

The Mirror Neuron System

A Neural Basis of Action Understanding

Ida Tidemann



Master of Philosophy in Psychology,
Cognitive Neuroscience

UNIVERSITY OF OSLO

May 2011

Acknowledgements

The study was initiated in collaboration with my supervisor Professor Claes von Hofsten and my co-supervisor Professor Annika Melinder, both at the Cognitive Developmental Research Unit (EKUP), Department of Psychology, University of Oslo. Owing to encouragement from my supervisors, I have acquired an insight and experience in all stages of the research process ranging from the application of ethical approval, recruiting and testing of participants, to the analysis and writing of the thesis. Professor von Hofsten has been of great assistance in developing the experimental paradigm, and in providing professional advice with regards to the theoretical framework and the eye tracking technology throughout the work on this thesis. I owe thanks to EKUP, under the direction of Professor Melinder, for allowing for a monetary compensation to the participants in this study and otherwise for including me in the research activity at the EKUP laboratory. I would also like to thank Dr. Kerstin Rosander for making the script used in the MATLAB analyses and for otherwise providing support and professional advice throughout all of the stages of this work. Lastly, I thank master student Marita Andreassen for assisting me through the testing of some of the participants for the current study.

Abstract

The ability to manually solve a tower building task as well as the capacity to predict the goal during the observation of the same task was investigated by the use of eye tracking in 12- and 18-month-old infants. The Mirror Neuron System is proposed to mediate a mapping of observed actions onto the individual's own motor system. This specialized system for perceiving actions guides predictive goal-oriented eye movements and is therefore understood as the neural basis for the important social competency of action understanding. The matching of observation and executing of goal-oriented actions is thought to be dependent on the individual's own motor experience and repertoire, implying that the emergence of such predictive gaze behavior is dependent on action development. The results from this study show that goal anticipation during action observation is dependent on performance on the manual task at a group level. In addition, a significant difference between the two groups in both their ability to predict the goal for the observed action and solve the manual task was demonstrated (only the older group were effective in both). In suggesting a link between manual ability and the ability to predict the goals of others' actions in infants, these results add to the direct matching hypothesis and provide support to its suggested developmental course.

Table of Content

Introduction	1
Gaze Behavior in Observing and Executing Action.....	2
A Neural Mechanism for Action Understanding.....	3
The Monkey MNS	4
The Human MNS.....	7
Electrophysiological evidence	7
Evidence from brain imaging studies	9
The MNS Hypothesis of Social Cognition	11
The Current Study	14
Method	16
Participants	16
Ethical Considerations	16
Study Design.....	17
Apparatus.....	17
Procedure	18
Data Analysis.....	19
Results	21
Discussion	25
Eye Tracking in Infancy Research.....	27
Implications of Findings	28
Future Directions	28
Concluding Remarks	29
References	30

Introduction

In this thesis, goal-oriented actions will be examined as the means by which action understanding arise as hypothesized to be mediated by the Mirror Neuron System (MNS) (Rizzolatti, Fogassi, & Gallese, 2001). The term action understanding is defined here as a motor behavior performed by an agent, conceived in relation to its goal state (Csibra & Gergely, 2007). The thesis is based on an eye tracking study focusing on the perception of goal-oriented action in typical infant development. I will review the importance of our gaze behavior and also the MNS from its discovery to its functional properties, both in the monkey and the human brain. This will be discussed as a neural system for matching observed and executed actions. Further, The MNS hypothesis for social cognition will be examined. Action understanding is here indicated by predictive gaze behavior. The results will be discussed in relation to a developmental neurocognitive perspective.

As we are members of a particularly social species, action understanding is essential for proper functioning in a complex social environment. Conversely, a failure to grasp others' minds will have tremendous consequences both for the individual and for our functioning in the society. Understanding the basis of these socio-cognitive processes and how they develop is an important part of understanding ourselves as human beings. The neural mechanism that is thought to render this ability possible is the MNS. It is posited that this system provides for a direct matching of observed events onto our own action system, thereby allowing for an internal replication of the event. As the mirror neurons respond in synchrony with the observed behavior of others, they make conceptual reasoning superfluous in grasping the goal of the observed action. In this way, the neuronal simulation (i.e. the mirroring) of the observed event yields a direct understanding of other's intentions and goals, thereby eliminating the need for more reflective thinking (Gallese, Keysers, & Rizzolatti, 2004).

The investigation of infants' ability to understand other's actions offers an interesting glimpse into the developmental course of the MNS, while also providing us with the opportunity to test several aspects of the MNS hypothesis. Before language develops, gaze behavior serves as the principal gateway into the infant's mind. Children's visual attention is closely related to their eye movements, thereby serving as an indirect measure of attention. Today's eye-tracking technology is very accurate with respect to the gaze position in time and space. As gaze position serves as a very good indirect measure of focal attention, it provides

useful insights into how different aspects of social understanding emerge in the infant (Gredebäck, Johnson, & von Hofsten, 2010).

Gaze Behavior in Observing and Executing Action

Our eye movements are in a sense what guide us physically through our environment, and looking is one of the very first behaviors to develop in the infant. On most occasions, our gaze precedes our motor actions. Accordingly, our eye movements must have an anticipatory quality that actively seeks information from the environment in order for us to produce the proper behavior. The oculomotor system does not just respond to stimuli by the means of a bottom-up approach, but also acts proactively with the involvement of a complex interaction between pure sensory mechanisms and more analytic processing systems (Land & Furneaux, 1997).

If our motor actions are to be successful, the proactive quality of our eye movements needs to be goal-oriented. One study concluded by the use of an eye tracking method that our gaze behavior (i.e. saccades and fixations) supports the planning of hand movements by marking the key positions to which the hand/object is directed. The requirements of the task at hand determine the salience of the gaze targets (Johansson, Westling, Bäckström, & Flanagan, 2001). Another study has demonstrated that participants' gaze predicts, rather than reactively follow the movements of the observed hand performing an action. The pattern of eye movements displayed in this study was highly similar to the one displayed when the participants themselves performed the same action. This indicates that people use action plans in order to guide the oculomotor system while observing others perform object-related, goal-oriented actions. These findings further imply that the motor system is involved in predicting the goals of other people's actions. It was also discovered that the gaze moved reactively to the observed action when the object moved by itself without involving the hand, supporting the hypothesis that goal-directedness and object-relatedness are both criteria in order for this internal matching process of observation and execution of actions to function (Flanagan & Johansson, 2003).

The view expressed by Flanagan and Johansson (2003) is in accordance with the quite so recent discovery of a system in the brain with mirroring properties unifying observation and execution of action. This mechanism, the MNS, is thought to transform sensory representations of the observed action into motor representations of the very same action in the observer's brain, giving rise to the first-person grasp of others' motor intentions and goals

(Rizzolatti & Sinigaglia, 2010). It has been postulated through numerous research projects during the last two decades that the MNS mediates this matching process as expressed in the direct matching hypothesis. Provided that this is correct, there is a coherence between MNS activity and proactive goal-oriented gaze behavior during action observation (Falck-Ytter, Gredebäck, & von Hofsten, 2006).

A Neural Mechanism for Action Understanding

The understanding of other people's actions can be mediated by mirror neurons, as indicated by a great number of experimental research findings in recent decades. This ability is at the core of social cognition in that it provides us with the necessary information in order to respond to our social environment. In the visual processing of action-related information, we are provided with the *how* and *what* of an observed event. The mapping of observed actions onto the individual's own motor system allows for a representation of the observed action in the observer's head and facilitates the comprehension of the *why* of the observed action, in that way allowing for the understanding of other people's actions (Iacoboni, et al., 2005). The matching mechanism of observation and execution implies that the brain regions that are normally activated in response to our own actions and sensations are also activated by seeing similar actions and sensations performed by others (Keysers, Kaas, & Gazzola, 2010). The generation of this internal representation may have several complementary functions, such as motor learning and the understanding of meaning of the observed action. This is also a possible neuronal basis for the process of imitation. We learn by imitation, and this way of acquiring new knowledge could be based on an observation/execution matching mechanism, as the one represented by the mirror neurons (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Our ability to plan and execute actions resulting in the predicted outcome is likely the result of an association between the representation of the motor act and the consequences of that action. This type of knowledge could be extended to actions performed by others. If the neural activity that corresponds to the observed action is evoked, we would have access to the meaning of that action through the internally generated chain of responses. In this way, classes of mirror neurons seem to code blueprints for specific actions, allowing individuals to perform simple motor actions without devoting much cognitive effort to it. In addition, this neuronal property facilitates a deeper understanding of others' actions by producing the firing pattern of the action in the passive observer's brain (Rizzolatti, Fogassi, & Gallese, 2006).

