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An Embodied Account of Action Prediction

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Abstract

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Being able to generate predictions about what is going to happen next while observing other people's actions plays a crucial role in our daily lives. Different theoretical explanations for the underlying processes of humans' action prediction abilities have been suggested. Whereas an embodied account posits that predictive gaze relies on embodied simulations in the observer's motor system, other accounts do not assume a causal role of the motor system for action prediction.

The general aim of this thesis was to augment current knowledge about the functional mechanisms behind humans' action prediction abilities. In particular, the present thesis outlines and tests an embodied account of action prediction. The second aim of this thesis was to extend prior action prediction studies by exploring infants' online gaze during observation of social interactions.

The thesis reports 3 eye-tracking studies that were designed to measure adults' and infants' predictive eye movements during observation of different manual and social actions. The first two studies used point-light displays of manual reaching actions as stimuli to isolate human motion information. Additionally, Study II used transcranial magnetic stimulation (TMS) to directly modify motor cortex activity.

Study I showed that kinematic information from biological motion can be used to anticipate the goal of other people's point-light actions and that the presence of biological motion is sufficient for anticipation to occur.

Study II demonstrated that TMS-induced temporary lesions in the primary motor cortex selectively affected observers' gaze latencies.

Study III examined 12-month-olds' online gaze during observation of a give-and-take interaction between two individuals. The third study showed that already at one year of age infants shift their gaze from a passing hand to a receiving hand faster when the receiving hand forms a give-me gesture compared to an inverted hand shape.

The reported results from this thesis make two major contributions. First, Studies I and II provide evidence for an embodied account of action prediction by demonstrating a direct connection between anticipatory eye movements and motor cortex activity. These findings support the interpretation that predictive eye movements are driven by a recruitment of the observer's own motor system. Second, Study III implicates that properties of social action goals influence infants' online gaze during action observation. It further suggests that at one year of age infants begin to show sensitivity to social goals within the context of give-and-take interactions while observing from a third-party perspective.

Keywords: Action prediction, biological motion, direct-matching, embodied simulation, eye movements, eye-tracking, give-me gesture, mirror neuron, motor cortex, point-light, social interaction, TMS

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To my grandfather Norbert

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I Elsner, C., Falck-Ytter, T., Gredebäck, G. (2012). Humans anticipate the goal of other people's point-light actions. *Frontiers in Psychology*, 3(120).
- II Elsner, C., D'Ausilio, A., Gredebäck, G., Falck-Ytter, T., & Fadiga, L. (2013). The motor cortex is causally related to predictive eye movements during action observation. *Neuropsychologia*, 51, 488-492.
- III Elsner, C., Bakker, M., Rohlfing, K., & Gredebäck, G. (2014). Infants' online perception of give-and-take-interactions. *Journal of Experimental Child Psychology*, 126, 280-294.

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Contents

Introduction	11
Humans' sensitivity to goal-directed actions.....	13
Biological motion perception	16
Embodied cognition theories	18
Eye-tracking as a tool to study action perception.....	20
Looking time measures	20
Action prediction and anticipatory eye movement paradigms	21
Predictive eye movements during action observation	22
The mirror neuron system.....	26
Evidence from non-human primates.....	27
The mirror neuron system in humans	28
Accounts of action prediction.....	32
Action resonance theories	32
The role of inferential and teleological reasoning	35
Statistical learning.....	38
Infants' online gaze during social interactions	41
Infants' development of social-communicative skills	42
Infants' gestural development.....	43
Infants' online gaze during observation of social interactions	44
Aims of the thesis	46
Methods.....	48
Participants	48
Stimuli	48
Apparatus.....	49
General procedure.....	50
Data analysis.....	51
Study I – Anticipation of biological motion.....	53
Design.....	54
Results	56
Discussion Study I.....	58
Study II – The role of the motor cortex during online action anticipation....	60
Design.....	61
Results	63

Discussion Study II.....	64
Study III – Infants’ online perception of give-and-take interactions	67
Design.....	68
Results	71
Discussion Study III	73
General discussion.....	76
An embodied account of action prediction.....	77
Prediction of social interactions	85
Future directions	91
Final conclusions	93
Acknowledgements	94
References	97

Abbreviations

AOI	Area of Interest
ASL	Associative Sequence Learning
AT	Anterior Tibialis
EEG	Electroencephalography
FDI	First Dorsal Interosseous
FEF	Frontal Eye Fields
fMRI	Functional Magnetic Resonance Imaging
IPL	Inferior Parietal Lobe
MEG	Magnetoencephalography
MEP	Motor Evoked Potentials
MNS	Mirror Neuron System
PMC	Premotor Cortex
PMCv	Ventral Premotor Cortex
PL	Point-light
SMA	Supplementary Motor Area
STS	Superior Temporal Sulcus
TMS	Transcranial Magnetic Stimulation

Introduction

“To naïve thought nothing is less problematic than that we grasp the actions of others, but it is precisely the task of psychology to remove the veil of self-evidence from these momentous processes.” Solomon E. Asch (1952)

In order to successfully navigate through our social world, it is necessary for people to make sense of others' actions. Of particular significance for many adaptive behaviors are movements of other living beings around us. Importantly, humans do not only develop the ability to detect and perceive biological motion from other living entities, but also to see actions around them as structured by goals and intentions (Allison, Puce, & McCarthy, 2000; Behne, Carpenter, Call, & Tomasello, 2005). Therefore, attending to goal-directed motion information from other living creatures, especially to human body motion, enables us to extract meaningful information about others' actions and behavior (Blakemore & Decety, 2001). This specific aspect of our visual perception also plays an evolutionarily fundamental role for survival, supports learning and the orientation to other socially relevant information and cues, such as faces, gaze or more complex intentions (Carpenter, Call, & Tomasello, 2005).

From birth, human infants are exposed to other people acting and interacting with them. By exploring and observing the world around them, infants develop the fascinating ability to quickly gain insights into others' minds (Barresi & Moore, 1996; Senju, Southgate, White, & Frith, 2009; von Hofsten, 2004). Importantly, while attending to and looking at others' behavior, infants learn to make online predictions about what is going to happen next, allowing them to act efficiently in the world (Bertenthal, 1996). This ability is foundational for successful interactions in our environment, such as staying ahead of competitors or coordinating our actions with other people (Henderson, 2003; Johansson, Westling, Bäckström, & Fanagan, 2001; Land, 2009). Further, the ability to prospectively look at others' actions in order to anticipate future events plays a central role for action planning and communication and, thus, constitutes a key feature of human social cognition (Hayhoe & Ballard, 2005; Hommel, Müsseler, Aschersleben, & Prinz, 2001; Schütz-Bosbach & Prinz, 2007a; Sebanz, Bekkering, & Knoblich, 2006). It is therefore crucial to understand what accounts for the ability to perceive and predict others' action goals, when this ability emerges and which underlying processes may guide our action anticipations.

Although successful social interactions rely on the ability to predict others' behavior, the processes underlying action prediction and understanding are not yet fully understood and still a matter of heated debates. Different theoretical accounts have been developed that aim to clarify the functional mechanisms and neural circuits involved in predicting and understanding others' goal-directed actions. According to an embodied account, embodied simulation processes in the observer's motor system underlie the ability to predict others' actions. This notion proposes that simulation or matching processes of perceived actions onto the observer's own motor plans account for action prediction (e.g. Rizzolatti & Craighero, 2004). However, other accounts have criticized the embodied account and do not assume a causal role of the motor system for action prediction and action understanding. Instead, proponents of opposing views have emphasized the role of efficiency considerations, statistical learning or goal saliency for action prediction. For instance, in contrast to an embodied account, Csibra and colleagues argue that we are able to understand and predict others' actions by means of specialized inferential processes taking place outside of the mirror neuron system (MNS) (Csibra & Gergely, 2007).

This thesis reports three studies on adult and infant subjects that were designed to increase current knowledge about the different mechanisms underlying our ability to predict other people's action goals. In particular, we examined the embodied account of action prediction by investigating the role of the motor system for anticipatory gaze processes. The presented studies will focus on human motor actions that are defined as purposeful and goal-directed movements toward a goal associated with a specific effect or outcome (von Hofsten, 2004). In this context, action understanding will be defined as observers' ability to represent perceived actions in terms of their underlying goal structure (Hamlin, Hallinan, & Woodward, 2008) and captured in participants' online gaze shifts to the goal of an observed action. That is, the term action prediction, or action anticipation, refers to observers' ability to prospectively gaze at the goal of an ongoing action before it is completed (for more detailed definitions of action anticipations and goal understanding see page 22).

Prior to presenting the empirical studies, the next sections aim to provide a general overview about previous research on the topic, introducing relevant theories related to action anticipation and eye-tracking as a measurement thereof. Specifically, the starting point of the introduction will be research on humans' ability to perceive other human actions as centered around goals. Related to this ability is sensitivity to biological motion information. Therefore, the subsequent section will review research exploring the special role of biological motion for social perception. Afterwards, two suitable eye-tracking measures for studying action perception and understanding will be described. As all three studies of this thesis employ anticipatory eye movement paradigms, the reviewed eye-tracking literature will concentrate on

studies measuring predictive eye movements. More precisely, the presented eye-tracking studies will shed light on the relation between action prediction and action production. In order to embed these findings in a broader theoretical framework, the account of embodied cognition will be introduced, followed by a description of neurophysiological evidence for the MNS as a potential neural network linking action perception and execution. Subsequently, I will provide an overview about the different theoretical views on the underlying processes behind action prediction and understanding. The last part of the introduction will extend the focus from understanding actions performed by a single individual to social interactions. As Study III tested an infant sample, the last sections will concentrate on a developmental perspective. This part will be introduced by a brief review about the origins of humans' social, especially gestural communication abilities. The last section will elaborate on prior research investigating infants' online gaze during observation of social interactions, serving as a motivation for Study III.

Humans' sensitivity to goal-directed actions

In everyday life, humans need to readily process a complex and ever-changing stream of information from unfolding activities around them. Despite this information overload, adults are strikingly proficient in perceiving a relevant structure in others' ongoing behavior that enables them to identify pursued action goals and to discern intentions from observed dynamic actions (Baird & Baldwin, 2001). There is common consensus that adults readily interpret other people's actions as goal-directed (Bekkering, Wohlschläger, & Gattis, 2000; Malle, Moses, & Baldwin, 2001), and this ability is so robust that even the motion of inanimate geometrical shapes is described as vivid, goal-directed and intentional (Heider & Simmel, 1944). When processing others' actions, adult observers rapidly distinguish between unintentional and purposeful human actions (Malle & Knobe, 1997) and they selectively recall parts of an observed action sequence that are related to the actor's previously ascribed intention (Zadny & Gerard, 1974). In addition, observers consistently parse action sequences in terms of meaningful units to discover segmental structure in the stream of ongoing events (Newtonson, 1973; Zacks, Tversky, & Iyer, 2001). Further support comes from studies assessing patterns of looking times (i.e., dwell-time) that have demonstrated observers' ability to process unfolding event streams as segmented and hierarchical (Hard, Recchia, & Tversky, 2011).

