 [PubMed: 11533734]

Rizzolatti G, & Sinigaglia C (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. Nature Reviews. Neuroscience, 11(4), 264–74. 10.1038/nrn2805 [PubMed: 20216547]

Rowe ML, & Goldin-Meadow S (2009a). Early gesture selectively predicts later language learning. Developmental Science, 12(1), 182–7. 10.1111/j.1467-7687.2008.00764.x [PubMed: 19120426]

Rowe ML, & Goldin-Meadow S (2009b). Differences in early gesture explain SES disparities in child vocabulary size at school entry. Science, 323, 951–953. 10.1126/science.1167025 [PubMed: 19213922]

Rowe ML, Ozçalişkan S, & Goldin-Meadow S (2008). Learning words by hand: Gesture's role in predicting vocabulary development. First Language, 28(2), 182–199. 10.1177/0142723707088310 [PubMed: 19763249]

Roy AC, Craighero L, Fabbri-Destro M, & Fadiga L (2008). Phonological and lexical motor facilitation during speech listening: A transcranial magnetic stimulation study. Journal of Physiology Paris, 102(1–3), 101–105. 10.1016/j.jphysparis.2008.03.006

Salo VC, Rowe ML, & Reeb-Sutherland BC (2018). Exploring infant gesture and joint attention as related constructs and as predictors of later language. Infancy. 10.1111/infa.12229

Schippers MB, Gazzola V, Goebel R, & Keysers C (2009). Playing charades in the fMRI: Are mirror and/or mentalizing areas involved in gestural communication? PLoS ONE, 4(8), e6801 10.1371/journal.pone.0006801 [PubMed: 19710923]

Schippers MB, Roebroeck A, Renken R, Nanetti L, & Keysers C (2010). Mapping the information flow from one brain to another during gestural communication. Proceedings of the National Academy of Sciences, 107(20), 9388–9393. 10.1073/pnas.1001791107

Seibert JM, Hogan AE, & Mundy P (1982). Assessing interactional competencies: The Early Social-Communication Scales. Infant Mental Health Journal, 3(4).

Shiller DM, Bourguignon N, Frak V, Nazir T, Cadoret G, Robert M, & Lemay M (2013). Word-induced postural changes reflect a tight interaction between motor and lexico-semantic representations. Neuroscience Letters, 555, 129–133. 10.1016/j.neulet.2013.09.021 [PubMed: 24051340]

Sommerville JA, Woodward AL, & Needham A (2005). Action experience alters 3-month-old infants' perception of others' action. Cognition, 96(1), B1–11. 10.1016/j.cognition.2004.07.004.Action [PubMed: 15833301]

Southgate V (2013). Do infants provide evidence that the mirror system is involved in action understanding? Consciousness and Cognition, 22(3), 1114–1121. 10.1016/j.concog.2013.04.008 [PubMed: 23773550]

Southgate V, Johnson MH, Karoui I. El, & Csibra G (2010). Motor system activation reveals infants' on-line prediction of others' goals. Psychological Science, 21(3), 355–359. 10.1177/0956797610362058 [PubMed: 20424068]

Southgate V, Johnson MH, Osborne T, & Csibra G (2009). Predictive motor activation during action observation in human infants. Biology Letters, 5(6), 769–772. 10.1098/rsbl.2009.0474 [PubMed: 19675001]

Stadler W, Ott DVM, Springer A, Schubotz RI, Schütz-Bosbach S, & Prinz W (2012). Repetitive TMS suggests a role of the human dorsal premotor cortex in action prediction. Frontiers in Human Neuroscience, 6, 20 10.3389/fnhum.2012.00020 [PubMed: 22363279]

Steinhorst A, & Funke J (2014). Mirror neuron activity is no proof for action understanding. Frontiers in Human Neuroscience, 8, 8–11. 10.3389/fnhum.2014.00333 [PubMed: 24478674]

Streltsova A, Berchio C, Gallese V, & Umiltà MA (2010). Time course and specificity of sensory-motor alpha modulation during the observation of hand motor acts and gestures: a high density EEG study. Experimental Brain Research, 205(3), 363–73. 10.1007/s00221-010-2371-7 [PubMed: 20680250]

Tenenbaum EJ, Sobel DM, Sheinkopf SJ, Malle BF, & Morgan JL (2015). Attention to the mouth and gaze following in infancy predict language development. Journal of Child Language, 42(6), 1173–1190. 10.1017/S0305000914000725 [PubMed: 25403090]

Thorpe SG, Cannon EN, & Fox NA (2016). Spectral and source structural development of mu and alpha rhythms from infancy through adulthood. Clinical Neurophysiology, 127(1), 254–269. 10.1016/j.clinph.2015.03.004 [PubMed: 25910852]

Tomasello M (2007). If they're so good at grammar, then why don't they talk? Hints from apes' and humans' use of gestures. Language Learning and Development, 3(3), 133–156. Retrieved from http://www.tandfonline.com/doi/abs/10.1080/15475440701225451

Tomasello M (2008). Origins of human communication. Cambridge, MA: MIT Press.