Several researchers have explored this unique set of neurons, by the means of different experimental paradigms, both in monkeys and humans. I will review some of these in the following sections while also providing a more thorough account for the various properties of these neurons. While several functional properties and social cognitive implications of the MNS have been proposed during the recent years, the focus of this thesis will be on the mechanism for matching observation and execution of action, and the process of understanding other peoples' actions.

The Monkey MNS

Different behavioral and single cell studies have shown that the primate agranular cortex (i.e. Brodmann area 6/ the ventral premotor area) is involved in cognitive functions in addition to its primary characterization as a premotor area. Area F5, one of the various agranular frontal areas in the monkey brain, has been especially interesting due to its complex functions. Stimulation and recording experiments have shown that this area is involved in both hand and mouth movements. The 'hand' neurons are extensively studied, and they show properties that indicate both specificity and diversity. They become active in response to specific goal-related movements such as grasping, tearing, manipulating and holding. Another finding concerning the F5 neurons is the fact that particular types of these neurons seem to become active in response to both the active movements of the monkey, and when the monkey observes meaningful hand movements performed by another individual. Because these neurons seem to directly reflect the action within the observer's brain, and not only in the acting agent's brain, this special class of F5 neurons was named mirror neurons (Gallese, et al., 1996).

Early evidence illustrating the properties of the F5 neurons was provided by Gallese, Fadiga, Fogassi, and Rizzolatti (1996) in Parma, Italy. They were recording activity from single neurons in the rostral part of inferior area 6 (sector F5) in two *Macaca nemestrina* monkeys. They first isolated the neuron of interest, and then tested its motor and visual properties. The latter was done by presenting different objects within and outside of reaching distance of the monkey. The monkey was trained to fixate the object and also to grasp for it as it was moved closer towards it. In order to see whether these recorded neurons only coded movements specific for hand-object interactions, they also recorded activity while performing the same tasks using tools instead of their hands, grasping in the absence of the object, and so on. All together, activity of 532 neurons from the area F5 was recorded. Out of these, 92

neurons displayed what is referred to as mirror-like qualities, i.e. they discharged both when the monkey made active movements and when it observed specific meaningful actions performed by the experimenter. The most effective visual stimuli in triggering the mirror neurons were shown to be actions in which the experimenter's hand or mouth interacted with objects. Instances where tools were used instead of the experimenter's hand were ineffective in evoking activity of the mirror neurons. The presentation of other interesting stimuli, as well as gestures with emotional meaning also proved ineffective (Gallese, et al., 1996).

Most of the mirror neurons responded to only one action. The relationship between the visual actions the mirror neurons respond to and the motor action they code for was considered in order to determine their degree of congruency. Strictly congruent mirror neurons were set to be those where the effective observed and executed action corresponded both in terms of the goal for the action and the way in which it was executed. The broadly congruent neurons were those who generalized action goals across different instances of a given action (Gallese, et al., 1996).

Besides from identifying several neurons with this mirroring property, different types of mirror neurons were also discovered. These were all categorized according to the action that triggered their response. In addition, some of the neurons also discriminated between other action-related factors. The motor responses of the mirror neurons were the same as those of the other F5 neurons in that they typically activated in response to specific goal-directed motor actions. EMG and single cell recordings were also executed in order to control for the possibility that motor activity related to the observed action was present during the action observation. None of the recordings showed any motor activity during the observation of the actions performed by the experimenter (Gallese, et al., 1996).

Since this early study, the properties of the mirror neurons have been confirmed by several researchers, while also extended to involve other aspects as well. Kohler, Keysers, Umiltà, Fogassi, Gallese and Rizzolatti (2002) found what they named audiovisual mirror neurons in the monkey premotor area. These responded to actions irrespective of whether they were performed, heard, or merely observed as measured using single cell recordings in three macaque monkeys. The auditory properties of these neurons were studied by using action-related and non-action-related sounds produced by the experimenter. The authors concluded that audiovisual mirror neurons could be used both to plan and execute actions, and to recognize the actions of others, even if they are only heard, by evoking motor ideas (i.e. actions represented in terms of their goals). It was further suggested by these authors that this

could help explain the origins of human language in that they code abstract contents and also are located in what is the homolog to the human Broca's area (Kohler, et al., 2002).

Another study also found support for the MNS as the mediator of action understanding while exploring the ventral premotor area of the macaque monkey. Here, what was of particular interest was the mirror neurons found to be broadly congruent in their generalization of the action goal across different instances of it. The fact that individuals for the most part are able to infer the goal of others' action, even when the target of the action is out of sight, led to the investigation of the F5 neurons response to two different experimental conditions: one in which the whole observed action was visible, and one in which the same action was shown except for that the goal/end state was hidden from the monkey. The majority of the recorded mirror neurons responded equally in the latter condition, providing support for the hypothesis that mirror neurons indeed are involved in action recognition (Umiltà, et al., 2001).

Not only the ventral premotor area has been appointed as the location for the MNS in the monkey brain. One of the major inputs to the STS comes from the inferior parietal lobule (IPL) and the two are reciprocally connected. Many of the neurons in this area have been shown to hold mirroring properties, while in addition, the inferior parietal lobule sends output to the ventral premotor cortex, including area F5 (Rizzolatti & Craighero, 2004). Cells in the macaque Superior Temporal Sulcus (STS) have been found to code for the direction of others' attention as well as the direction of body movement, thereby concluded to support the detection of intentional actions (Jellema, Baker, Wicker, & Perrett, 2000). The STS seems to have a larger repertoire of movements they code compared to area F5, maybe because it is connected to the entire ventral premotor region, and not only to F5. The STS does not appear to have motor properties. The neurons described as broadly congruent by Gallese et al. (1996) are believed to be the source of the ability to predict the goals of an observed action as indicated by the fact that mirror neurons in the IPL were found to discriminate between identical observed motor acts depending on the superior goal of the action (Fogassi, et al., 2005).

Taken together, it seems as if the MNS, at least in the monkey brain, consists of the ventral premotor area and the IPL, connected by the STS (Rizzolatti & Craighero, 2004).

In sum, the monkey mirror neurons are characterized by two main properties: activation in response to the sight of object-related, goal-oriented actions, and activation during one's own active movements. In addition, some of the mirror neurons are able to code the observed action on the basis of its superior goal independent of the action type. This

indicates that, in monkeys, the representations of actions and action goals are facilitated by the MNS. This is used for online planning and controlling of own movements in addition to understanding the actions performed by others (Fogassi, et al., 2005). These neurons are not limited to the visual domain, but are also found to activate in response to sounds.

The Human MNS

The experimental paradigms used in studies exploring the human MNS usually originate from the assumption that the motor system during observation of an action is activated in the same manner as when the action is being performed. In addition, certain other prerequisites are assumed to be necessary in order for the mirror neurons to activate, as indicated by the studies reviewed above on the monkey MNS. Several indirect measures supporting the effects of a human MNS have been provided by utilizing electrophysiological and brain imaging studies. Throughout the next sections, some of the different studies on the human MNS will be reviewed.

Electrophysiological evidence

Microelectrode recordings have an advantage over other electrophysiological recordings in that the source conveying the signal easily can be detected. However, due to ethical considerations, this is not used in research on human subjects except in clinical cases of e.g. epilepsy. Still, using electroencephalography (EEG) and magnetoencephalography (MEG) recordings generates good insight on the temporal distributions of the neuronal activity, while deducing the measured signal distribution also prove quite good in identifying the neuronal structure generating the signals. These electrophysiological measures offer a noninvasive view “through the skull” on the activation patterns of the human cerebral cortex (Hari & Salmelin, 1997). Researchers using electroencephalography (EEG) typically distinguish between two different EEG rhythms at rest, both within the alpha frequency range: a posterior alpha rhythm and a central mu rhythm. There is a functional difference between these two as well as a difference in location. The alpha rhythm is measurable when the sensory systems are not activated, in particular the visual system, disappearing with the onset of sensory stimuli. And the mu rhythm is present during motor rest, disappearing during active movements and somatosensory stimulation (Rizzolatti, et al., 2001). Providing evidence that both observation and execution of actions share the same human cortical circuit, Cochin, Barthelemy, Roux and Martineau (1999) utilized quantified electroencephalography

(qEEG) as human subjects were observing and executing finger movements and while resting. Electrode locations corresponding to the motor and the frontal cortex displayed a decrease in activity on the mu rhythm frequency for both the observation- and the execution task compared to resting (Cochin, Barthelemy, Roux, & Martineau, 1999). It is argued that observation and execution mechanisms are important in understanding the meaning of action (Gallese, et al., 1996) and a common cortical network thereby allows for the adaptation of motor skills during interpersonal experience as well as for the acquisition of social conventions (Cochin, et al., 1999; Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; Southgate, Johnson, Osborne, & Csibra, 2009).