The development of humans' sensitivity to goal-directed actions

Understanding the intentions and goals behind other people's actions is fundamental in order to make sense of others' behavior (Tomasello, 1999). Being sensitive to the goal-directed nature of others' actions facilitates social

learning, serves as a precursor for understanding other people's behavior and is seen as a base for suitable reactions in social interactions (Hamlin et al., 2008). In order to disentangle the origins of humans' sensitivity to goal-directed actions, the development of this ability has been extensively studied (e.g. Carpenter et al., 2005; Hofer, Hauf, & Aschersleben, 2005; Király, Jovanovic, Prinz, Aschersleben, & Gergely, 2003; Woodward & Sommerville, 2000). For instance, it has been shown that from early on, infants attend to a variety of social stimuli when observing others, such as eye contact or facial expressions (Farroni, Csibra, Simion, & Johnson, 2002). Already two-day-old babies have shown sensitivity to visual cues indicating purposeful and goal-directed actions, such as the direction of an arm movement, the presence of a goal object or hand shaping (Craighero, Leo, Umiltà, & Simion, 2011). Further, research has revealed that infants from 3 months of age are able to attribute goals to non-human agents, e.g. to a self-propelled box (Csibra, 2008; Luo & Baillargeon, 2005; Luo, 2011). Starting from around six months of age, infants represent observed human actions in terms of goal-relevant aspects (Carpenter et al., 2005; Legerstee, Barna, & DiAdamo, 2000; Woodward, 1998). In a seminal looking time study, Woodward (1998) has provided evidence for infants' sensitivity to the underlying goal structure of observed human actions. Six- and 9-month-olds were habituated with an actor reaching for one of two toys. During the following test phase, the location of the toys was switched and the actor reached either for the same goal object in a new location or kept the movement trajectory but grasped the new goal in the old location. Infants at both 6 and 9 months of age dishabituated and looked longer at the test event in which the actor reached for a new goal in the old location compared to the event in which the actor reached for the old toy in a new location. Importantly, infants only showed this novelty response when they saw a familiar human grasping or pointing action (Woodward & Guajardo, 2002), but they did not differentiate between the two events when the actions were performed by a mechanical claw (Woodward, 1998) or when an unfamiliar back-of-the-hand movement was presented (Woodward, 1999). The findings support the interpretation that infants represented and encoded the observed reaching action as goal-directed.

Later research has extended the knowledge about infants' perception of goal-directed actions. For example, it was also shown that infants at seven months of age selectively imitate goal-directed actions compared to goal-ambiguous actions (Hamlin et al., 2008) and that they differentiate whether an action was performed by a human actor or a mechanical claw (Hofer et al., 2005). Using a preferential looking paradigm, Daum, Prinz, and Aschersleben (2008) showed that infants' sensitivity to others' goal-directed actions becomes more mature over time. They demonstrated that 6- and 9-month-olds are able to infer a goal even from an uncompleted human reaching action if the action was presented from an allocentric perspective.

Additionally, infants at this age encode the specific way a reaching action is performed in order to infer the size of a goal object from the aperture size of the observed grasping hand (Daum, Vuori, Prinz, & Aschersleben, 2009). Between 9 to 12 months, infants also begin to encode human pointing as an object-directed action (Woodward & Guajardo, 2002) and 9-month-olds begin to discriminate between different intentional actions, e.g. if an actor is unwilling or unable to pass infants a toy they wanted (Behne et al., 2005). At one year, they further encode goals from other communicative cues, such as emotional expressions (Phillips, Wellman, & Spelke, 2002). After their first year of life, infants expand this ability and they begin to show sensitivity to the common goal structure of an observed joint action between two collaborating individuals (Fawcett & Gredebäck, 2013; Henderson & Woodward, 2011).

Several theoretical accounts put forth the idea that action experience contributes to action understanding and, therefore, infants' own emerging action abilities support the development of their understanding of actions and goals (e.g. Gallese, Rochat, Cossu, & Sinigaglia, 2009; von Hofsten, 2004, 2007). For instance, Bertenthal and colleagues (Bertenthal, Campos, & Kermoian, 1994) found that infants' locomotor experience affected their performance in the visual-cliff task. Infants with more crawling experience showed increased fear of heights and higher heart rate accelerations when crawling over the deep side of the visual cliff. Similarly, several EEG studies have revealed how motor experience modulates brain activity (Reid & Kaduk, 2011; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). For instance, van Elk and collaborators found stronger activation over motor areas while infants were watching crawling compared to walking videos, and infants' motor resonance was closely related to their crawling experience. In line with these findings, it has been proposed that infants' own motor experience also affects the understanding of others' actions. Thus, being able to represent own actions in terms of goals also facilitates understanding of other people's goal-directed actions. In order to test this hypothesis, Sommerville and colleagues (Sommerville, Woodward, & Needham, 2005) experimentally modulated the grasping experience of pre-reaching infants and assessed its effects on their goal attribution abilities. During a training phase, 3-month-olds, who typically do not have grasping abilities yet (Needham, Barrett, & Peterman, 2002), were wearing mittens covered with Velcro that allowed them to effectively swipe at and pick up objects when touching them. After the training experience, infants were presented with a habituation paradigm similar to the paradigm in Woodward's seminal experiment. Infants' looking times indicated that only infants with prior mitten training showed sensitivity to the changed goal structure of the reaching-grasping actions, i.e. they viewed the action as goal-directed (see also Skerry, Carey, & Spelke, 2013; Sommerville, Hildebrand, & Crane, 2008). In another habituation study, Loucks and Sommerville (2011) showed that

10-month-olds' ability to process observed precision grasps in relation to their functional consequences was closely related to infants' own motor abilities. Recent research (Gerson & Woodward, 2014) provides further evidence for the view that infants' active rather than observational experience with sticky mittens accounts for their enhanced sensitivity to the goal-directed nature of the observed action. In a similar vein, Daum, Prinz and Aschersleben (2011) demonstrated that 6-month-olds' ability to differentiate between expected and unexpected outcomes of observed grasping actions was related to their ability to perform thumb-opposite grasping actions.

Together, a large body of empirical evidence demonstrates humans' sensitivity to goal-relevant aspects of others' actions. In addition, developmental research has indicated that already young infants are selectively sensitive to human goal-directed actions, and that infants' action experience plays an important role for their action and goal understanding (Hunnius, & Bekkering, 2014). As human actions carry biological motion information, the following section will elaborate on the special role of biological motion for social perception. Later sections will expand the focus from single-person actions to social interactions as the base of human social cognition depends to a large degree on the human ability to encode and understand human social interactions between individuals (Blakemore & Decety, 2001; Sebanz et al., 2006).

Biological motion perception

Every day, we experience visual motion, but we are especially fascinated and interested in motion from other living beings around us (Allison et al., 2000). Besides our sensitivity to motion patterns from other living creatures, the visual system is also able to extract socially and biologically relevant information from biological motion with apparent ease and readiness. Humans' remarkable ability to identify living creatures based on perceptual motion cues is well established (Blakemore & Decety, 2001). Historically, Gunnar Johansson was the first to use the point-light (PL) technique to demonstrate how particularly sensitive the human visual system is to motion of biological entities (Johansson, 1973). In these so-called PL animations, motion cues of human body movements have been reduced to points of lights from reflective markers that were attached to the major joint positions of a human body. Interestingly, the captured motion of these PL action sequences provides observers sufficient information to readily and unequivocally identify coordinated walking actions.

During the last decades, a particular interest of developmental studies has been infants' perception and sensitivity to biological motion information. Recent work on human newborns' perception of biological motion showed that already two-days-old infants discriminate between a PL animation de-

picting biological motion of a walking hen from both an inverted display or a scrambled non-biological version (Simion, Regolin, & Bulf, 2008). With regard to human motion, Fox and McDaniel (1982) demonstrated in their classical preferential looking study that also 4- to 6-month-old babies exhibit a visual preference for an upright PL display from a walking person compared to an inverted PL walking action (for a similar study with 3-month-olds, see Bertenthal, Proffitt, & Cutting, 1984). Further, starting from five months of age, typically developing infants demonstrate an enhanced sensitivity to human motion compared to animal motion, such as from spiders or cats (Pinto, 2006). This “perceptual tuning” could indicate a developing specialization of infants’ visual system for human motion. Along this line, infants’ sensitivity to human motion was also revealed in Event Related Potentials (ERP) studies in which 8-month-olds were presented with upright and scrambled or inverted PL walkers (Hirai & Hiraki, 2005; Reid, Hoehl, & Striano, 2006).

The particular role of human body motion becomes evident when comparing the developmental trajectories of infants’ sensitivity to either dynamic or static depictions of human bodies. In contrast to the early emerging sensitivity to human motion, infants younger than 18 months are not able to reliably differentiate coherent and scrambled static body stimuli (Slaughter, Heron, & Sim, 2002). However, it also needs to be noted that electroencephalography (EEG) studies have revealed that infants younger than 9 months differentiate static pictures from congruent and incongruent pointing and grasping actions (Bakker, Daum, Handl, & Gredebäck, 2014; Gredebäck, Melinder, & Daum, 2010).

Given the evolutionary adaptive purpose of biological motion detection for survival (Troje & Westhoff, 2006) and based on the early emergence of a sensitivity toward coherent, dynamic biological motion from social agents, Johansson (1973) and others (e.g. Bardi et al., 2014; Johnson, 2006; Simion et al., 2008) suggested the existence of a “life detector” capacity of the visual system that is already present at birth. This predisposed perceptual tuning for biological motion from living creatures is assumed to be present across vertebrates. Later research has revealed that even newly-hatched chicks manifest a spontaneous preference for a PL display of a walking hen compared to a scrambled non-biological version of the display (Vallortigara, Regolin, & Marconato, 2005) or to a hen-like object rotating around the vertical axis (Bardi, et al., 2011).

Humans’ apparent sensitivity to biological motion information expressed by PL displays has also initiated extensive research efforts in adults. It has been shown how accurately adult observers are able to detect and categorize the gender (Barclay, Cutting, & Kozlowski, 1978; Kozlowski & Cutting, 1977), emotional states (Atkinson, Dittrich, Gemmell, & Young, 2004; Dittrich & Troscianko, 1996) or the age of an observed PL walker (Montepare & Zebrowitz-McArthur). In just a fraction of a second, humans

are also able to recognize familiar individuals (Cutting & Kozlowski, 1977) and to derive information about intentions (Blakemore & Decety, 2001) or some personality traits (Troje, 2008) from PL displays. Even nuanced information, such as the weight of a lifted box (Runeson & Frykholm, 1981), can be discerned from biological motion animations.

Of important note for this thesis will be the role of biological motion for action prediction, as this source of sensory input provides crucial information for predicting other people's actions (Blakemore & Decety, 2001). At the same time, biological motion PL displays are suitable stimuli to isolate motion information from visual information normally associated with human actions (van Kemenade, Muggleton, Walsh, & Saygin, 2012). Thus, this type of stimulus will be used to address the research questions from Studies I and II, i.e. whether biological information provides sufficient information to elicit predictive eye movements during observation of goal-directed PL actions.

Prior to presenting empirical work on action prediction, the next section will introduce the account of embodied cognition as a theoretical framework that emphasizes the importance of action experience and perception for cognition.

Embodied cognition theories

While classical accounts describe human cognition as abstract information processes based on internal cognitive processes and symbolic representations, proponents of opposing accounts have been emphasizing the contribution of action and perception to cognitive processes, especially the role of our body acting in the environment. Of central interest for this thesis is the role of embodied processes for action perception and anticipation. Historically, the idea that the motor system is involved in action perception has already been a part of philosophical theories from Kant (1787/1965), Reid (1785/1969) or Merleau-Ponty (1945/2005) who highlighted the role our body's experiences for knowledge and understanding. In contrast to purely mentalistic explanations to cognition, modern theorists began to emphasize the connection between mental and perceptual-motor processing (for a review see Barsalou, 2008). For example, both William James (1890/1981) and Jean Piaget (1953) stressed the importance of sensorimotor abilities for the development of cognitive abilities. These emerging ideas about how embodied representations contribute to social cognition and understanding have been labeled as accounts of embodied cognition. Although these approaches cannot be unified in a single theory of embodied cognition (Saphiro, 2010), all embodied theories assume that "body matters" for cognitive processes, i.e. that the body influences the human mind. In other words, the notion of embodied cognition assumes that cognitive processes

are closely related to the physical body and body representations (Goldman & de Vignemont, 2009). Thus, cognitive mechanisms are considered as being shaped by bodily interactions with objects in the environment and as deriving from sensorimotor abilities and experiences of human actions (Chemero, 2009; Clark, 1997; Lakoff & Johnson, 1999; Varela, Thompson, & Rosch, 1991). Deriving from the idea that action and perception are tightly linked, Gibson (1979) proposed in his ecological psychology that both our actions and the environment are central for cognition. His more radical account of embodied cognition emphasizes not only how perceptual processes guide our actions but also the importance of affordances. Gibson views affordances as intrinsic properties of objects in the environment that provide necessary information for our behavior. More precisely, such affordances are directly perceivable opportunities for interactions and possibilities for use, action or intervention (see also Study III, Experiment 2).