Tomasello M, Carpenter M, Call J, Behne T, & Moll H (2005). Understanding and sharing intentions: the origins of cultural cognition. The Behavioral and Brain Sciences, 28(5), 675–91–735. 10.1017/S0140525X05000129 [PubMed: 16262930]

Tomasello M, & Farrar MJ (1986). Joint attention and early language. Child Development, 57(6), 1454 10.2307/1130423 [PubMed: 3802971]

Tomasello M, Kruger AC, & Ratner HH (1993). Cultural learning. Behavioral and Brain Sciences, 16(3), 495 10.1017/S0140525X0003123X

Umiltà MA, Kohler E, Gallese V, Fogassi L, Fadiga L, Keysers C, & Rizzolatti G (2001). I know what you are doing. Neuron, 31(1), 155–165. 10.1016/S0896-6273(01)00337-3 [PubMed: 11498058]

Urgesi C, Candidi M, & Avenanti A (2014). Neuroanatomical substrates of action perception and understanding: an anatomic likelihood estimation meta-analysis of lesion-symptom mapping studies in brain injured patients. Frontiers in Human Neuroscience, 8, 344 10.3389/fnhum.2014.00344 [PubMed: 24910603]

Van Overwalle F, & Baetens K (2009). Understanding others' actions and goals by mirror and mentalizing systems: A meta-analysis. NeuroImage, 48(3), 564–584. 10.1016/j.neuroimage.2009.06.009 [PubMed: 19524046]

Vanderwert RE, Simpson EA, Paukner A, Suomi SJ, Fox NA, & Ferrari PF (2015). Early social experience affects neural activity to affiliative facial gestures in newborn nonhuman primates. Developmental Neuroscience, 37(3), 243–52. 10.1159/000381538 [PubMed: 26022835]

Virji-Babul N, Rose A, Moiseeva N, & Makan N (2012). Neural correlates of action understanding in infants: Influence of motor experience. Brain and Behavior, 2(3), 237–242. 10.1002/brb3.50 [PubMed: 22741097]

Volterra V, Capirci O, Caselli MC, Rinaldi P, & Sparaci L (2017). Developmental evidence for continuity from action to gesture to sign/word. Language, Interaction and Acquisition, 8(1), 13–41. 10.1075/lia.8.1.02vol

Volterra V, Caselli MC, Capirci O, & Pizzuto E (2005). Gesture and the emergence and development of langauge In Slobin D & Tomasello M (Eds.), Beyond Nature-nurture: Essays in Honor of Elizabeth Bates (pp. 3–40). Mahwah, NJ: Lawrence Erlbaum Associates.

Vukovic N, Feurra M, Shpektor A, Myachykov A, & Shtyrov Y (2017). Primary motor cortex functionally contributes to language comprehension: An online rTMS study. Neuropsychologia, 96, 222–229. 10.1016/j.neuropsychologia.2017.01.025 [PubMed: 28122198]

Wakefield E, Novack MA, Congdon EL, Franconeri S, & Goldin-Meadow S (2018). Gesture helps learners learn, but not merely by guiding their visual attention Developmental Science, p. e12664 Wiley/Blackwell (10.1111) 10.1111/desc.12664

Wakefield EM, Novack MA, & Goldin-Meadow S (2018). Unpacking the Ontogeny of Gesture Understanding: How Movement Becomes Meaningful Across Development. Child Development, 89(3), e245–e260. 10.1111/cdev.12817 [PubMed: 28504410]

Watkins KE, Strafella AP, & Paus T (2003). Seeing and hearing speech excites the motor system involved in speech production. Neuropsychologia, 41(8), 989–994. 10.1016/S0028-3932(02)00316-0 [PubMed: 12667534]

Woodward AL (2004). Infants' use of action knowledge to get a grasp on words In Hall DG & Waxman SR (Eds.), Weaving a Lexicon (pp. 149–172). Cambridge, MA: MIT Press.

Woodward AL, & Guajardo JJ (2002). Infants' understanding of the point gesture as an object-directed action. Cognitive Development, 17(1), 1061–1084. 10.1016/S0885-2014(02)00074-6

Yoo KH, Thorpe SG, & Fox NA (2016). Neural correlates of motor learning in infants. Paper presented in N. A. Fox (Chair) Neural correlates of action from infancy to early childhood. The Biennial International Conference on Infant Studies, New Orleans, LA.

Zambrana IM, Ystrom E, Schjølberg S, & Pons F (2013). Action imitation at 1½ years is better than pointing gesture in predicting late development of language production at 3 years of age. Child Development, 84(2), 560–73. 10.1111/j.1467-8624.2012.01872.x [PubMed: 23033814]