Transcranial magnetic stimulation (TMS) studies have also shown mirror properties in the human motor system. In studies of brain function, TMS has been used by interrupting processing of different tasks at different points in time. When applied to the motor cortex, motor-evoked potentials (MEPs) can be recorded from contralateral extremity muscles. The measured potentials are modulated by the behavioral context, and will in that way be used to assess the central effects of different experimental conditions (Rizzolatti & Craighero, 2004).

In one study utilizing the TMS technique on human participants, Fadiga, Fogassi, Pavesi and Rizzolatti (1995) found that the MEPs from hand muscles were significantly increased while the participants were observing different movements where the hand was in use, as opposed to conditions where no moving object was involved. The pattern measured while the participants observed these actions reflected the pattern measured while the participants themselves performed the same actions. The researchers concluded from this that a system matching observation and execution of actions exist, resembling the mirror neuron system observed in monkeys (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995).

Nishitani and Hari (2002) found that still pictures of human lip forms implying motion activated the MNS in a temporal manner using the MEG technique. The information reaches Broca's area with its counterpart in the right hemisphere, from the STS region via the IPL, in this given sequence (Nishitani & Hari, 2002).

A single-cell recording study on humans has also been reported recently. Mukamel, Ekstrom, Kaplan, Iacoboni and Fried (2010) recorded activity from cells in the human frontal and medial cortices while epileptic patients performed or observed hand grasping actions or emotional facial expressions. The neural response during action observation and action execution was examined for each action. A large number of the measured neurons in supplementary motor area, hippocampus and surrounding areas responded both to action

observation and action execution, suggesting that several systems in the human brain may hold mirroring properties (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010).

Evidence from brain imaging studies

The functional magnetic resonance imaging (fMRI) technique in neuroscience has allowed for a more direct way of localization of function in the brain during the last few decades. This technique offers good spatial and temporal resolution, as well as being noninvasive and adaptable to many different types of experimental paradigms (Huettel, Song, & McCarthy, 2009).

Buccino et al. (2001) carried out an fMRI study investigating the active brain areas when the participants were observing others performing an action. The participants were scanned while asked to observe videotapes of others performing different actions utilizing different effectors (i.e. mouth, arm/hand, and foot). The actions were both object-, and non-object-related. The results were in line with the author's aims for the study, and showed that the premotor cortex activated in a somatotopic manner dependent on the different effectors used. There was a clear shift in premotor cortex activation from ventral to dorsal when the effector used changed from mouth to hand/arm and to foot. This in turns shows that the mirror system is not only limited to hand actions, and also that the activation of Broca's area is not due to a verbalization of the observed actions. If that was the case, this area should have been the main point of activation regardless of the effectors used. Also, a large difference between object-related and non-object-related actions was observed. The parietal lobe was strongly activated at any time when an object was the target of the observed action, also showing a somatotopic organization. The fundamental role of the parietal lobe is seen as to describe objects for action, indicating that a "pragmatic" analysis of the observed object-related action is carried out during tasks like this where one is observing others. It can therefore be implied that action understanding is not dependent on higher-order analyses, since the opposite would render this parietal involvement unnecessary (Buccino, et al., 2001).

Another fMRI study conducted by Iacoboni et al. (2005) yielded evidence for the MNS circuit's role in the understanding of intention. While premotor mirror neuron areas were previously thought only to be involved in action recognition, this study demonstrated that attribution of intention requires inference of a forthcoming new goal, an operation performed automatically by the motor system. Intention, as described in this study, indicates the *why* of the action. It was hypothesized that if the MNS mediates understanding of

intentions the way it is described here, then the same action performed in two different contexts, reflecting two different meanings, should modulate activity in the MNS. The results showed that the activity in mirror neuron areas of the inferior premotor cortex was greater for observing grasping actions embedded within context compared to that in absence of context and while observing the context alone. The conventional way of viewing intention understanding upholds that the description of an action and the interpretation of the actor's intentionality rely on different mechanisms. This is in contrast with the findings of these authors suggesting that this is mediated by the activation of a neuronal chain constituted by mirror neurons coding the observed motor act together with mirror neurons coding the motor acts that are most likely to follow the observed one in that given context (Iacoboni, et al., 2005).

Results from an event-related fMRI paradigm suggest that the neural basis underlying imitation learning lies within the MNS. In all phases of the scanning in this study (i.e. from action observation to action execution) the MNS was strongly activated. This is taken to indicate that the process of imitation work from vision to action, but not in distinct stages. Rather, the observed action is visually processed in higher order visual areas causing the corresponding motor representations to resonate. A selection and recombination of these motor units is then necessary to reproduce the observed action. All of these processes are suggested to occur within the MNS (Buccino, Vogt, et al., 2004).

It is also suggested that the MNS, in concert with the anterior insula and the amygdale, is involved in decoding the emotions of others. The embodied model of emotion understanding was based on an fMRI study where human subjects either imitated or simply observed emotional facial expressions. It was concluded that these two tasks activated a largely similar network of brain areas involving the action representation network discussed earlier, as well as limbic areas provided in the insula. It is suggested from this that representations of the actions associated with the emotions we are witnessing needs to be formed in order for us to empathize (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2008).

In gaining knowledge of an observed action, a motor representation of this action is activated by the means of the MNS. The ability to understand these actions and the intentions behind it provides a feeling of personal knowledge, a way of experiencing the action from “within” as opposed to from the “outside” as would be the case if no motor representation was activated. In that instance, the action would be recognized on the basis of the visual properties of the action.

A prerequisite for the action to be mapped onto the observer's motor system is therefore that the action belongs to the person's action repertoire (Buccino, Lui, et al., 2004). In studying whether the MNS uses specialized motor representations or general processes of visual inference and knowledge to infer and understand the meaning of observed actions, Calvo-Merino, Grèzes, Glaser, Passingham, and Haggard (2006) used fMRI to reveal the neural bases of motor influences on action observation. The research group measured brain activity during observation of intransitive actions in two groups differing in their motor skills but with the same visual experience of the observed actions. They made use of the fact that some ballet moves are gender-specific (i.e. only one gender will perform these moves), while both genders will have equal visual experience with the moves in that both genders train together. This results in both genders having the visual knowledge of all of the moves, while they will have additional motor representations for those specific to their own gender. In measuring the activity while the male and female dancers were watching videos of gender-specific moves of both genders, the researcher could dissociate the brain responses related to motor representation from those related to visual knowledge. These two opposing sets of responses were clearly separated and the results demonstrated that the MNS activity depended on the motor representation of the action, and not only on the visual analysis and knowledge of the observed. The brain areas' activity in this respect were the parietal, premotor and cerebellar cortices, demonstrating that action understanding is acquired motorically via the MNS, and not only by the means of a visual analysis of the observed action (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Mukamel, et al., 2010).

The MNS Hypothesis of Social Cognition

From first being described in the monkey F5 area, the mirror neurons and the system it is a part of is thought to be composed of several brain areas, also in humans. The capacity to remove the self-other barrier may be a prerequisite for the development of social cognition, allowing for meaningful social bonds between individuals, a capacity that is proposed to be mediated by the MNS.

As opposed to a need for a complete visual analysis and the involvement of the extrastriate visual areas in order to achieve an understanding of others' actions, the functional properties of the mirror neurons speak for an alternative route to action and intention understanding (Rizzolatti, et al., 2001). As demonstrated by Umiltà et al. (2001), this understanding can also be inferred without the need of the action goal in sight, suggesting that

this can be mediated by the mirror neurons in complete absence of visual processing. It is suggested, on the basis of the recent findings (as previously reviewed), that a system of direct matching constitutes the mediation of this capacity. An automatically induced motor representation of the observed action is generated in the premotor cortex. This corresponds to the activation that would occur during active action, and therefore also conveys the same information as if this was the case. The goal state of the observed action is being read as if the reader was the acting agent (Rizzolatti & Craighero, 2004).

On the presumptions that the demonstrated functional properties of the MNS is in fact correct, the observed action must be within the observer's action repertoire in order for the MNS to be able to excite the motor system. The motor resonance allows for the action to be experienced from within, removing the need for a complete analysis of the visual patterns of the observed. In cases where the observer's motor repertoire is not sufficient, the feeling of personal knowledge will be lacking and the observed action will be recognized on the basis of a more analytic processing. The experience will be one where the human sense of "knowing what you are feeling" is missing (Rizzolatti & Craighero, 2004). The action perspective on the acquisition of social competencies also sets other demands on the action being observed, one being the need for an action directed towards a goal. The motor system is strongly influenced by the goal of the action to be performed, as in cases of imitation, again indicating that areas relevant to motor preparation and execution are tuned in to mapping goal-oriented actions (Gallese, et al., 1996; Koski, et al., 2002).