While embodied accounts have influenced many areas of research, e.g. cognitive linguistic or memory theories, the thesis will concentrate on its role for action understanding and prediction. In this context, modern embodied accounts have been focusing on the role of simulation mechanisms in human social cognition (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Decety & Grèzes, 2006; Gallese & Sinigaglia, 2011; Goldman, 2006). In general, simulation theories presume that observers represent other people's actions or minds using simulations of their own actions or minds (Barsalou, 2008; Gallese, Keysers, & Rizzolatti, 2004). The idea that simulation processes in the motor system, i.e. in the MNS, influence action understanding has added a neurophysiological level to the embodied account (Rizzolatti & Craighero 2004). In line with the assumption that action and perception are closely intertwined (Clark, 1997; Hommel et al., 2001), this notion proposes that we use acquired sensory-motor and introspective states from our own experience and apply them to perceived actions. Accordingly, action understanding is achieved by simulating a perceived action in the motor system, i.e. in neural networks that are also involved in the processing of sensory-motor information from own actions. Thus, observers are able to understand and predict others' actions reenacting own perceptual or motor states (Barsalou, 2008). Consequently, prediction during observation of others' actions would reflect that own action plans are triggered in the observer (Falck-Ytter, 2012; Flanagan & Johansson, 2003).

The following sections review empirical evidence and theoretical views both supporting and challenging the idea that embodied simulation processes play a central role for action perception and understanding. As anticipatory eye movement paradigms provide a suitable behavioral measurement for studying online action processing, evidence from eye-tracking studies in relation to embodied and non-embodied accounts of action prediction will be described. At the same time, the presented literature will focus on recent

neurophysiological findings illuminating the underlying neural processes and assumed mechanisms behind action understanding and action prediction.

Eye-tracking as a tool to study action perception

As reviewed above, the visual perception of goal-directed actions and biological motion has mostly been investigated by means of eye-tracking using looking times measures and, more recently, anticipatory eye movement paradigms. Therefore, the following section elaborates on how online measurements of eye-tracking were used to study predictive eye movements during observation of others' manual actions, focusing on the relation between predictive gaze and the motor system.

Looking time measures

Since the first and seminal studies on infants' looking behavior in the 1950s (Fantz, 1958), looking time measures have been one of the most commonly used behavioral methods to study action perception (Aslin, 2000). In the context of action understanding, measuring novelty responses by means of habituation paradigms has provided detailed information about the relevant aspects of an action that observers attend to. Moreover, this method has been used to examine how manipulations of these aspects shape observers' detection, discrimination or learning abilities (Aslin, 2000). Despite the importance of looking time studies for our knowledge about action perception, especially with respect to infants' development and cognitive abilities, this method comes along with some disadvantages compared to other eye-tracking techniques (Aslin, 2012; Heyes, 2014; Hunnius & Bekkering, 2014). With regard to the temporal resolution, a shortcoming of looking time measures is that they do not provide detailed information about participants' online gaze behavior. In habituation paradigms, looking times are often measured after a presented event or action has occurred and, therefore, they capture observers' sensitivity to changes in specific aspects of an observed action rather than their online gaze behavior. However, in everyday life, we need to evaluate and predict observed actions as they unfold. Thus, whereas looking time studies often measure post-hoc evaluations of observed actions (Cannon & Woodward, 2012; Daum, Attig, Gunawan, Prinz, & Gredebäck, 2012), the eye-tracking measure of predictive gaze can provide important information about observers' online predictions and evaluations about upcoming events.

Action prediction and anticipatory eye movement paradigms

As reviewed above, action prediction, i.e. the ability to direct gaze to the goal of an action ahead of time, plays a crucial role in many different contexts of our lives. For instance, humans are able to predict future physical events during extrapolation tasks, such as the reappearance of self-propelled objects rolling behind an occluder (Green, Kochukhova, & Gredebäck, 2014; Rosander & von Hofsten, 2004). Further, perceptual predictions contribute to prospective motor planning, action production and action control (Claxton, Keen, & McCarty, 2003; Land, 2006; von Hofsten & Fazel-Zandy, 1984; von Hofsten, 2004). Research has shown that the kinematics of adults' goal-directed reaching actions are shaped by future intended actions, i.e. depending on what adults plan to do with an object after grasping it (Flanagan, Vetter, Johansson, & Wolpert, 2003; Land & Hayhoe, 2001; Marteniuk, Mackenzie, Jeannerod, Athenes, & Dugas, 1987). Thus, while executing a manual action, action prediction assists in guiding and adjusting the final approach of the hand to the size and shape of an action goal (Bertenthal, 1996; Johansson et al., 2001). Already 9- to 13-month-old infants are able to adapt their hand shaping to the size of the target they are reaching for (von Hofsten & Rönqvist, 1988). These findings demonstrate that the prospective planning of motor actions as an essential part of action production is necessary for the activation of future action plans (Johansson et al., 2001; Sailer, Flanagan, & Johansson, 2005). Importantly, when performing a visuomotor task, action prediction not only facilitates well-timed motor responses but also permits compensating for the internal processing lag of our oculomotor system (von Hofsten, 2007).

In addition to its importance for action execution, prediction also plays a central role for the processing of others' goal-directed actions. Being able to form expectations about what is going to happen next whilst observing other people's actions allows us to prepare appropriate and timely responses during cooperative or competitive actions. For instance, when walking a busy intersection, we make predictions about where others will walk in order to avoid bumping into them (Patla & Vickers, 2003). Also, in more coordinated interactions such as sports, predictions are necessary to foresee what a person from the opposite team is going to do next. These predictions help to adjust strategies in order to score the winning goal (Land & McLeod, 2000). Hence, predictions form the basis of efficient coordination with others during social interactions that require fine-grained temporal reactions (Bekkering et al., 2009; Schütz-Bosbach & Prinz, 2007b).

The ability to predict upcoming events is captured in prospective gaze shifts to future action goals. When observing actions, both adults and infants exhibit anticipatory gaze shifts toward the goal of an action ahead of time. These visual anticipations serve as a measure of observers' expectations about future actions, e.g. which goal object a person is going to grasp

(Cannon & Woodward, 2012). To date, eye-tracking research measuring anticipatory eye movements as an index of adults' or infants' action prediction abilities has become quite prevalent. Anticipatory gaze shifts are a particularly suitable measure of participants' online evaluations as it is a non-invasive and comparably quick measurement with a high temporal and spatial resolution (Aslin, 2012). Consequently, this method has played an important role for studying prediction of human motor actions, especially manual reaching actions (Ambrosini, Costantini, & Sinigaglia, 2011; Falck-Ytter, Gredebäck, & von Hofsten, 2006; Henrichs, Elsner, Elsner, Wilkinson, & Gredebäck, 2014; Johansson et al., 2001).

Within the framework of this thesis, anticipations are operationalized as goal-directed gaze shifts toward action goals that occur before an action goal is reached. That is, fixating an action goal before the goal is achieved is defined as action anticipation, or action prediction. In this thesis, both terms are used interchangeably, i.e. both are operationalized as participants' ability to look toward the future location of an observed goal-directed action ahead of time (Gredebäck, Johnson, & von Hofsten, 2010). By this conceptualization, the corresponding goal of an action generally refers to the object that is attained by the observed intentional motor behavior toward it. Anticipatory gaze shifts toward these action goals are viewed as a marker of participants' online action understanding (Gredebäck et al., 2010; Holmqvist, 2011). As action understanding is a complex and broad concept, it comprises representing and comprehending goals on multiple levels (Uithol & Paulus, 2013; Woodward & Gerson, 2014). More precisely, goal-directed actions can be seen in relation to a hierarchy of goals, ranging from proximate goals, such as reaching for a cup to obtain the cup, to more complex intentions, such as reaching for a cup to drink in order to avoid dehydration (Hunnius & Bekkering, 2014). In the context of the thesis, action or goal understanding relates to proximal goals rather than higher-order intentions. In this framework, the ability to predict the future endpoint of observed goal-directed action requires representing a viewed action with respect to its underlying goal structure, but not a representation of higher-level goals.

In this thesis, all reported studies use anticipatory eye movement paradigms to investigate adults' and infants' online gaze, i.e. their future-oriented, goal-directed eye movements during observation of different manual and social actions. Therefore, the next section reviews prior research examining adults' and infants' anticipatory gaze during action observation.

Predictive eye movements during action observation

Predictive eye movements play an essential role in movement planning and control during object-related manual actions (Bowman, Johansson, Johansson, & Flanagan, 2009; Hayhoe & Ballard, 2005; Land, Mennie, &

Rusted, 1999). It is well documented that during execution of object manipulation tasks, people exhibit task-specific predictive gaze shifts to forthcoming grasp or landing sites, i.e. they fixate on the goal object before the hand arrives there (Johansson et al., 2001; Land, Mennie, & Rusted, 1999). In their seminal eye-tracking study, Flanagan and Johansson (2003) made the intriguing discovery that humans showed similar predictive gaze shifts when people performed an object manipulation task (block stacking task) or when they observed an actor performing the same action. That is, observers generate predictive eye movements that resemble the ones produced during action execution. This striking ability allows them to predict and not simply track other people's actions as they unfold. Later research has extended these findings, showing that adult observers are also able to predict manual actions with multiple potential targets (Rotman, Troje, Johansson, & Flanagan, 2006) and that they are able to take advantage of action-specific cues (Ambrosini et al., 2011; Webb, Knott, & Macaskill, 2010). On the contrary, it was shown that observers do not implement the same proactive eye movements when viewing self-propelled objects (e.g. blocks or balls) moving along the same trajectory as a hand during an object manipulation task (Falck-Ytter et al., 2006; Flanagan & Johansson, 2003).

Based on the intriguing finding of similar predictive eye movements during action execution and action observation, Flanagan and Johansson (2003) have put forward the idea that a recruitment of analogous motor representations drive predictive eye movements both when performing an action and when observing another person doing the same action. This notion is consistent with the direct-matching hypothesis, proposing that observed action plans are mapped onto the observer's own action plans, which allows observers to decode and predict other people's actions (e.g. Rizzolatti, Fogassi, & Gallese, 2001; Rotman et al., 2006, see page 32).

The resemblance of proactive gaze when performing or observing an action has inspired developmental research to investigate how infants' ability to anticipate observed action goals emerges, and how this ability is related to their own motor repertoire. In addition, studying predictive gaze from a developmental perspective allows us to gain information that increases the understanding of the underlying processes behind action prediction.

In line with the findings from the eye-tracking study by Flanagan & Johansson (2003), Rosander and von Hofsten (2011) revealed a close coupling between infants' own hand and eye movements both during action observation and execution of a manual transport action. Historically, Falck-Ytter and colleagues (2006) were one of the first to study infants' online gaze anticipations during action observation. In their eye-tracking experiment, they presented 6- and 12-month-olds and a group of adults with three different transport actions while measuring latencies of goal-directed gaze shifts. Participants were either presented with a manual displacement action in which a human actor transported a ball into a bucket, or they observed a

self-propelled ball moving along the same trajectory toward the bucket and with identical motion as the model's hand (self-propelled condition) or along a linear trajectory (mechanical motion condition). Adults and 12-month-olds, but not 6-month-olds, predicted the goal of the manual displacement action and shifted their gaze to the bucket before the hand had arrived there. At the same time, participants did not exhibit anticipatory eye movements when they saw the ball flying to the bucket in a self-propelled manner. These findings indicate that by one year of age, infants are able to predict observed manual transport actions. Interestingly, infants around that age are competent at reaching and grasping and they are already able to perform transport actions, such as transferring objects into containers (Bruner, 1970; von Hofsten, 1991). The authors interpreted their findings as evidence for a developmental correspondence between infants' ability to perform the observed manual action and their ability to look at the action goal before that action is completed.

Later studies have demonstrated that specific goal properties are also important for predictive gaze in adults (e.g. Ambrosini et al., 2011) and infants (e.g. Henrichs, Elsner, Elsner, & Gredebäck, 2012). Specifically, these studies showed that latencies of goal-directed gaze shifts were influenced by the visual saliency of the action goal, such as the presented end-effects (Eshuis, Coventry, & Vulchanova, 2009), or by the overarching goal of an action. That is, infants' predictive gaze shifts depended on whether the final goal of an observed reaching action was to place objects into containers or to displace them on a board (Gredebäck, Stasiewicz, Falck-Ytter, von Hofsten, & Rosander, 2009).