Examining the developmental path of the acquiring of social competencies also provides insights as to how these come to function. With action understanding constituting such a fundamental basis for social functioning, its course of development could potentially also yield a more complete sense of the underlying problems of certain deficiencies in this particular domain. The MNS mediates the foundation for several important branches of social competencies, such as imitation, "Theory of Mind", communication and action understanding, according to the MNS hypothesis (Gallese, et al., 2004; Rizzolatti & Craighero, 2004). If it is hypothesized correctly, the MNS should operate simultaneously with or before the infant is capable of displaying such competencies. Furthermore, the neuronal mapping of the observed action onto the observer's action system, and thereby also the understanding of others' actions, require that the infants are able to perform these actions themselves (Falck-Ytter, et al., 2006). In one study, making use of the eye tracking method, it was found that a system for action understanding is guiding proactive goal-oriented eye movements (the MNS as hypothesized), and that this system come to develop during the second half of the first year of

life. The proactive goal-oriented eye movements were dependent on the observation of an interaction between the hand of the agent and an object, as demonstrated by the comparison of gaze behavior in a “human agent” and a “self propelled” condition (Falck-Ytter, et al., 2006). Gredebäck and Kochukhova (2010) found that goal anticipation during action observation is dependent upon the manual ability to perform the same action. This was concluded after the comparison of the performance in manually solving a puzzle and observing a human agent performing a similar action of 18- and 25-month-olds (Gredebäck & Kochukhova, 2010). Also in line with the MNS hypothesis are the findings from Gredebäck, Stasiewicz, Falck-Ytter, Rosander and von Hofsten (2009). They found that 14-month-old infants displayed (as measured by the means of eye tracking) anticipatory gaze behavior during the observation of goal-oriented reaching tasks, as opposed to 10-month-old infants. The gaze behavior was dependent on the different goals of the observed actions, and in the control condition with just a moving fist, the displayed gaze behavior was reactive, rather than predictive. Together, these results point to an incorporation of information regarding both action type and goal type in the assessment of other’s actions in 14-month-old infants (Gredebäck, Stasiewicz, Falck-Ytter, Rosander, & von Hofsten, 2009).

All of the proposed functions of the MNS are important for adults, but emerges in infancy and early childhood. The maturation of the neural circuits at work during these processes is rarely studied in the human infant, but the demonstrated mu rhythm desynchronization during goal-oriented and object-related action observation as measured using the EEG technique was utilized in order to point to a functioning MNS in 6-month-old infants in one study. The ERP results showed a significantly higher amplitude to observation of goal-oriented action as compared to non-goal-oriented action and moving/static dot observation, and the time course indicated that the measured effects reflected MNS activity (Nyström, 2008).

Even though an impressive amount of research has provided results in support of the MNS’s role in action understanding, in part by emphasizing its course of development, this field of research has not reached complete consensus on how the ability to understand others’ actions arise. Gergely and Csibra (2003) point to the discrepancy between the age at which “Theory of Mind” first emerges (about four years of age (Wellman, 2007)) and studies demonstrating an understanding of others’ intentional goal-oriented actions (by the first year of age, e.g. Falck-Ytter et al. (2006)). The “modularist” account disclaims this gap arguing that the action understanding demonstrated in early infancy in fact is indicative of an innate mechanism for mental state attribution driven by stimulus cues. Further, the MNS hypothesis

of social cognition disavow this qualitative gap in development by theorizing that the subjective mental state of others are mapped onto the person's own action system, providing a neural representation of the observed action by the means of the MNS (Gergely & Csibra, 2003).

The teleological stance theory, however, offers an alternative explanation, seeing human search for rationality as the foundation for action understanding, while viewing the MNS as a reflection of action understanding, rather than the origins of it. Behind the rationality principle lies the criteria that future goal states are brought about as a function of action, and that the most rational action within the constraints of the situation is used as the means to realize the action goals (Eshuis, Coventry, & Vulchanova, 2009; Gergely & Csibra, 2003). It is also argued that teleological reasoning is required in social learning of new means actions and artifact functions, something that is not provided by simulation procedures generally well suited for on-line action monitoring and prediction (Csibra & Gergely, 2007).

While these views are contradictory in several respects, Gredebäck and Melinder (2009) provide a dual-process account for infants' understanding of everyday social interactions. They recorded 6- and 12-month-olds' eye movements while they observed rational and irrational feeding actions. It was found that the older group displayed predictive gaze behavior in that they fixated on the target of the action before the food arrived, also depending on their experience of being fed. In addition, both age groups dilated their pupils in response to observing the irrational feeding action, an effect interpreted as a reaction to the violation of their expectations about rationality. This study concludes that infants require less experience to evaluate rationality than what is needed to predict the goals of others' actions, thereby arguing for a dual process account of the development of such competencies. Their ability to evaluate rationality is based on the criteria put forward by Gergely and Csibra (2003), whilst their ability to predict action goals is based on a direct matching process, as believed to be mediated by the MNS (Gredebäck & Melinder, 2009).

The Current Study

The current study is grounded on recent theorizing on the role of the MNS in action understanding and how it develops. It has earlier been established that predictive eye movements are important for the planning and execution of action. When a goal-oriented manual action is performed, predictive eye movements accompany it. This is logical because then the action can be monitored from the goal position. It has also been proven that we use

the same pattern of eye movements when we observe similar actions performed by others, indicating that motor plans are involved in both instances. If the MNS mediates this matching process, there should be a direct coherence between MNS activity and proactive goal-oriented eye movements also during the observation of actions (Falck-Ytter, et al., 2006). Furthermore, according to the MNS hypothesis, if the observer maps the observed actions onto the motor representation of those actions, then the prediction and understanding of others' action goals cannot arise until the individual can perform these actions. In this way the proactive goal-oriented eye movements should only be displayed if the observed action is within the individual's action repertoire (Falck-Ytter, et al., 2006). Measurements of eye movements allow for the testability of this hypothesis (Flanagan & Johansson, 2003).

In the current study, eye tracking was used on typically developing infants in order to examine the assumptions about infant development deriving from the MNS hypothesis. By using a live scene with dynamic action, as in the current experiment, the infant's gaze behavior is also likely to resemble the spontaneous eye movements exhibited outside of the experimental paradigm. Particular attention was directed to the MNS hypothesis' assumptions stating that when the performance level of a certain action increases it is expected that the accompanying eye movements while observing others performing the same task should become more predictive. The action chosen for the study was building towers of small wooden blocks. This particular action was chosen because it is something most infants enjoy and because age-related norms of their ability to construct towers are well established, such as in the Bayley Scale of Infant Development (Bayley, 1969). For example, in the Bayley Scale, 13.8 months old infants (range = 10-19 months) can build a two-level tower on average, and 16.7 months old infants (range = 13-21 months) can build a three-level tower on average (Bayley, 1969). The two groups of infants tested in this study therefore consisted of 12- and 18-month-olds. Taking the MNS hypothesis into account, the expected outcome of this study was for the 12-month-old infants to display less predictive eye movements in observing the tower building as compared to the 18-month-olds. In addition, it was expected that this would correlate positively with their ability to build the towers themselves. The ability to perceive the perceptual information (i.e. the blocks, their size and shape) and the appropriate motor action as a coherent whole, suggests that the entire sequence is governed by an overreaching goal as demonstrated by Chen, Keen, Rosander and von Hofsten (2010). Building blocks is a typical activity for children around 12-24 months of age in that it reflects their ability to both form and pursue a goal by repeatedly performing sequential actions. Chen et al. (2010) found by registering toddlers' sequential movements in a two-stage tower building task, that

movement planning was engaged in a manner extending beyond the available perceptual information, and that this planning was incorporated with the final goal of the tower building task (Chen, Keen, Rosander, & von Hofsten, 2010).

Two hypotheses were put forward for this study. First, it was expected that the two age groups would differ with respect to their gaze behavior in that the older group was expected to display more predictive eye movements in the observation task compared to the younger group. Second, the latency between the experimenter's hand and the infant's gaze was predicted to correlate positively with the infant's ability to perform the task; the more predictive gaze behavior, the more blocks stacked on top of each other (Gredebäck & Kochukhova, 2010).

Method

Participants

Twelve 12-month-old (range = 11.4-14.7 months) and ten 18-month-old (range = 17.5-21 months) typically developed infants participated in this study. In the older group, two additional infants were recruited, but they withdrew before the time for testing was scheduled. Letters, formulated according to the norm set by the Regional Ethical Committee (Regional Etisk Komité), were sent to families in the Oslo area with children in the particular age range relevant for this study. Their addresses were collected from the Norwegian national register (Folkeregisteret/Skatteetaten). The families who answered the inquiry were contacted either by e-mail or phone. This procedure of recruiting is according to the standard routine developed by the Unit for Cognitive Developmental Psychology (EKUP) at the University of Oslo. In addition, some of the participants were recruited by way of contact with different acquaintances.