In addition to studies investigating the effect of goal properties on predictive gaze, the focus of most recent research efforts has been on the role of observers' own motor abilities. For instance, Kanakogi and Itakura (2011) compared 4- to 10-month-old infants' and adults' reaching-grasping abilities with their ability to predict others' action goals. The prediction task included three different action sequences showing either a human reaching action toward one of two toys, a mechanical claw or the back of a hand moving toward one of the goal objects, respectively. They found that the onset of infants' own reaching ability corresponded with their action anticipation ability. Importantly, this correlation was only significant for the condition showing the human grasping action. In detail, they demonstrated that starting from 6 months, infants begin to anticipate the human reaching-grasping action, but not the actions performed by the mechanical device or the back of the hand. At this age, infants were also able to perform simple reaching actions. At the same time, 4-month-olds' grasping abilities were significantly lower and younger infants tracked all presented actions in a reactive manner. Altogether, these findings indicate that infants' ability to predict an observed action is modulated by their motor ability to perform that same action, supporting an embodied account of action prediction.

The tight coupling between motor experience and action perception receives further support from eye-tracking studies showing that 12-month-olds' latencies of goal-directed gaze shifts depend on their life experience with feeding actions (Gredebäck & Melinder, 2010) or that goal anticipations relate to 25-month-old infants' manual ability to solve a puzzle (Gredebäck & Kochukhova, 2010). In addition, Ambrosini and colleagues (2013) found that infants from 8 months of age show a pre-shape advantage not only during anticipation of whole-hand grasps, but also for precision grasps (Ambrosini et al., 2013). The direct link between infants' ability to execute specific actions with whole-hand or precision grasps and their saccadic latencies during observation of corresponding pre-shaped grasping actions further suggests the ability to predict the goal of an action is closely connected to the type of action observed and to one's own motor repertoire. Thus, infants with competent motor skills can use relevant motor cues, e.g. the pre-shaping of a reaching hand, for action anticipation.

Besides the large number of studies looking at the connection between the onset of different motor abilities and the onset of the ability to predict the corresponding motor actions, another approach has been taken to study the relation between infants' own experience and their action perception. Researchers tested whether training infant's action production system facilitates action perception. Using the same experimental design as Falck-Ytter et al. (2006), Cannon and colleagues tested whether infants' engagement in containment activities affects their action anticipation abilities, which were assessed directly afterwards (Cannon, Woodward, Gredebäck, von Hofsten, & Turek, 2012). Indeed, they found a relation between infants' own activity level in the motoric task (placing objects into containers) and their anticipatory gaze performance during the following observational task.

In addition, eye-tracking studies with adult samples have provided further evidence for the influential idea that a recruitment of the observers' own motor system accounts for action anticipation during action observation. For example, Cannon and Woodward (2008) conducted an eye-tracking study on adults that tested if concurrent motor activity or effortful cognitive processes interfere with action anticipation. During observation of a manual displacement action (similar stimuli as Falck-Ytter et al., 2006), participants were performing either a finger-tapping or working memory task while goal-directed gaze shifts were recorded. Interestingly, only simultaneous finger-tapping, but not the concurrent non-motor task, affected latencies of goal-directed gaze shifts, suggesting that the motor system is involved in anticipations of observed motor actions.

Whereas this experiment demonstrates a clear interference effect of simultaneous motor tasks on gaze predictions, other adult eye-tracking studies revealed how even more subtle modulations of perceived motor information affect predictive eye movements. For instance, it was shown that adult observers benefit from specific motor cues, e.g. the hand configuration

(Ambrosini et al., 2011) or that predictive eye movements are modulated by action experience (Land & McLeod, 2000; Sailer et al., 2005). Specifically, Ambrosini and colleagues demonstrated that observers use information about the hand preshaping in order to anticipate an observed reaching action toward one of two differently sized goal objects. When the moving hand was shaped as a precision grip, observers shifted their gaze to the small object in a predictive manner, and when the reaching hand formed a whole-hand grip, observers fixated at the big goal object ahead of time. In addition, Costantini, Ambrosini and Sinigaglia (2012a) found that the compatibility between observed and produced prehension influences gaze anticipations, indicating that proactive eye movements are affected by the readiness of the observers' own motor representations. They further demonstrated that anticipatory gaze performance is selectively impaired when observers' hands are tied behind their backs during observation of reaching-grasping but not touching actions (Ambrosini, Sinigaglia, & Costantini, 2012). Based on these findings, the authors concluded that whether observers are in a position to perform an observed action or not has an impact on their action anticipation abilities. On a related note, it was shown that predictive gaze behavior is modulated by object reachability, i.e. depends on whether the presented object falls within the actor's reaching space or not (Costantini, Ambrosini, & Sinigaglia, 2012b). Specifically, observers exhibited predictive gaze shifts significantly earlier when an observed actor is able to reach for and act on a goal object than when an object is out of the actor's reach.

Together, the available evidence from the reviewed anticipatory eye movement paradigms in infants and adults suggests that, in some action observation scenarios, the motor system plays an important role for action anticipation. In addition, findings from Cannon and Woodward (2008) support the assumption that gaze anticipations during observation of a manual action might depend on a recruitment of motor areas that are also involved when observers perform the same action themselves. On a neural level, it has been suggested that mirror neurons form a network for matching perception and execution of motor actions (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996), and that the MNS provides the neural basis for action prediction through motor resonance (Rizzolatti & Craighero, 2004).

The mirror neuron system

As reviewed above, a large body of research indicates that the ability to process and anticipate others' actions is closely connected to the activation of the observer's own motor system. An assumed underlying neural basis linking action production and perception is the MNS. In connection to the previously described eye-tracking literature, it has been suggested that this mirror neuron circuit is involved in action prediction. Before elaborating on

different theories specifying the role of the MNS for predictive gaze, revealed evidence for the existence of brain areas with mirror properties in non-human and human primates will be reported.

Evidence from non-human primates

In their seminal single-cell recording studies, a group of Italian researchers at the University of Parma discovered a new class of visuomotor neurons in area F5 of the ventral premotor cortex (PMCV) and in area PF of the inferior parietal lobe (IPL) of macaque brains with special firing properties (Gallese et al., 1996). That is, these neurons discharged both when the monkey executed hand or mouth actions (e.g. grasping actions) as well as when it viewed another individual performing the same actions (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Thus, for this class of neurons, watching somebody do something is similar to when the monkey would perform the same action itself. Due to this unique firing property that allows the brain to duplicate (i.e. ‘mirror’) the movements it sees, these neurons have been called mirror neurons. The cortical pathways of this mirroring network are assumed to begin with visual processing in the superior temporal sulcus (STS), an area that is activated by biological motion and movements (Allison et al., 2000; Puce & Perrett, 2003), but lacks mirror properties. From there, important output signals are sent to temporal regions with mirroring properties, mainly to the IPL. Subsequently, the IPL projects visual information up to the PMCV including area F5 (e.g. Keysers & Gazzola, 2014; Rizzolatti & Craighero, 2004).

The area F5 of the PMCV consists of two populations of cells, the so-called ‘mirror neurons’ and the ‘canonical neurons’ (Gallese et al., 1996). The latter set of cells fire during execution of a manual action and they are triggered by passive observation of graspable objects, but they do not respond during observation of object-directed grasping actions (Rizzolatti & Luppino, 2001). On the contrary, mirror neurons fire during execution or observation of any action that involves an interaction between a biological effector (e.g. hand or mouth) and an object. Since the initial discovery, mirror neurons coding effector-specific manual (e.g. grasping) or mouth actions (e.g. cracking a peanut) and specific goal states, e.g. grasp-to-eat, have been identified (Casile, 2013; Fogassi et al., 2005). Furthermore, another set of neurons, strictly congruent mirror neurons, fire only when observed and performed motor actions are identical with respect to the involved effector and object. At the same time, two thirds of mirror neurons display a broader congruence in terms of their similarity between visual and motor acts. That is, the discharge of broadly congruent mirror neurons is independent of the motor details and movement specifics (e.g. grasping with precision or whole-hand grip) of an observed or executed action (Gallese et al., 1996).

Therefore, this class of neurons was proposed to be in charge of encoding overarching action goals (Uithol, van Rooij, Bekkering, & Haselager, 2011).

Given that a monkey is aware of an object behind a screen, it has been shown that mirror neurons also fire when a monkey observes a goal-directed reaching-grasping action in which the final hand-object interaction is not visible (Umiltà et al., 2001). Based on this finding of mirror neuron discharge during observation of manual actions toward occluded action goals, Umiltà and colleagues concluded that the MNS decodes specific goal-directed movements and not the kinematics for executing them. This finding is consistent with a single-cell recording study by Fogassi et al. (2005), which looked at the temporal activation patterns of mirror neurons. They found that certain cells fire before a goal is achieved, e.g. during the initial grasping phase. This capacity was interpreted as evidence for anticipatory processes set in place in the MNS.

On a related note, a recent study has directly investigated the relationship between monkeys' gaze behavior and mirror neuron activity by simultaneously recording eye position and mirror neuron discharge in area F5 of two macaques during observation of grasping actions (Maranesi et al., 2013). They demonstrated that anticipatory eye movements do not only occur during execution of manual actions, but also during action observation, providing first evidence for macaques' ability to exhibit proactive gaze shifts during observation of goal-directed grasping actions. Further, they found that the onset of mirror neuron discharge was connected to the onset of the actor's movements, and that gaze behavior influences mirror neurons' firing rate. That is, mirror neurons fired stronger when the monkey's gaze was predictive than when it was reactive, and the mirror neurons' firing rate was more influenced by 'when' rather than by 'how long' monkeys gazed at the goal of the observed action during its unfolding. Besides, when the monkey exhibited anticipatory eye movements, gaze-dependent mirror neurons showed the strongest discharge during the pre-contact phase (i.e. before the hand-object interaction), whereas reactive gaze behavior was associated with higher mirror neuron discharge after the hand contacted the goal object. Together, this study reveals a close correspondence between monkeys' gaze behavior and mirror neuron response during action observation, supporting the idea that motor representations could play a crucial role in directing anticipatory eye movements.

The mirror neuron system in humans

The spectacular discovery of action mirroring neurons in the macaque brain has initiated an extensive and vivid scientific discussion about a human MNS and its potential functions. Generally speaking, many neurophysiological studies have shown that the processing of goal-directed human actions does not only occur in visual brain regions, but relies also on cortical

motor areas (Bonini & Ferrari, 2011). The findings of visuomotor neurons activated during action execution and observation add a potential neural basis to the concept of embodied cognition, providing an explanation on a neural level for the assumed embodied processes linking action and perception (Gallese & Sinigaglia, 2011). However, the idea that humans possess a special circuitry in the brain that helps them to connect with other people was applied to a wide range of other social skills. That is, a large body of research has emphasized the importance of action mirroring for a variety of social functions. For instance, mirror neurons have been proposed to subserve imitation (Buccino et al., 2004; Iacoboni, 1999), emotion recognition (Jabbi, Swart, & Keysers, 2007), feelings of empathy (Gazzola, Aziz-Zadeh, & Keysers, 2006), intention inferences (Fogassi et al., 2005) or language processing and acquisition (Arbib, 2005). But it needs to be pointed out that the functional contribution of mirror neurons with regard to various human social abilities or disorders is still a matter of heated and controversial debates (for instance see Dinstein, Thomas, Behrmann, & Heeger, 2008; Heyes, 2010; Hickok & Hauser, 2010; Hickok, 2009).

Neurophysiological evidence for a human MNS

Since invasive single-cell recordings are not feasible for human studies due to ethical reasons, much effort has been directed into different behavioral and neurophysiological methods to indirectly demonstrate the existence of an analogous mirroring circuitry in humans. The first neurophysiological evidence for a tight link between action and perception systems in humans came from electrophysiological studies showing that both observing other people's actions or performing these actions leads to sensorimotor mu rhythm desynchronization (Altschuler et al., 1997; Pineda, 2005). Originating in the sensorimotor cortex with a frequency around 10 Hz at rest (Arnstein et al., 2011), the mu rhythm was found to be suppressed not only during action execution, but also during action observation (Muthukumaraswamy, Johnson, & McNair, 2004). Therefore, mu rhythm desynchronization has been used as a neural marker for mirroring activity in the human MNS. As a recent example, Cannon et al. (2014) tested the effect of active motor experience versus passive observational experience on adults' mu rhythm suppression. Compared to novices or observers, participants who received active tool-use training showed the greatest desynchronization during subsequent observation of grasping actions with a mechanical claw. The results indicate that short-term sensorimotor experience, but not passive observation, is sufficient to alter mirror neuron activity (Cannon et al., 2014; see also Paulus, Hunnius, van Elk, & Bekkering, 2012). Recently, EEG mu rhythm suppression analysis has also become a popular neurophysiological measure for demonstrating a recruitment of infants' motor system during action observation (e.g. Marshall, Saby, & Meltzoff, 2013; Nyström, Ljunghammar, Rosander, & von Hofsten, 2011). At the same time,

magnetoencephalography (MEG) studies (e.g. Hari et al., 1998; Hari, Bourguignon, Piitulainen, Smeds, & Tiège, 2014) found a similar post-stimulus rebound, i.e. a reduction of 20 Hz-activity as an indicator of motor cortex activation, both during object manipulation and action observation (see also Järveläinen, Schürmann, & Hari, 2004; Nishitani & Hari, 2002).

Since more than a decade, neuroimaging has been employed in order to pinpoint the exact locations of mirror mechanisms in humans (e.g. Iacoboni & Dapretto, 2006; Kilner, Neal, Weiskopf, Friston, & Frith, 2009). For instance, in functional brain imaging experiments, participants were scanned while they executed hand or mouth actions themselves or while they observed another person performing the same action (Buccino et al., 2004). In line with findings from the EEG study by Cannon et al. (2014), fMRI studies also linked specific activation patterns in fronto-parietal areas to acquired motor skills and motor expertise, for instance in expert ballet dancers, tennis players or other athletes (Balsler et al., 2014; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006).

Several meta-analyses of neuroimaging data aimed to identify common neural correlates across studies and consistently activated cortical regions with mirror properties (Caspers, Zilles, Laird, & Eickhoff, 2010; Molenberghs, Cunnington, & Mattingley, 2012; Van Overwalle & Baetens, 2009). Analogously to the macaque brain, the human mirror neuron network has been presumed to exist in the premotor cortex (Brodmann areas 44 and 6, corresponding to monkey's area F5) and the IPL (corresponding to monkey's area PF). Both receive input from the posterior STS (corresponding to the monkey's STS). However, the human MNS seems to reside well beyond the assumed classical fronto-parietal mirror circuit. Several studies have found additional areas with mirroring activity in the primary somatosensory cortex or superior parietal lobe (Caspers et al., 2010; Keysers, Kaas, & Gazzola, 2010). Nevertheless, little is known about the exact cortical connections of these regions with other mirror neuron areas. Compared to the monkey MNS, the human MNS appears to be more widespread (Gazzola & Keysers, 2009; Landmann, Landi, Grafton, & Della-Maggiore, 2011; Molenberghs et al., 2012). For instance, the medial temporal lobe and the supplementary motor area (SMA) have also been identified to contain a large proportion of neurons firing both during action execution and observation (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). Importantly, the study by Mukamel et al. (2010) was also the first to use single-cell recordings in epilepsy patients who observed or executed hand-grasping actions or facial expressions, providing the currently most direct evidence for cells with mirroring properties in humans.

In summary, many studies show that the MNS is involved in action processing and activated during action observation. However, central to the claims that action understanding is based on mirroring processes is to examine whether motor activation is causally related to action understanding

and action prediction (Avenanti & Urgesi, 2011). An answer to this could come from brain lesion studies or brain stimulation studies, which are able to overcome some disadvantages of fMRI procedures. That is, TMS permits online modulation of brain activity and direct testing of the effects on performance and behavior, such as on action perception (Avenanti, Candidi, & Urgesi, 2013; Mattiassi, Mele, Ticini, & Urgesi, 2014). By means of repetitive TMS or single pulses applied to a particular area of the cortex through an electromagnetic coil, changes in the induced magnetic field affect brain activity. This non-invasive method alters for instance the activation of neurons in the motor cortex for a very short time period. Thus, using TMS protocols makes it possible to test a causal relation between TMS-induced manipulations and its direct effects on participants' performance (Glenberg, 2011). In a first TMS study measuring cortico-spinal excitability during action observation, Fadiga et al. (1995) found a specific increase of motor-evoked potentials (MEPs) from hand and arm muscles elicited when participants observed manual goal-directed actions, but not during observation of three-dimensional objects or during an attention demanding detection task.¹ Further, a functional contribution of the motor system to speech comprehension has been demonstrated in another TMS study (D'Ausilio et al., 2009). Double TMS pulses on the lip or tongue areas of the primary motor cortex during the discrimination of lip- and tongue-articulated phonemes had a facilitatory effect on the discrimination of concordant speech sounds and an inhibitory effect on the classification of discordant speech sounds. While these findings suggest a tight link between action and language systems, they are particularly interesting because they show a clear somatotopical effect for speech perception. Further research applying TMS over motor cortical areas in healthy human participants demonstrated interference effects and performance impairments during perception of biological motion and PL displays (Grossman, Battelli, & Pascual-Leone, 2005; van Kemenade et al., 2012), goal recognition tasks (Jacquet & Avenanti, 2013), visual action discrimination tasks of whole body movements (Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007), or during action outcome predictions (Stadler, Ott, et al., 2012), e.g. in soccer players (Makris & Urgesi, 2014). With respect to action prediction, Aglioti and colleagues (2008) investigated the role of motor expertise for action anticipation abilities in elite basketball athletes. More explicitly, they found that professional basketball players were more accurate and faster at verbally predicting successful outcomes of basket shots compared to novices or visually trained observers, especially in the early phases of the action, i.e. before the ball left the player's hand. By using TMS, they also demonstrated a selective and time-specific increase in motor excitability in the athlete group when verbally predicting the fate of

¹ Increased cortico-spinal excitability as measured by MEPs during action observation has been interpreted as an index of mirror activity (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995).

the observed shot at the basket. Their findings indicate that the elite players were able to extract and use kinematic cues from body movements to successfully predict the outcome of observed basketball shots (Aglioti, Cesari, Romani, & Urgesi, 2008).

Jointly, the reported neurophysiological studies using multiple methods provide converging evidence that during the processing of others' actions the human motor system is activated in a similar way as when observers would perform the same actions themselves. This suggests that mirror neuron activity plays a central role in many processes of action perception, e.g. in simulating future action outcomes (see also Cook, Bird, Catmur, Press, & Heyes, 2014; Press, Cook, Blakemore, & Kilner, 2011). These findings are consistent with an embodied account promoting that the motor system is actively involved in action understanding and prediction. However, in relation to predictive eye movements, direct evidence for the causal role of the motor system to action prediction is still lacking. Importantly, other theories on the underlying processes behind action prediction have been proposed as well. In the following section, I will review the different theoretical approaches that researchers have developed with regard to the functional mechanisms mediating action prediction.

Accounts of action prediction

While the studies reviewed above emphasize the role of the motor system for action anticipation, other theories explain action prediction without the reliance on the MNS. However, it needs to be mentioned that the vast literature on action prediction has focused on the importance of the motor system for anticipatory gaze processes and only few studies have opposed this view by testing other theories. Despite this imbalance, the existing theories can generally be divided into embodied and non-embodied accounts. In order to provide an overview about the different, and often contradictory theoretical perspectives, the most prominent theories about the underlying processes guiding action understanding and action prediction will be presented in more detail in the following sections.

Action resonance theories

The simulation theory, also referred to as action resonance theory, assumes that simulation processes of visual descriptions from perceived motor acts drive action understanding. In detail, during this embodied simulation (Gallese & Sinigaglia, 2011; Gallese, 2005) internal representations of the observed movements are recruited and they 'resonate' with the observer's own motor system, as if the observer was acting him-/herself (Iacoboni & Dapretto, 2006; Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004).

Mapping sensory information onto the motor representation of the same action allows recognition of the observed motor action and corresponding motor goal by means of the observer's own 'motor knowledge' (Fogassi et al., 2005; Umiltà et al., 2001). As Rizzolatti and colleagues (2011) suggested, action understanding could be achieved by resonating and duplicating an observed action in the motor system because the observer "knows the outcome when he does it" (Gallese et al., 2004, p. 396).

Important for this thesis, proponents of an embodied account of action prediction have suggested that these simulation processes also play an important role for predictive gaze. Specifically, the reported evidence from previous predictive eye movement studies (see page 22) has revealed support for the idea that observers recruit their own action plans to generate predictions about others' action goals. Thus, according to an embodied simulation account, predictive eye movements reflect the activation of the observer's own corresponding motor plans. For example, when observing a sequence of actions, e.g. someone grasping and lifting a bottle of water, the motor plans of the perceived actions are mirrored onto our own motor plans, allowing us to predict the sensory implications of that action. Thus, by reusing our own motor plans and attributing them to the sensory representations of another's action (Gallese & Sinigaglia, 2011) we are able to predict and differentiate between a grasping action that will ultimately result in drinking and one which will result in water being tossed at us. Importantly, this resonance-based model proposes that these simulation processes play a causal role for our ability to predict and comprehend others' proximal motor goals, without the necessity of additional higher-level inferential processes outside of the MNS (Miall, 2003).

One account for action prediction deriving from the action resonance theory is the direct-matching hypothesis. According to the direct-matching theory, the visual representations of perceived kinematics are mapped onto the corresponding motor representations in the observer (Ambrosini et al., 2011). Thus, sensory input elicits motor activation similar to when observers plan to perform an action. Particularly relevant to the present thesis, the direct-matching process has been suggested to play a crucial role for comprehending and predicting others' motor actions (Ambrosini et al., 2011; Flanagan & Johansson, 2003; Urgesi et al., 2010; Urgesi, Moro, Candidi, & Aglioti, 2006). In line with this idea, Flanagan and Johansson (2003, see page 22) found that observers spontaneously exhibit predictive eye movements not only when they perform a manual action themselves but also when they observed someone else performing the action. Flanagan and Johansson suggested that analogous eye motor programs are triggered during action execution and observation, and that a recruitment of the observer's motor plans accounts for anticipatory eye movements toward future end states of observed actions. They interpreted the common patterns of anticipatory gaze as evidence for a direct-matching process, assuming that sensory-motor

transformations of observed actions onto the observer's corresponding motor plans guide gaze anticipations. Specifically, they assumed that when observing another person executing a manual goal-directed action, observers activate their own action system, i.e. covert action plans and motor schema required to perform that action (Land & Furneaux, 1997; Rizzolatti et al., 2001). Hence, when observing other people's action, this direct-matching process in the MNS allows observers to internally simulate others' actions and, thus, to encode and predict their behavior.

With respect to the reviewed eye-tracking literature (page 22), the revealed interference effects of simultaneous motor tasks (Cannon & Woodward, 2008; Kilner, Paulignan, & Blakemore, 2003) and the facilitatory effects of specific motor cues such as hand pre-shaping (Ambrosini et al., 2011; Costantini et al., 2012a) indicate that gaze anticipations may indeed rely on a recruitment of the observer's own action plans. Previously reviewed infant eye-tracking studies have also demonstrated that infants' own motor experience plays a crucial role in shaping how they perceive and anticipate others' actions. Many studies have revealed a tight relation between infants' motor repertoire and their action anticipation abilities (Cannon et al., 2012; Falck-Ytter et al., 2006; Kanakogi & Itakura, 2011). From a direct-matching perspective, researchers concluded that only if infants have the ability to perform a certain motor action, the observed actions could be mapped onto the infants' own motor representation of that action.