Ethical Considerations

The study was approved by the Regional Ethical Committee before the recruiting of participants started, and was conducted in accordance with the ethical standards specified in the 1964 Declaration of Helsinki. The parents were briefed about the purpose of the study in the inquiry received by post in addition to a more thorough review when they arrived at the laboratory. It was emphasized that they could withdraw from the study at any time, no

questions asked. Afterwards, they signed an informed consent form on behalf of their children. The experimental procedure was designed with the infant's and the parent's safety and comfort in mind.

Study Design

The eye movements of the infants were recorded during action observation in order to determine if they were able to predict the goal of simple manual actions performed by another person. Both groups of infants were exposed to the same experimental design, which consisted of two separate parts. In the first part, the infant watched the experimenter build towers of blocks on a live scene while the infant's eye movements were registered. In the second part, the infant was given the opportunity to play with the same blocks, attempting to build their own tower while being videotaped. Two measures were therefore included in this study: The goal prediction as determined by the difference in time between the experimenter's hand reaching the goal (i.e. the tower) and the infant's eyes reaching the goal, and the infants' ability to build a tower themselves measured and scored after the number of blocks placed on top of each other. A live scene was chosen instead of displaying a recorded set of actions on a screen. This, to better ensure that the eye movements registered during the experimental procedure resemble the ones displayed outside of the experimental setting.

Apparatus

The infants' eye movements were measured by a method based on cornea reflection. The reflections of reference light on the cornea are measured relative to the pupil. The Tobii Eye Tracker X50 uses near infrared diodes for this purpose. The strength of the infrared light is about the same as normal daylight. These reflection patterns, together with other visual information about the person are collected by a camera. When the curvature of the eye is taken in to account (as done by a calibration procedure), an exact measure of the gaze direction in time (50 Hz) and space ($<0,4^\circ$ of visual angle) is obtained.

Another camera is installed at the side of the participants' head, videotaping the scene from the participant's perspective. The second part of the session was videotaped by the use of a camera installed in front of the participant.



Figure 1. The experimental setting from the participant's perspective. The infant is placed in the parent's lap, directly in front of the TOBII eye tracker. A camera, capturing the infant's viewpoint, is installed on the left hand side of his/her head.

Procedure

The parents and their children were welcomed and informed of the experimental procedure and the aims of the study. The infants' name, date of birth, and whether or not the infant was premature was registered in a data file. After a short period of familiarization with the experimenter and the environment, the infants were seated in their parent's lap in front of the eye tracker. Participant and camera positions were adjusted to obtain satisfactory gaze tracking status and the parent was asked to look away by turning his/her head slightly during the following procedures in order to prevent the eye tracker from registering the wrong set of eyes. The infant's eyes were then calibrated to the apparatus using a five-point calibration employing a blinking object accompanied with sound to attract the infant's attention. The actual experiment started immediately after.

The experimenter was seated behind small scene in front of the participant. The experimenter's face was hidden behind a curtain in order to prevent the infant from directing his/hers attention more towards the experimenter's face than to the actual task at hand. Six wooden blocks (4 cm cubes) in different colors were placed on the scene and the experimenter started building towers (see figure 1). Six blocks were used for each tower. After each tower

had been built, the experimenter tore it down and started rebuilding a new one. A mark on the scene floor showed where the towers on each side of the scene were to be built (27 cm apart) in order to ensure that each trial would be of approximately the same length and otherwise the same across all participants. This was done eight times, four on each side of the scene while the infants' eye movements were registered. The number of towers built for each participant did however depend on the infant's patience and mood.

After this first part of the procedure, the blocks were put on a mat on the floor in another part of the room, encouraging the infants to play with them and building a tower themselves. This second part of the procedure was videotaped. After ended session, the parents viewed the videotape showing the infants' eye movements projected on the scene, and they received a compensation for their participation (a gift card worth 100 NOK).

Data Analysis

The eye tracker saves the recorded data in a text file including gaze position relative to time as well as the validity of each sample (lasting 16-20 ms). In addition, the gaze position is projected on to the video recording of the experimental procedure (showing each fixation as a "dot" on the screen, while the saccades are traced by a line in the software, Clearview (TOBII inc)). See Figure 2.

In conducting the experiment live for every participant, it was important that the towers were built in approximately the same speed every time, while also at the same locations on the scene. This was done in order to keep the conditions equal for all participants. VirtualDub 1.8.8 media player, which allows for frame by frame analysis of recordings, was used to analyze the experimental trials for each participant. This made it possible to investigate the arrival of the infant's gaze at the goal relative to the arrival of the experimenters hand at the goal. The exact time for the arrival of both the hand and the gaze at the goal for each trial was registered, rendering possible the calculation of a mean difference (i.e. hand arrival at goal minus gaze arrival at goal) for each participant. The criterion for the hand having reached the goal was set to be the instance when half the block to be placed on the top of the pile was directly above the other block(s). The criterion for the gaze having reached the goal was set to be the instance when the participant's eyes fixated on the tower, regardless of the point in the vertical plane (we were only interested in the horizontal plane relative to time for these analyses).

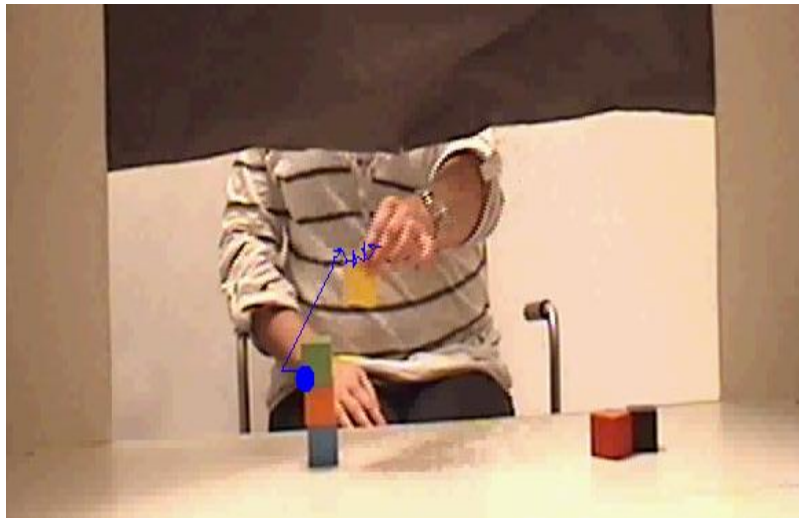


Figure 2. Sample picture of the experimental paradigm used in the study. The blue “dot” indicates where the participant’s eye are fixating at that given moment in time, whereas the blue line behind it indicates the saccades prior to the fixation.

In order to validate the time-stamps of the gaze arrival manually registered from the recording and to assure the reliability of the registrations, the data file from 1/3 of the experiments were automatically analyzed in MATLAB. The analysis done in MATLAB consisted of a series of discrete steps. First, all the invalid trials were eliminated from the analysis, providing a measure of the percentage of invalid trials. Next, the time course of valid gaze data in the horizontal dimension of the frontal plane was analyzed and converted into a graph showing when in time significant displacements were made (see Figure 3). When the graph was plotted, each point of interest (i.e. each fixation on the goal) could be marked and the exact time-stamp for this event would be registered. Accordingly, the mean time differences could be calculated and compared to those manually registered by the experimenter, ensuring the reliability of the rating. These calculations showed that the manually and automatically registered time-stamps only differed by 0.04 s on average, an insignificant difference without any impact on the additional analyses. Further, with the MATLAB script being very sensitive with respect to the tracking status of the participant (i.e. the validation of the gaze data produced by the eye tracker software), using MATLAB for registration of the timestamps would have led to far fewer registered trials per participant, thereby decreasing the validity of the experiment.

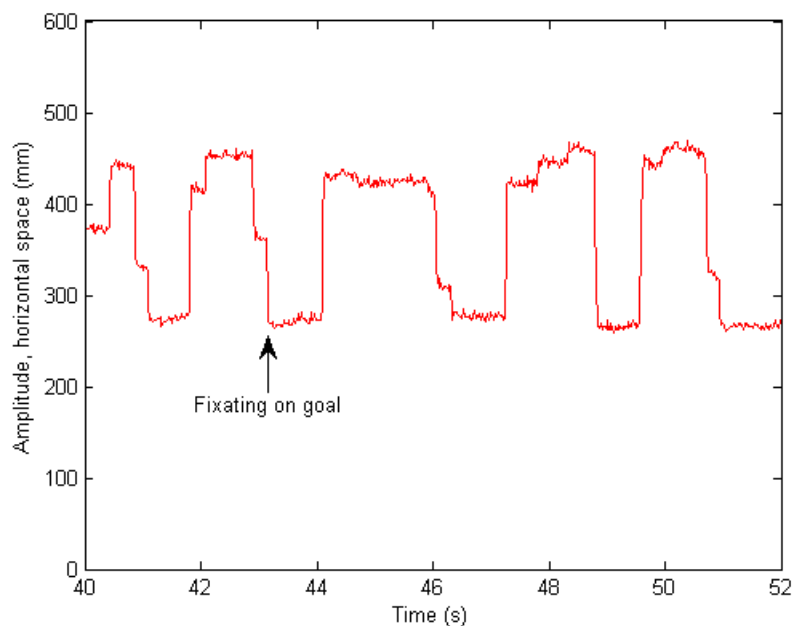


Figure 3. Sample graph exported from MATLAB illustrating the eye movements in the horizontal dimension of the fronto-parallel plane (Y-axis) of one participant within a given time frame (X-axis). Within this particular time frame, the participant has watched the experimenter build one tower consisting of 6 blocks, equaling 5 fixations on the goal, i.e. the tower. A higher amplitude indicates fixations to the right on the scene, while a lower amplitude indicates fixations to the left. Each full cycle indicates the participant having followed the experimenters hand from picking up a block, moving it towards the target, and then going back again to pick up yet another block.

The video recordings of the infants' building towers were analyzed individually, and their performance (0-6) was scored according to the number of blocks stacked on top of each other. In addition, the participants could be given 0.5 points reflecting whether they had attempted to build yet another block but failed. Finally, all of the data was imported into SPSS for further analyses regarding group differences and correlations.

Results

The average number of towers built was 6.2, resulting in the average number of trials being 31.2, one trial equaling each block moved by the experimenter's hand to the tower (the towers had six levels, but the first level was not considered because it constituted the goal for the infants' fixations). Some of the trials were invalid due to poorer gaze tracking, so the average number of registered eye movements per participant was 20.4.

An independent-samples t-test was conducted to compare the means of the two age groups' eye movements in relation to the hand. There was a significant difference in the scores for the 12- ($M = -0.10$, $SD = 0.07$) and the 18-month-old infants ($M = 0.21$, $SD = 0.19$); $t(10.98) = -4.87$, $p = .00$ (two-tailed). The magnitude of the differences in the means (mean difference = -0.31 , 95% CI: -0.44 to -0.17) was moderate (eta squared = $.072$). See Figure 4.

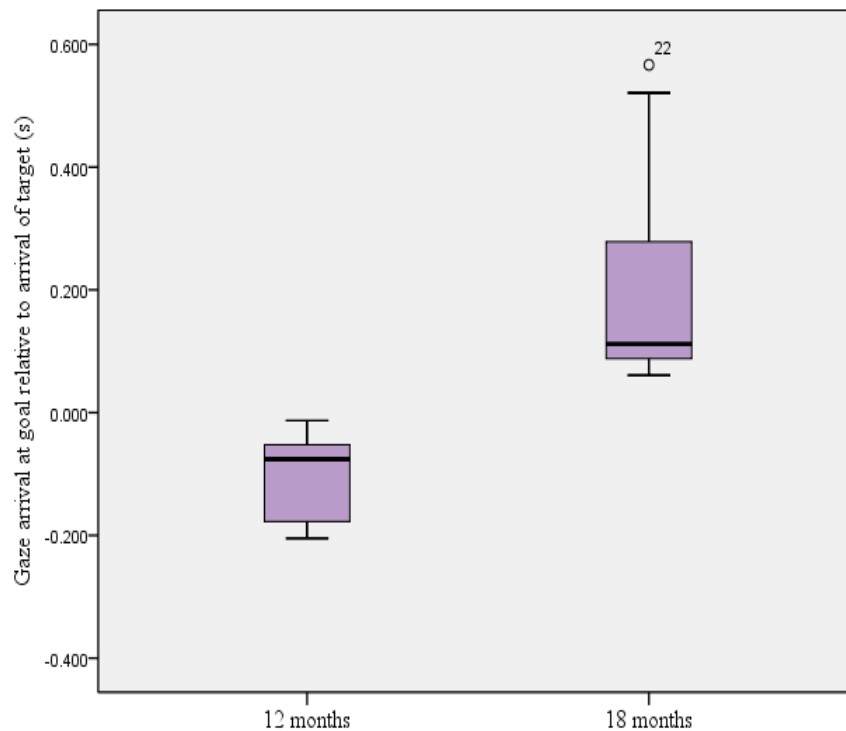


Figure 4. Boxplot illustrating the distribution of the gaze arrival at goal relative to the arrival of the target for each age group. The length of the box illustrates the interquartile range and contains 50% of the cases, while the line across the box represents the median value. The whiskers protruding from the box go out to the smallest and largest registered values. One outlier is identified.

An independent-samples t-test was also conducted in order to compare the number of blocks built for each of the two age groups. There was a significant difference in scores for 12-month-olds ($M = 0.73$, $SD = 0.34$) and 18-month-olds ($M = 4.61$, $SD = 1.45$); $t(8.74) = -7.84$, $p = .00$ (two-tailed). The magnitude of the difference in the means (mean difference = -3.88 , 95% CI: -5.01 to -2.76) was large (eta squared = $.181$). See Figure 5.

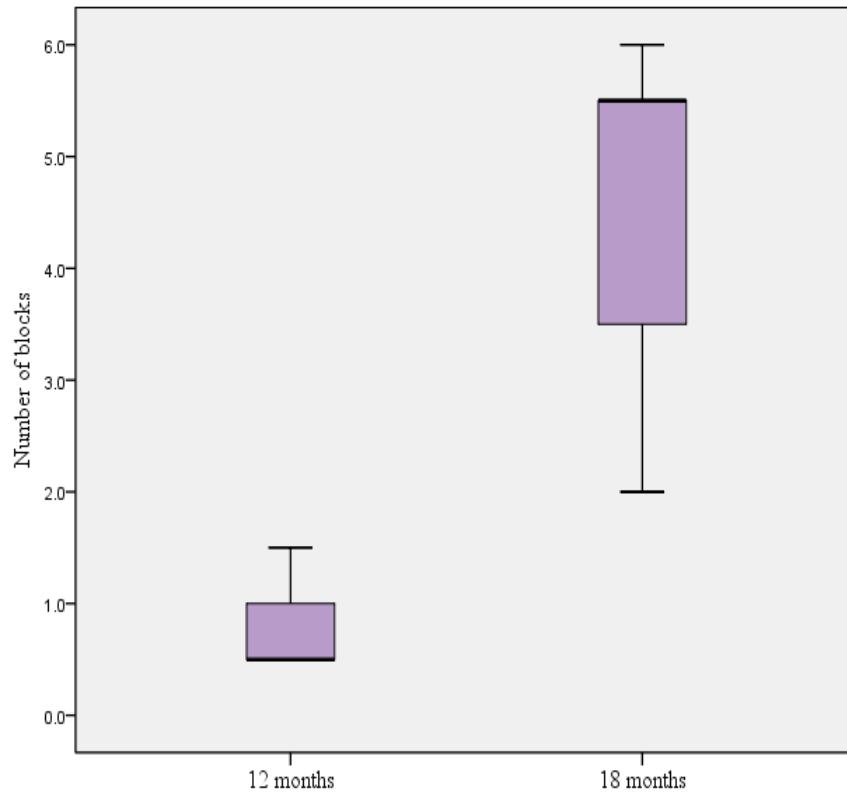


Figure 5. Boxplot illustrating the distribution of the number of blocks built for each age group. The length of the box illustrates the interquartile range and contains 50% of the cases, while the line across the box represents the median value. The whiskers protruding from the box go out to the smallest and largest registered values.

The relationship between the infants' eye movements and their ability to build the towers themselves was investigated using Pearson product-moment correlation coefficient. There was a strong, positive correlation between the two variables, $r = .701$, $n = 20$, $p < .001$, with more predictive eye movements associated with the infants building higher towers themselves. The infants' ability to build towers helped explain 49% of the variance in the infants' eye movements. See Figure 6. See Table 1 for the correlation coefficients for the measures (i.e. eye movements and number of blocks).