Altogether, the findings from these studies provide evidence for the direct-matching process as the driving mechanisms for predictive eye movements. Other, more recent accounts have refined or extended the direct-matching hypothesis to explain how others' action goals and intentions can be inferred through action observation. For instance, the predictive coding account combines predictions relying on prior knowledge and context information with predictions based on observed kinematics (Kilner & Frith, 2008). At the core of the predictive coding framework is the idea that observed actions are represented at hierarchically organized levels. Specifically, the predictive coding theory assumes that contextual cues and prior experience lead to predictions about another person's intention. Based on these general expectations, observers form predictions about proximate goals, which are then used for and matched with predictions on a kinematic level (Press, Heyes, & Kilner, 2011). That is, predictions about another person's intention and the most likely action outcome are generated and constantly updated in simultaneous forward-connections. Thereby, predictive errors are minimized by comparing predictions in feedback-loops between the sub-ordinate representation level and the goal or intention level (Kilner, Friston, & Frith, 2007). Compared to the direct-matching account, this theory incorporates predictions generated outside of the MNS.

Altogether, action resonance theories highlight the central role of the motor system for action prediction, suggesting that mirroring processes are

crucial for action perception, prediction and understanding. Besides the excitement about mirror neurons, which have been called the “the most hyped concept in neuroscience” in the last decades (Jarrett, 2012), other scientists have formulated criticism about the assumed functions of the MNS (e.g. de Vignemont & Haggard, 2008; Jacob & Jeannerod, 2005; Jacob, 2009). In relation to action processing, opposing theories to the resonance-based account have been proposed, suggesting alternative mechanisms that drive action perception and understanding. In the following, the most prominent non-embodied accounts of action perception will be presented.

The role of inferential and teleological reasoning

One alternative account assumes that, rather than by motor-simulation recruiting the MNS, action understanding is mediated by an inferential interpretive system (e.g. Dennett, 1987; Gergely & Csibra, 2003). That is, inferential models (hereafter labeled as ‘inference account’) state that action understanding is a product of intention reading abilities and not a result of simulation processes in the motor system (Uithol & Paulus, 2013). Advocates of this alternative view criticized the direct-matching theory by arguing that a recruitment of observer’s motor representations does not play a crucial role in inferring and representing other people’s actions and goals. According to the critics of action resonance theories, there is a conceptually missing link between the recruitment of motor representations and the representation of others’ goals or intentions. Further, Gergely and Csibra argue action understanding does not rely on simulation processes of observed motor actions, as there are different ways to achieve a specific goal, e.g. different ways of reaching for an object. In the same vein, proponents of the inference account demonstrated that action understanding can be achieved even when the observer is not able to execute an action him-/herself and that evaluations of rationality are not solely based on prior experience with similar events (Csibra, 2008; Wood, Glynn, Phillips, & Hauser, 2007). Further support comes from studies showing that humans readily ascribe goals and intentionality to non-human agents (e.g. geometrical shapes) by means of non-kinematic behavioral animacy cues, such as equifinal action variation, self-propulsion and causal action-effect relations (e.g. Bíró & Leslie, 2007; Heider & Simmel, 1944; Luo & Baillargeon, 2005; Luo, 2011; Ramsey & Hamilton, 2010).

According to the inference account, we understand other people’s action goals and intentions based on teleological or inferential processes. At core of inferential theories are efficiency evaluations that are applied when processing others’ actions in relation to their goals. If these efficiency considerations and teleological interpretations satisfy the so-called principle of rational action, humans and even young infants are able to assign goals to observed actions (Gergely & Csibra, 1997). According to this principle, ob-

servers expect agents to plan rationally and to choose actions efficiently in order to achieve their goals and desires. In other words, people assume that others tend to obtain goals by the most efficient and optimal means present in a specific situation. Hence, an observed action can be explained by evaluating the relation between a desirable goal state, the most efficient action toward that goal state and the given situational constraints of physical reality (Csibra & Gergely, 1998). Csibra and colleagues reasoned that if information about at least two of the three action components (the action, the goal and the environment) is available, any third aspect could be inferred by the principle of rational action (Gergely, Nádasdy, Csibra, & Bíró, 1995). As an example of this teleological stance, an agent's most likely behavior could be determined if information about a desired goal state, e.g. a point or object in the environment, and the specific constraints of a situation, such as the agent's location or the presence of obstacles, are available. Central to the teleological reasoning theory are three assumptions. First, the principle of rational action can be applied to situations including both human and non-human agents. Second, inferences based on this principle do not require experience and can be made by already by young infants (Lou, 2011). Third, teleological reasoning might constitute a precursor of higher-level mentalistic processes evolving in later life (Gergely & Csibra, 2003).

Empirical evidence for infants' ability to use the rationality principle has been provided by habituation studies in which infants' looking times were compared when observing a self-propelled agent (e.g. a jumping circle) approaching a goal in an efficient or inefficient way (e.g. Csibra, Bíró, Koós, & Gergely, 2003; Csibra, 2003, 2008). It was shown that infants as young as 3 months of age are able to differentiate rational and non-rational actions and that they expect different animated or human agents to act in a rational manner, even when the environment changes (Csibra et al., 2003; Kamewari, Kato, Kanda, Ishiguro, & Hiraki, 2005; Wagner & Carey, 2005). Similarly, in their eye-tracking study measuring infants' pupil dilations in response to rational or non-rational feeding actions, Gredebäck and Melinder (2010) found that 6-month- and 12-month-old infants reacted with surprise, i.e. their pupils dilated more, when observing irrational feeding actions.

In addition to behavioral studies suggesting that already infants possess the ability to take a "teleological stance" when observing actions from human and non-human agents, brain-imaging studies on adults examined the neural processes behind action understanding. For instance, in their fMRI experiment, Brass et al. (2007) investigated the role of the inferential and mirror neuron network for action understanding, respectively. Specifically, they identified activated brain regions in the MNS or in the inferential reasoning network while participants observed novel plausible or implausible actions that required context-based inferences. The revealed data provide support for the inference account, showing stronger brain activations in the inferential network when observing an unusual and implausible action com-

pared to observing the same action in a more plausible context. At the same time, no differential brain activation between situations with varying plausibility was observed in the MNS (Brass, Schmitt, Spengler, & Gergely, 2007). Also de Lange and colleagues (2008) used functional brain imaging to assess the contribution of brain areas involved in motor simulation or inferential processes for action and intention understanding. Adult participants were presented with actions in which an actor carried out an ordinary or an extra-ordinary action with respect to either its motoric manner or underlying intention. Additionally, they varied whether participants had to focus on the perceived intention or motoric manner of the presented action across trials. They found that while parts of the MNS automatically process intentionality based on the visual properties of the observed action, the inferential network is specifically activated when participants paid attention to the intention of an observed action. Based on their results, the authors suggest that both networks are not mutually exclusive, but may play complementary roles in understanding others' actions and intentions (de Lange, Spronk, Willems, Toni, & Bekkering, 2008). Further support for rational inference mechanisms in adults' goal understanding comes from a study by Baker, Saxe and Tenenbaum (2009). They developed a computational framework using Bayesian inference for modeling action understanding based on the principle of rational action. In their behavioral experiments, in which they evaluated the model's predictions, they show that adults use rational inference mechanisms in order to deduce the goals of animated agents moving in simple mazes.

Predictive gaze

With regard to action prediction, the inferential account challenges the idea that predictive eye movements are mediated by mirroring processes in the MNS. Csibra and colleagues claim that action understanding and goal predictions are governed by action reconstruction processes and that motor activation does not causally contribute to, but rather constitutes a consequence of action understanding. In line with this idea, Southgate and Begus (2013) found a similar decrease in motor activation (i.e. attenuated sensorimotor alpha) during an action prediction task for actions in and outside of infants' own motor repertoire. Based on their findings, they concluded that predictive eye movements are the consequence of inferential processes and that the motor system is only recruited to predict how an action will unfold. Specifically, once action predictions have been generated outside of the MNS, motor activation that takes place during action observation only supports emulation processes of motor commands that are necessary to achieve an observed action goal (Southgate, 2013).

In relation to predictive gaze shifts, Csibra and Gergely (2007) have been arguing that predictive eye movements are generated on the basis of efficiency considerations following the principle of rational action. In general,

advocates of the inference account posit that anticipatory eye movements reflect non-motor inferential processes that originate outside of the MNS. In contrast to action resonance theories, this account proposes that direct-matching processes are not causally related to predictive eye movements during action observation. Some proponents of this view have claimed that these inferential processes underlying predictive gaze are higher-level processes (Eshuis et al., 2009), whilst others suppose that they could be non-mentalistic as well (Gergely & Csibra, 2003). More precisely, Eshuis and collaborators highlighted that predictive gaze shifts can be implemented even when there are only few motor cues available, e.g. when observers predict a salient end state of moving self-propelled, non-human objects. They claim that predictive gaze requires an observer to understand an agent's intention to achieve a goal and that human motion is not necessary for predictive gaze shifts to occur. In line with their findings, Biró (2013) showed that 13-month-olds are able to prospectively gaze at the goal of moving self-propelled objects, and that they shift their gaze faster when the self-propelled objects move in a rational compared to an irrational way.

Altogether, models of inferential and teleological reasoning propose that goals and intentions of observed actions are identified by non-motor inferential processes. Moreover, this approach assumes that predictive gaze shifts are driven by inferential processes, without the necessity of simulation processes in the MNS. Instead, the assumed inferential processes could recruit brain areas that are part of a “mentalizing network”, such as the temporoparietal junction, the midline structures posterior cingulate and medial prefrontal cortex, together with the STS (de Lange et al., 2008). In conclusion, the inference account provides a potential alternative explanation for the processes guiding predictive eye movements. Additionally, this account revealed challenging findings for the idea that the motor system is causally involved in anticipatory gaze processes and action understanding. Future research needs to obtain more direct evidence to shed light on the underlying processes of predictive gaze.

Statistical learning

Humans also rely on information about the regularity and patterns of observed events when forming expectations about others' behavior (Aslin & Newport, 2012). Already infants demonstrate sensitivity to statistical relationships between co-occurring events (Hunnius & Bekkering, 2010; Kirkham, Slemmer, & Johnson, 2002). For instance, statistical learning affects the perceptual processing of visual action sequences (Fiser & Aslin, 2001) and language development (Saffran, Aslin, & Newport, 1996). Interestingly, infants are also able to learn visual associations on the basis of probabilistic reasoning that are independent from their own experience (Téglás et al., 2011; Wentworth & Haith, 1998). In addition, Cicchino, Aslin

and Rakison (2011) were the first to demonstrate that the experienced regularities in the visual environment predict infants' understanding of the social world surrounding them. Further, Baldwin and colleagues provided evidence for the influence of statistical learning on action segmentation in adults (Baldwin, Andersson, Saffran, & Meyer, 2008).

Of importance for action prediction studies are findings showing that information about statistical regularities in the environment also influence predictive gaze behavior. For example, evidence for infants' statistical learning abilities has been provided by Paulus et al. (2011) who showed that both adults and 9-month-olds use frequency information for predicting the reappearance of an animated non-human agent. Recently, these findings have been extended to human goal-directed actions. Henrichs, Elsner, Elsner, Wilkinson and Gredebäck (2014) demonstrated that at one year of age, infants rely on information about the certainty of goal selection when predicting human reaching actions toward multiple goal objects. In detail, 12-month-olds showed significantly earlier predictive gaze shifts when observing a hand reaching for the same goal object across trials (frequent condition) compared with when they observed a hand reaching for a different goal in each trial (non-frequent condition). Additionally, only infants in the frequent condition rapidly learned to predict the goal-directed action over the course of trials, but not in the case of uncertainty (non-frequent condition). Together, the findings from this study implicate that at one year of age, infants are able to use information about certainty and statistical regularity of observed actions, here in terms of goal selection, to make predictions about others' action goals. In a similar vein, a recent eye-tracking study investigated the effect of visual learning on 8-month-old infants' predictive gaze behavior (Green, Li, Lockman & Gredebäck, submitted). Interestingly, they found that not only infants' motor repertoire, but also their visual experience depending on the individual cultural context influenced predictive gaze performance.

With respect to humans' ability to infer others' goals and intentions, Baker, Tenenbaum and Saxe (2006) proposed a framework that emphasized the statistical nature of people's intentional reasoning. They aimed to extend the teleological stance by adding a probabilistic approach to action understanding. According to their Bayesian model, inferences about an agent's goal are influenced by both efficiency considerations about the observed behavior based on the principle of rational action and, after successive observations, by the prior probability of a specific goal. They provide empirical and computational evidence for their probabilistic framework that takes into account how observers predict and infer others' goals when observing an agent acting in novel situations, i.e. when initial conditions for the agent's behavior changed.