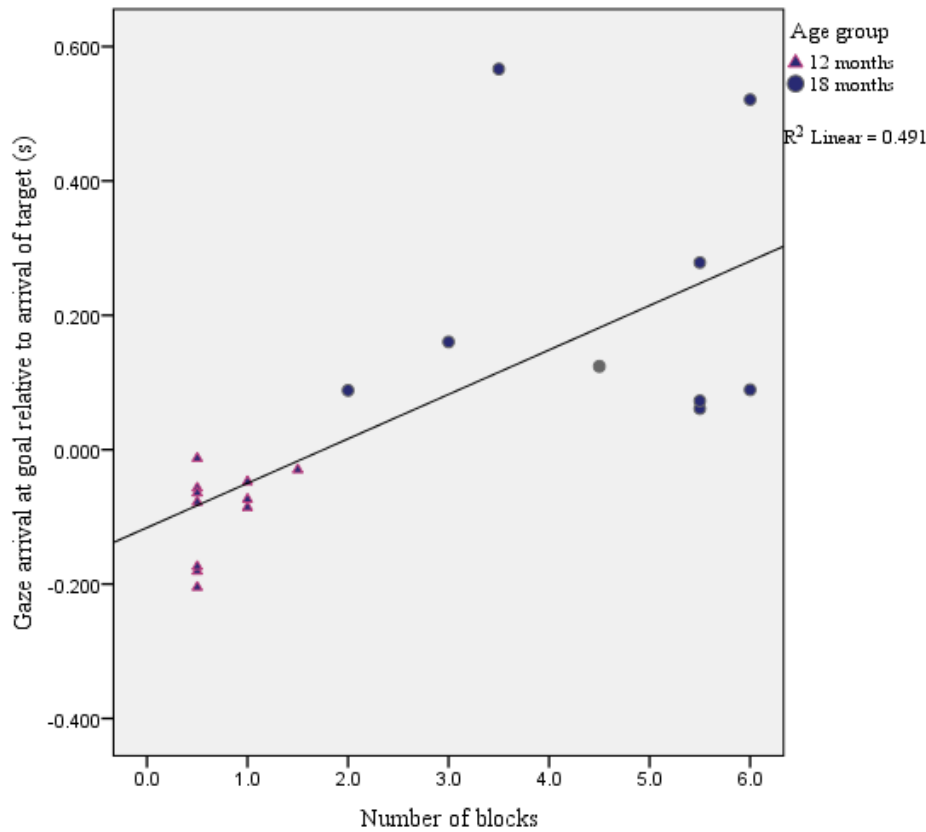


Figure 6. Scatterplot illustrating the positive correlation between the registered gaze arrivals relative to target arrival and the number of blocks built by the infants.

Partial correlations were conducted in order to see how much the age of the infants contribute to the relationship between ability to build towers and gaze behavior. By statistically removing the influence of this variable, it was expected to yield a more accurate indication of the relationship between the two variables of interest. This analysis usually demands for the confounding variable to be continuous, so for this instance the infants' age was regarded as belonging to a continuum (with age as the number of days since birth) rather than just being divided into two groups. The partial correlation between the number of blocks stacked on top of each other and predictive eye movements, controlling for age, was not significant with a weak positive correlation, $r = .141$, $n = 20$. In inspecting the zero-order correlation ($r = .701$) this suggests that controlling for age has an effect on the strength of the relationship between these two variables (see Table 1).

In considering the relationship between the two variables of interest within each age group, the correlations between ability to build a tower and predictive eye movements for the younger age group was not significant, but with a moderate correlation, $r = .430$, $n = 11$, remaining about the same when controlling for age, $r = .429$. In the older age group, the

correlations were very weak and not significant, $r = .036$, $N = 9$. However, when controlling for age in this instance, the correlation increased, $r = .228$, but did still not reach significance (See Table 1).

Table 1

Pearson product-moment correlations and partial correlations between measures of predictive eye movements and number of blocks

Correlation	Group level ^a	12 months ^b	18 months ^c
Zero order	.701*	.430	.036
Controlling for age	.141	.429	.228

Note. * $p < .001$ (two-tailed). Correlation coefficients indicating the relationship between the displayed predictive eye movements and the number of blocks built. ^aBetween group pearson correlation analysis. ^bPearson correlation within the younger group. ^cPearson correlation within the older group.

Discussion

The results from the current study indicated that when watching another person performing actions on a live scene, 18-month-old infants looked at the goal of the actions ahead of the moving hand. This was significantly more so than the 12-month-old infants who, on average, followed the hand towards the goal in a slightly reactive manner. In addition, a significant difference between the two groups in their ability to perform the observed task themselves was found. The infants in the older group were able to build higher towers than the ones in the younger group, correlating strongly and significantly with the two group's eye movements (Gredebäck & Kochukhova, 2010). The predictive gaze behavior, as displayed in the older age group, is advantageous in many real-life situations in that it makes it possible to respond to the observed event faster than if the action was observed reactively. Previous studies have found that both adults and infants use predictive eye movements in action observation (Falck-Ytter, et al., 2006; Gredebäck & Kochukhova, 2010). This occurs by mapping the observed action onto one's own motor representations of that action according to the direct matching hypothesis. These findings are replicated in this study and also provides additional support for the hypothesis owing to the fact that the ability to build a two-level tower develops on average at the age of 14 months as reported in previous studies (Bayley, 1969; Chen, et al., 2010). When controlling for age, the relationship between the two variables decreased to a lower correlation below significance.

It was expected that the relationship between goal-oriented, predictive gaze behavior and manual ability also would correlate significantly within the older group. However, the correlations here were weaker and not significant, also when eliminating age as a confounding variable. One of the participants in each group was removed from the analyses for not wanting to participate in the tower building after ended eye tracking, leaving especially the older group low in participants. It is speculated that the within-group analyses' weaker correlations is due to the number of participants being too low and is expected to rise with more participants. It is also speculated that the older group's scores on the tower building task is reflecting a ceiling effect in that the variance in this variable is no longer measured when the participant scores above a certain level. The task at hand may be one where the infants require more motivation in order to build higher towers, even though they are motorically capable of doing so. This is indicated by a congestion of scores at the upper level. Age has a clear mediating effect in this study, demonstrating its importance in the development of the manual task proficiency. However, it is also shown that, within the older age group, controlling for age contributes to the correlation with goal-oriented gaze behavior in a positive manner. As the proficiency of the manual task increases with age, so does the ability to predict the goal of the observed action, making the two hard to evaluate separately. However, other studies have demonstrated that prior experience in the manual task at hand have not effected the latency of goal-oriented gaze behavior (Gredebäck & Kochukhova, 2010)

Still, a relationship between the latency of goal-directed gaze behavior and manual ability is demonstrated on a group level in this study, as contradictory to the teleological stance theory that views goal anticipation as mediated through an attribution of rationality to human actions (Eshuis, et al., 2009). Both of the groups should be able to perceive the experimenter's actions as rational, and therefore also be able to attribute goal-directedness and predict the goal of the observed action as infants well below 12 months have been found to demonstrate sensitivity to the rationality of intentional agents (Gergely & Csibra, 2003).

The importance of the observed action to belong to the observer's action repertoire, as demonstrated by Calvo-Merino et al. (2006), substantiates that action understanding by the means of the MNS is dependent on the observer's own proficiency in the observed action and that this goal anticipating ability develops within context.

The ERP measures of the MNS in infants demonstrated by Nyström (2008) also provides evidence for an early onset of MNS functioning in the human brain. The higher ERP

activation for goal-oriented action observation in the 6-month-old infants in that study clearly indicated a MNS in operation.

Eye Tracking in Infancy Research

The use of corneal reflection eye tracking in research offers a unique way of investigating the attentional abilities of infants to reflect the ongoing processes of the MNS. In calibrating the infants' eye directions, it is possible to infer what the infant looks at. In this study, the live calibration procedure was adapted to be appropriate for infants at 12 and 18 months of age by having a small toy accompanied by a sound appear in the five different calibration points. The critical aspect of capturing the infants' eyes at all times during the calibration and the experimental procedure was reassured by placing the infants in their parents' lap. The eye tracking equipment used, also had the advantage of capturing both eyes as well as allowing for head movements. Some data was lost during the procedures due to a loss of the infants' attention. Still, this was compensated for by building several towers during the eye tracking procedure so that a satisfactory amount of data could be registered in order to perform the intended analyses (Gredebäck, et al., 2010).

The measuring of infants' gaze as they observe others engaging in meaningful goal-oriented actions provides a unique insight into an emerging social competence. In analyzing the gaze data from social cognitive studies, one often relies on a comparison between when an actor performs certain actions and how the infants scan these events. These analyses often rest on inspections of areas of interest (AOI) that define spatial locations in the presented events. In this study however, an AOI-based analysis was not suitable due to the use of a live scene. When using AOIs it is necessary to have the location of the goal in exactly the same position at all times, and this was not possible with a live presentation (Gredebäck, et al., 2010).

The ability to anticipate future state of affairs minimize the possibility that predictive gaze behavior is guided by purely visual properties of the observed event, namely because the event has not yet occurred. This property of eye tracking is one that helps reduce the gap between observable behavior and the underlying processes. Another advantage gained by using this technology is that it is relatively inexpensive compared to some other means of gathering data in psychology research (e.g. brain imaging). It is also well suited to infancy research in that nothing needs to be applied on the infant in addition to the accuracy and objectivity it offers in studying real life action observation (Gredebäck, et al., 2010).