Based on the reported findings, it has been suggested that predictive gaze could also be explained by statistical learning mechanisms. For instance,

while action resonance theory argues that the emergence of infants' ability to predict others' actions might be causally related to their own motor abilities, it is also possible that their visual experience accounts for predictive gaze. That is, infants might be able to extract certainty information from repeated and frequent observations of others' behavior and actions, and this visual information might drive infants' action prediction abilities (Southgate, 2013). In sum, visual experience and the deriving information about statistical regularities of specific events, patterns, actions or behaviors may guide predictive gaze, without an involvement of motor processes.

Summary

While the statistical learning account suggests that actions could be predicted on a mere visual basis and on reliance of frequency information, action resonance theories emphasize the functional role of mirroring processes for action prediction. According to a direct-matching account, anticipatory eye movements during action observation are guided by an engagement of the observers' own motor representations and occur as a result of motor simulation processes in the MNS. Whereas embodied simulation theories provide evidence for the active role of the motor system in perception of others' actions, other accounts have highlighted the effect of additional factors, such as the saliency of action goals, on action prediction.

On a different vein, the inference account posits that non-motor inferential processes form the basis of humans' ability to predict observed actions and to understand others' intentions. That is, proponents of this view stress the impact of inferences generated outside of the motor system, such as higher-level cognitive processes or efficiency considerations according to the principle of rational action. To date, the different functional mechanisms behind action understanding and prediction are still controversial. Strikingly, most of the conducted empirical studies that aimed to test and evaluate the different theoretical accounts of action prediction did not include a direct manipulation of the involved brain areas, and therefore, direct evidence for an embodied account of action prediction has been missing (Falck-Ytter, 2012). In order to increase our knowledge about the processes driving predictive gaze performance, neurophysiological studies need to directly modify and measure brain activity in regions of the assumed underlying neural circuits of action understanding and action prediction. In the attempt to fill this gap, Studies I and II aim to test the role of the motor cortex for predictive gaze by employing TMS and eye tracking.

In addition, Study III targets another limitation of prior research, which concerns the degree to which the revealed results can be generalized to a variety of everyday life situations. More explicitly, the bulk of previous studies on the topic concentrated on actions performed by a single actor. However, the ability to predict others' actions is particularly relevant during social interactions, where predictions form the basis of timely and

appropriate reactions in response to others' behavior (Sebanz et al., 2006). Consequently, in order to gain insight in the full spectrum of daily life, we need to examine actions as performed by more than one person. Therefore, the third study of this thesis will shift the focus from individual to social interactions. Accordingly, the last section of the introduction will elaborate on prior research investigating action prediction during social interactions.

Infants' online gaze during social interactions

One limitation of most prior action anticipation studies is the focus on manual actions performed by a single person (Ambrosini et al., 2011; Henrichs et al., 2012, 2014). That is, the vast majority of previously reviewed eye-tracking studies were limited in scope in that they presented infants or adults with individual manual displacement actions. However, we live in a social world where we constantly observe and decode social interactions. Hence, to understand how humans perceive other people's behavior in real-world scenarios, we need to study their perception of others' actions in a social and interactive context. In support of this notion, Tremblay and Rovira (2007) found a facilitatory effect of social context for early communication abilities in young infants who observed dyadic interactions in comparison to single-person interactions with objects. With respect to action prediction, so far, little is known about predictive gaze during social interactions, but there are a few exceptions, e.g. a study by Bakker, Kochukhova and von Hofsten (2011) that investigated the development of children's predictive gaze behavior during observation of social and non-social turn-taking events in conversations. While several studies have examined eye movement patterns during conversations (e.g. Richardson, Dale, & Kirkham, 2007; von Hofsten, Uhlig, Adell, & Kochukhova, 2009), our knowledge about human gaze behavior during non-verbal communication is peculiarly limited.

In addition to the lack of insight into this area of action prediction, the developmental trajectories of the ability to predict others' behavior in social interactions remain widely unexplored. Consequently, a crucial next step is to gain further insights into the origins of humans' ability to understand and predict non-verbal social interactions. The third study of this thesis will address this gap and, in doing so, test an infant sample. In order to embed the study's objectives in a broader theoretical framework, the following section will provide a general overview about prior research on the development of infants' social-communicative abilities and gestural communication. Serving as a motivation for Study III, the last section will describe previous studies investigating infants' online gaze behavior during observation of social interactions.

Infants' development of social-communicative skills

Prior research studying the origins of human joint actions has investigated how infants begin to participate in ritualized dyadic interactions and simple social games during the first year of life (Ross & Lollis, 1987) and how they gradually engage in more complex interactions over age (Hay, 1979). Already in their first weeks of life, infants begin to actively engage in social interactions by responding to parent's smiles with smiling back (Goren, Sarty, & Wu, 1975). Further, infants' remarkable social capacities become evident in their early sensitivity to turn-taking structures in dyadic face-to-face interactions, for instance between the mother and the infant (Kozak-Mayer & Tronick, 1985) or strangers and the infant (Gredebäck, Fikke, & Melinder, 2010). Moreover, by three to six months of age, infants' ability to engage in joint visual attention - to look in the same general direction toward an object or event as the caregiver - starts to emerge (D'Entremont, Hains, & Muir, 1997; Gredebäck et al., 2010). Around this time, the development of more precise gaze following in the presence of communicative cues enables first communication in triadic social interactions and serves as a foundation for later language acquisition and for more complex activities with shared goals (Adamson & Bakeman, 1991; Brooks & Meltzoff, 2005; Flom, Deák, Phill, & Pick, 2004). As infants grow older, they also begin to process and evaluate agents based on their social behaviors. For instance, already young infants prefer to look at or reach for pro-social geometric shape agents that previously helped another compared to agents that previously expressed anti-social behavior (Hamlin, Wynn, & Bloom, 2007, 2010). In line with these findings, we recently demonstrated that 6-month-olds' neural activity, measured by the ERP component P400, differed when observing agents that previously helped compared to agents that previously hindered others (Gredebäck et al., submitted). In addition, infants from around 8 to 10 months of age begin to use another person's facial or behavioral expressions as social referent points to regulate their own behavior in ambiguous and novel situations (Feinman, 1982; Striano & Rochat, 2000).

Toward the end of the first year of life, infants begin to actively take part in cooperative interactions including give-and-take actions (Bruner, 1981; Hay, 1979). From around two years of age, infants start to initiate and coordinate their actions during more unfamiliar or less routinized social activities and across different contexts (e.g. Bakeman & Adamson, 1984; Brownell, 2011; Warneken, Chen, & Tomasello, 2006). More precisely, as their social cognitive repertoire expands, infants become more sensitive to the social context of an action. For instance, by 18 months of age, infants begin to use social context to bind individual actions into a collaborative sequence (Fawcett & Gredebäck, 2013). Further, Fawcett & Liszkowski (2012) demonstrated that infants at this age are able to encode a joint goal, to learn by social demonstrations and to reproduce observed joint activity. Similarly,

Henderson and colleagues found that infants' ability to detect the common goal structure of an observed joint action between two collaborating individuals develops between 10 and 14 months of age (Henderson, Wang, Matz, & Woodward, 2013; Henderson & Woodward, 2011). Using visual habituation paradigms, they demonstrated that 14-month-olds represented common rather than individual goals of an observed collaborative action sequence, while 10-month-olds perceived an observed collaborative activity as directed towards a joint goal only after active experience.

Together, these remarkable early social skills deriving from first experiences in social interactions serve as a foundation for more sophisticated social competences in later life (Brownell & Carriger, 1990; Mundy & Newell, 2007; Tomasello, 1999). As gestures are an important tool of non-verbal communication, research about gestural communication and development will be presented in the following section.

Infants' gestural development

With increasing age and progressing social-cognitive abilities, infants begin to apply gestures within their communicative repertoire. Typically expressed by fingers, hands and arms, gestures are exhibited to convey specific intentions and goals (Crais, Douglas, & Campbell, 2004). Gestural communication plays an important role during social interactions, in which gestures may be used for expressing emotions or other interpersonal information between communicative partners, such as drawing others' attention to specific events or objects (Carpendale & Carpendale, 2010). The majority of developmental research on gestures has been centered around infant pointing (e.g. Tomasello, Carpenter, & Liszkowski, 2007). Infants start to point to objects from around 11 to 12 months of age to engage and cooperate with a communicative partner by sharing interest and attention, while they also try to repair misleading communication (Carpenter, Nagell, & Tomasello, 1998). According to Liszkowski, Carpenter and Tomasello (2007) infants' declarative pointing begins to follow some collaborative structures by 12 months of age. In contrast to the large amount of research on pointing gestures, the give-me gesture - an extended face-up palm hand directed toward the observer when requesting or receiving an object (Mundy, Sigman, Ungerer, & Sherman, 1986) - has received less attention. Due to its communicative relevance during social interactions, for instance as a communicative signal for expressing requests between adults and infants, the current thesis aims to augment our knowledge about the give-me gesture. Observational paradigms assessing infants' production of give-me gestures during give-and-take interactions obtained evidence that infants start to give and request objects between 9 and 12 months (Carpenter et al., 1998; Crais et al., 2004; Masur, 1983). More precisely, Messinger and Fogel (1998) have demonstrated the proportion of infants offering and requesting objects in

mother-infant play sessions increases from 9 to 15 months. Several subsequent longitudinal studies (Carpenter et al., 1998; Crais et al., 2004) revealed that infants begin to use declarative gives (i.e., giving objects to share and direct attention) around 9 to 13 months, whereas imperative giving (i.e., giving as a means to direct others' behavior) emerges at around 12 to 13 months of age.

While these studies capture developmental trajectories of give-me gesture production, they do not address the question of how infants understand the use of give-me gestures during third-party interactions. With respect to adults' understanding of gestures from a third-person perspective, i.e. during observation of other people interacting with each other, Shibata, Gyoba and Suzuki (2009) investigated the neural correlates of adults' perception of third-party give-and-take interactions. When presenting adult participants with either appropriate (shape of receiving hand matching the giving action) or inappropriate (shape of receiving hand not matching the giving action) receiving actions, observers' N400 components were larger during presentation of inappropriate compared with appropriate receiving actions. The authors interpreted these results as evidence for semantic processing in adults and their ability to predict action sequences between individuals. In relation to infants' understanding of gestural communication in third-party interactions, it was shown that infants start to comprehend communicative cues from non-verbal gestures, such as gazing ostensively and pointing to the location of a hidden toy, from 18 months of age (Gräfenhain, Behne, Carpenter, & Tomasello, 2009). Besides this exception, little is known about how infants look at and encode nonverbally expressed communicative intentions in the context of third-party interactions.

Infants' online gaze during observation of social interactions

From a broader perspective, the ability to discern the social motives behind others' gestures is related to action understanding at large, i.e. closely linked to the ability to detect social interactions and to read the underlying intentions behind other people's actions (Crais et al., 2004; Sebanz et al., 2006). Observing these communicative interactions from a third-party perspective, for instance between parents, provides infants with a rich source of information about their surrounding social world. More specifically, attending to actions that are addressed to third parties allows infants to learn about their culture (Baldwin, 2000) and facilitates the development of their own communicative skills (Sebanz et al., 2006, for a relevant study of autism see Falck-Ytter, von Hofsten, Gillberg, & Fernell, 2013).

Despite the importance of these observational experiences, the majority of prior experimental research on infants' communication abilities is centered around their understanding of dyadic interactions in which the infant is directly and actively engaged. In relation to infants' gaze behavior during ac-

tion observation, the focus of most research effort has been on infants' perception and comprehension of individual actions, e.g. one person interacting with an object, but not of social interactions between other individuals. Nevertheless, first studies have started to unravel and explore how infants look at and detect social interactions that are not directed to them (e.g. Fivaz-Depeursinge, Favez, Lavanchy, de Noni, & Frascarolo, 2005). In terms of verbally expressed communication, several eye-tracking studies have examined infants' perception of social turn-taking events, such as conversations between two people. They demonstrated that during observation of a conversation, typically developing infants pay selective attention to the speaker, in particular to his/her face (von Hofsten et al., 2009), and show sensitivity to communicative cues such as body orientation (Augusti, Melinder, & Gredebäck, 2010), even from static visual information (Handl, Mahlberg, Norling, & Gredebäck, 2013). With regard to infants' predictive gaze behavior, prior research obtained evidence that the ability to predict turns in conversations increases over time and that children exhibit more predictive gaze shifts when they observe a human conversation compared to a conversation between non-human agents (Bakker et al., 2011).