Implications of Findings

The implications of the findings from this study, as well as other studies demonstrating the MNS role in action understanding are numerous and versatile. A system for matching observation and execution of actions, dependent on our own action repertoire has implications for how we view the development and functioning of highly complex social abilities as action understanding. The neural network mediating this has, as reviewed in this paper, been suggested to be the MNS. The reviewed characteristics of the MNS suggests that it plays an important role in several social functions such as language, imitation and action understanding, as well as the understanding of others' emotions (Buccino, Vogt, et al., 2004; Gallese, et al., 2004; Kohler, et al., 2002; Rizzolatti & Craighero, 2004). Predictive eye movements in action observation play a vigorous part in goal- and object-directed actions with others by providing means for attention-synchronizing. The current study, in focusing on infant development, thereby has relevance for the understanding of social and emotional difficulties as well, both for further theoretical progress and for the purpose of treatment.

Future Directions

For future directions on this field of work, more studies taking advantage of the possibilities opened up by the use of eye tracking is suggested, especially in investigating infant development. Making use of this technique's versatile nature as far as live settings and real world social interactions are concerned is also recommended. The use of pupil size as an element of surprise, length of fixations, and speed of gaze shifts are other measures available with this technology. They can also be integrated with other measures as EEG, and heart rate. All of these approaches are likely to contribute to the understanding of infants' perceptual, cognitive and social abilities (Gredebäck, et al., 2010). Many questions regarding the MNS, its functional and cognitive role, and its course of development still remain debated and unanswered. Whether the MNS is the neural mediator of predictive eye movements in action observation is also still a matter of debate, making demands for future studies shedding light on the link between specific brain areas and gaze behavior in action observation. As a pursuance of the current study, more infants will be tested in order to be able to strengthen the correlations. In addition, an investigation of how the anticipatory ability changes with the ability to build higher towers will be included. Longitudinal research can also be valuable in gaining insight into the development of social and emotional impairments, focusing on high-risk groups of the population.

Concluding Remarks

Mirror neurons are units in the monkey frontal and parietal cortices that activates both during the passive observation and the active execution of goal- and object-oriented actions. During the recent years of research, a similar system is proposed in the human brain as well. The human MNS is proposed to be comprised of the premotor cortex, the IPL, and the STS, while other areas have been suggested to be involved as well. The functional properties of this neural network have been investigated by research utilizing several different technologies, but the area of focus for the current study has been the MNS as the possible underlying mechanism for the understanding and prediction of others' actions.

The MNS hypothesis of social cognition proposes that the projection of an observed action on the observer's action representations gives rise to an understanding of the meaning of the action "from the inside". This ability is dependent on the individual's action repertoire and sensorimotor experience. In order to investigate the MNS role in action understanding, eye tracking data from 12- and 18-month-old infants in observing a tower building task were compared to their ability to build towers using blocks themselves. The predictive gaze behavior displayed in the older group, along with the group-level correlation between the latency between hand and gaze and the performance in the manual task, provides further support for the hypothesis. In addition, this also yields more evidence in support of the early onset of MNS functioning.

Despite the great many findings in support of the role of the MNS in various branches of social cognition, many questions still stand open with regard to functional properties and implications. Together, these make promise of an interesting and flourishing field of research.

References

- Bayley, N. (1969). Manual for the Bayley Scales of Infant Development. *New York: Psychological Corporation.*
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal of Neuroscience, 13*(2), 400-404.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al. (2004). Neural Circuits Involved in the Recognition of Actions Performed by Nonconspicuous: An fMRI Study. *Journal of Cognitive Neuroscience, 16*(1), 114-126.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H.-J., et al. (2004). Neural Circuits Underlying Imitation Learning of Hand Actions: An Event-Related fMRI Study. *Neuron, 42*(2), 323-334.
- Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or Doing? Influence of Visual and Motor Familiarity in Action Observation. *Current Biology, 16*(19), 1905-1910.
- Carr, L., Iacoboni, M., Dubeau, M.-C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences of the United States of America, 100*(9), 5497-5502.
- Chen, Y.-p., Keen, R., Rosander, K., & von Hofsten, C. (2010). Movement Planning Reflects Skill Level and Age Changes in Toddlers. *Child Development, 81*(6), 1846-1858.
- Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (1999). Observation and execution of movement: similarities demonstrated by quantified electroencephalography. *European Journal of Neuroscience, 11*(5), 1839-1842.
- Csibra, G., & Gergely, G. (2007). 'Obsessed with goals': Functions and mechanisms of teleological interpretation of actions in humans. *Acta Psychologica, 124*(1), 60-78.
- Eshuis, R., Coventry, K. R., & Vulchanova, M. (2009). Predictive Eye Movements Are Driven by Goals, Not by the Mirror Neuron System. *Psychological Science, 20*(4), 438-440.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of Neurophysiology, 73*(6).

- Falck-Ytter, T., Gredebäck, G., & von Hofsten, C. (2006). Infants predict other people's action goals. *Nat Neurosci*, 9(7), 878-879.
- Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, 424(6950), 769-771.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal Lobe: From Action Organization to Intention Understanding. *Science*, 308(5722), 662-667.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119(2), 593-609.
- Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, 8(9), 396-403.
- Gergely, G., & Csibra, G. (2003). Teleological reasoning in infancy: the naïve theory of rational action. *Trends in Cognitive Sciences*, 7(7), 287-292.
- Gredebäck, G., Johnson, S., & von Hofsten, C. (2010). Eye Tracking in Infancy Research. *Developmental Neuropsychology*, 35(1), 1 - 19.
- Gredebäck, G., & Kochukhova, O. (2010). Goal anticipation during action observation is influenced by synonymous action capabilities, a puzzling developmental study. *Experimental Brain Research*, 202(2), 493-497.
- Gredebäck, G., & Melinder, A. (2009). Infants' understanding of everyday social interactions: A dual process account. *Cognition*, 114(2), 197-206.
- Gredebäck, G., Stasiewicz, D., Falck-Ytter, T., Rosander, K., & von Hofsten, C. (2009). Action Type and Goal Type Modulate Goal-Directed Gaze Shifts in 14-Month-Old Infants. *Developmental Psychology*, 45, 1190-1194.
- Hari, R., & Salmelin, R. (1997). Human cortical oscillations: a neuromagnetic view through the skull. *Trends in Neurosciences*, 20(1), 44-49.
- Huettel, S. A., Song, A. W., & McCarthy, G. (2009) *Functional Magnetic Resonance Imaging* (Second ed.). Sunderland, Massachusetts, U.S.A.: Sinauer Associates, Inc.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the Intentions of Others with One's Own Mirror Neuron System. *PLoS Biol*, 3(3), e79.
- Jellema, T., Baker, C. I., Wicker, B., & Perrett, D. I. (2000). Neural Representation for the Perception of the Intentionality of Actions. *Brain and Cognition*, 44(2), 280-302.

- Johansson, R. S., Westling, G., Bäckström, A., & Flanagan, J. R. (2001). Eye-Hand Coordination in Object Manipulation. *The Journal of Neuroscience*, *21*(17), 6917-6932.
- Keysers, C., Kaas, J. H., & Gazzola, V. (2010). Somatosensation in social perception. *Nat Rev Neurosci*, *11*(6), 417-428.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing Sounds, Understanding Actions: Action Representation in Mirror Neurons. *Science*, *297*(5582), 846-848.
- Koski, L., Wohlschläger, A., Bekkering, H., Woods, R. P., Dubeau, M.-C., Mazziotta, J. C., et al. (2002). Modulation of Motor and Premotor Activity during Imitation of Target-directed Actions. *Cerebral Cortex*, *12*(8), 847-855.
- Land, M. F., & Furneaux, S. (1997). The Knowledge Base of the Oculomotor System. *Philosophical Transactions: Biological Sciences*, *352*(1358), 1231-1239.
- Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-Neuron Responses in Humans during Execution and Observation of Actions. *Current Biology*, *20*(8), 750-756.
- Nishitani, N., & Hari, R. (2002). Viewing Lip Forms: Cortical Dynamics. *Neuron*, *36*(6), 1211-1220.
- Nyström, P. (2008). The infant mirror neuron system studied with high density EEG. *Social Neuroscience*, *3*, 334-347.
- 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.
- Pfeifer, J. H., Iacoboni, M., Mazziotta, J. C., & Dapretto, M. (2008). Mirroring others' emotions relates to empathy and interpersonal competence in children. *NeuroImage*, *39*(4), 2076-2085.
- Rizzolatti, G., & Craighero, L. (2004). THE MIRROR-NEURON SYSTEM. *Annual Review of Neuroscience*, *27*(1), 169-192.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci*, *2*(9), 661-670.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2006). Mirrors of the mind. *Sci Am*, *295*(5), 54-61.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews Neuroscience*, *11*(4), 264-274.

- Southgate, V., Johnson, M. H., Osborne, T., & Csibra, G. (2009). Predictive motor activation during action observation in human infants. *Biology Letters*, 5(6), 769-772.
- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., et al. (2001). I Know What You Are Doing: A Neurophysiological Study. *Neuron*, 31(1), 155-165.
- Wellman, H. M. (2007). *Understanding the Psychological World: Developing a Theory of Mind*: Blackwell Publishers Ltd.