With respect to non-verbal communication, Gredebäck and Melinder (2010) showed that 12-month-old infants are able to anticipate actions of two adult actors feeding each other. Specifically, infants observed one actor bringing the food either to the recipient's mouth (rational condition) or placing it on her hand (irrational condition). They found that 1-year-old infants shifted their gaze toward the recipient of the food significantly earlier when the feeding action was executed in a rational than in an irrational manner. Another anticipatory eye movement study revealed that 18-month-olds' online gaze is influenced by the social context of an observed interaction, i.e. by the prior social engagement of the actor (Fawcett & Gredebäck, 2013). They showed that infants make anticipations depending on whether they saw an actor aiming to achieve an individual or joint action goal.

Together, these studies show that infants are able to form expectations about future outcomes and shared goals in observed verbal or non-verbal social interactions. In addition, previous studies have demonstrated that latencies of goal-directed gaze shifts are modulated by properties of action goals, such as goal saliency (Ambrosini et al., 2011; Henrichs et al., 2012). However, it is unknown whether infants' gaze anticipations are influenced by properties of social goals, for example by the receiving hand in a give-and-take interaction. Further, information about infants' ability to make predictions in social interactions including gestural communication is limited. In conclusion, it remains unresolved whether infants are able to predict a give-me gesture as a social goal in a third-party interaction that involves responses to a request. Thus, more research is needed to further examine how infants look at give-me gestures in the context of social interactions.

Aims of the thesis

The overarching aim of this thesis is to gain a deeper insight into how adults and infants perceive and predict other people's actions. As reviewed in the introduction, previous research has developed different theoretical accounts providing alternative explanations for the underlying functional mechanisms of humans' action anticipation abilities. The present thesis aims to augment current knowledge about the mechanisms underlying action prediction and, in particular, intends to test the embodied account of action prediction. Accordingly, the first major goal of the thesis is to assess the role of direct-matching processes for online gaze anticipations. Second, the thesis intends not only to expand the focus from predicting actions performed by a single individual to those within social interactions, but also from adult to infant populations. Together, the reported eye-tracking studies aim to expand our understanding about predictive gaze during observation of different manual or social actions as well as the underlying mechanisms that drive anticipatory goal-directed eye movements.

The objective of Study I was to examine adults' online gaze during observation of a reaching action presented as a PL display. The main goal of the first study was to test whether biological motion information from an observed manual action is sufficient to elicit anticipatory eye movements. While prior research has demonstrated humans' general sensitivity to biological motion, the first eye-tracking study aims to investigate the role of biological motion for gaze anticipations. That is, Study I tests whether adult observers are able to use biological motion information in order to anticipate an observed PL action.

Based on prior behavioral data and on the findings from Study I, a neurophysiological study was designed to provide more direct evidence about the underlying mechanisms behind goal-directed eye movements. Deriving from the hypothesis that anticipatory eye movements are driven by a recruitment of the observer's own motor system, the purpose of Study II was to directly test the functional connection between real-time gaze anticipations and activation of the observer's own corresponding action plans. Thus, Study II used TMS in order to assess the contribution of the motor cortex to anticipatory gaze processes. Thereby, Study II aims to extend current knowledge about the role of the MNS for online anticipation of others' goals and actions.

Whereas the first two eye-tracking studies were designed to inspect the role of biological motion information and the contribution of motor brain areas for online gaze anticipations, the third eye-tracking study adds a developmental perspective by assessing how infants by one year of age look at a social interaction between two individuals. Since information about infants' gaze behavior during observation of non-verbal third-party interactions is limited, Study III addressed this gap by examining infants' online perception of a social give-and-take interaction. In addition, the third eye-tracking study investigates the question whether latencies of infants' goal-directed eye movements are influenced by properties of a social goal, such as a give-me gesture in a give-and-take interaction.

Methods

Participants

The first two eye-tracking studies included adult participants that were either tested in Sweden (Study I) or Italy (Study II). In Study I, the final sample consisted of 38 adult students (26 females) that were recruited at the campus area of Uppsala University. For Study II, a total of 21 Italian adults (mainly University students, 10 males) participated in the experiment. None reported any history of neurological disease or psychiatric syndrome. All included participants had normal vision and were right-handed (Oldfield, 1971). In both studies, all participants gave their informed consent for the experimental procedures and received a voucher (approximately 10 euros, Study I) or 25 euros (Study II) as compensation for their participation. In Study I, five additional participants with not enough valid trials were excluded from the analysis. In Study II, three additional participants had to be excluded from the analysis because of failure to fulfill the inclusion criteria.

In Study III, infants were recruited from local birth records in Uppsala. Parents received an introductory letter with general information about the Uppsala Child and Baby Lab. Parents who were interested in participating with their infant and who returned the response letter (mainly Northern European middle class families) were contacted via telephone and were informed about the study's purpose. Experiments 1 and 2 each included 34 twelve-month-olds (15 boys and 19 girls in Experiment 1, 19 boys and 15 girls in Experiment 2). An additional 14 twelve-month-olds were tested in Experiment 3 (5 boys, 9 girls) and Experiment 4 (8 boys and 6 girls), respectively. Across all four experiments of Study III, 20 additional infants were tested but excluded because of fussiness or lack of attention. Each family received a gift certificate (approximately 10 euros) for their participation.

All studies were approved by the regional ethical committee and conducted in accordance with the 1964 declaration of Helsinki.

Stimuli

In Study I and Study II, stimuli were movies of a manual PL display showing a reaching-grasping action toward an occluded goal object (see

Figures 1 and 4). For each experiment, the 3D motion of a manual reaching action was recorded in a motion capture system (Qualysis, Gothenburg, Sweden) by attaching reflective PL markers to the major joints of the hand and right arm. For each study, a 2D movie of the recorded PL display was generated in Matlab (MathWorks Inc, Natick, USA) and integrated in a virtual environment using Cinema 4D (Maxon, Friedrichsdorf, Germany). The virtual environment contained a goal object (toy bear or toy dinosaur) and a barrier that covered the final approach and contact between the PL markers and the goal object. Additionally, in Study I, a non-biological motion version of the PL display was created as stimuli for the control condition (see Figure 1). In Study II, 25 static background dots (same size and color as the PL markers) were added in the stimulus movie to increase the difficulty of the task and to avoid ceiling effects (Fig. 4). Further, the final stimulus movie from Study II was mirrored on the vertical axis in Adobe Premiere (Adobe Systems, San Jose, USA) in order to create a second stimulus version showing reaching from the left to the right.

In Study III, stimulus movies were recorded from live scenes and edited in Adobe Premiere. In Experiment 1, the final movie contained an everyday social interaction between two individuals. Infants were presented with a give-and-take interaction in which an object (ball with colorful flowers) is passed from one individual to another. The receiving hand formed either a give-me gesture or an inverted hand shape (hand shaped as a give-me gesture but presented upside-down). The movie clip was shown from a third-party perspective and included only the hands and arms of the two agents (see Figure 6). In Experiment 2, the presented action sequences were identical to those in Experiment 1, except that the receiving hand was replaced with a three-dimensional object shape (a skin-colored u-shaped metal bar, similar to the form of a give-me gesture; Fig. 6). In Experiments 3 and 4, the stimuli were live recordings of a moving a ball attached at the end of a wooden stick (Experiment 3) or held by a human hand (Experiment 4) and two human hands positioned across from each other, respectively (Fig. 7).

Apparatus

In all studies, gaze was measured with a Tobii T120 near infrared eye tracker (sampling rate 60 Hz, accuracy 0.5°, Tobii, Stockholm, Sweden). The corneal-reflection eye-tracking system measures participants' eye movements by near infrared illumination that causes reflection patterns on participants' cornea and pupil. Prior to the stimulus presentation, a calibration is performed in which the participant is looking at five set locations (in each corner and in the center of the screen, see Gredebäck, Johnson, et al., 2010). Gaze position is calculated by computer algorithms

comparing the infrared light reflection in the cornea and in the pupil center (Aslin & McMurray, 2004). Pupil center corneal reflection technique estimates gaze position with a high temporal and spatial resolution and high accuracy (Aslin, 2012). In each eye-tracking experiment, stimuli were presented on a 17-inch monitor, in which the infrared light camera is integrated below the screen.

In addition to eye-tracking technique, in Study II, TMS was applied to participants' primary motor cortex. An articulated Manfrotto arm (Manfrotto, Italy) maintained the coil in a stable position and stabilized participants' head during the experiment. TMS was delivered using a biphasic stimulator (Magstim, Whitland, UK) through a figure-of-eight coil (70 mm). The mapping procedure and threshold estimation were performed via wireless EMG recordings (Aurion, ZeroWire EMG) using a standard tendon-belly montage (Ag/AgCl electrodes). Signals were band-pass filtered at 10-1000 Hz and digitized at 2000 Hz. EMG traces were then acquired using a CED power 1401 board and visualized with the software Signa 13.09 (Cambridge Electronic Design Limited, UK). The onset of the TMS train was triggered by a photodiode placed in the upper left corner of the screen, detecting the appearance of a white square.

General procedure

All participants from Studies I and Study III were tested in the laboratory of the Uppsala Child and Baby Lab (Department of Psychology) at Uppsala University. All adults participating in Study II were tested at the Italian Institute of Technology in Italy. After participants' arrival in the lab, adult participants or the infant's caregiver received further information about the experimental procedures and they were asked for their written consent prior to the experiment. In the two adult eye-tracking studies, participants were seated approximately 60 cm in front of the eye-tracker on a chair (modified dentist chair in Study II in order to minimize head and body movements). In all experiments of Study III, infants were seated on the caregiver's lap in front of the eye-tracking monitor and a curtain covered infants' lateral view. In every study, before stimulus presentation both the monitor as well as participant's sitting position were adjusted and a standard 5-point calibration (Gredebäck, Johnson, et al., 2010) was performed. Adult participants were instructed to only passively observe the stimuli movies. Consistent with prior anticipatory eye movement studies (e.g., Falck-Ytter et al., 2006; Kochukhova & Gredebäck, 2010), one stimulus movie was presented several times (varying between 10-48 trials across experiments). All studies were conducted as between-subject designs, but Study II had an additional within-factor (TMS vs. No-TMS). In each study, attention-grabbing movies were presented between stimulus presentations to maintain participants' attention.

In Studies II and III, the stimulus movies (showing reaching or giving from the left or from the right) were alternated between consecutive trials to avoid quick habituation. After watching the stimuli, participants from Study I and II filled out a questionnaire and were asked to describe the presented PL stimuli and whether they recognized the PL display as a specific object or event. In Study I and III, each adult participant and respectively each family spend around 20 minutes in the lab. The TMS experiment (Study II) lasted approximately one hour.

Data analysis

Recorded gaze was exported as text files from tobii studio. For all studies, data analyses were performed in Matlab using custom-made analysis scripts. As dependent measure of adults' and infants' action anticipation, unfiltered raw gaze data were analyzed with respect to saccadic latencies. Saccades are defined as fast gaze shifts from one location to another (Land, 2006), here from an actor's moving hand toward an action goal. In the framework of this thesis, the action goal refers to the object the hand is reaching for (Study I and II), or to the give-me gesture (Study III).

At the beginning of each data analysis, two rectangular areas of interest (AOI) were defined in Matlab. In general, one AOI covered the action goal (Goal AOI) and the other the reaching hand (Hand AOI), i.e. either the PL hand (Study I-II) or the human hand (Study III). Analogously to prior action anticipation studies (e.g. Gredebäck et al., 2009), the Goal AOI captured the goal object plus one visual degree in each direction in order to account for possible measurement inaccuracy. The same size adjustment was done for the Hand AOI. The Matlab program extracted gaze positions from the exported data files and identified participant's first saccade from the Hand AOI to the Goal AOI for each trial, respectively. In order to be counted as a valid gaze shift, participants had to first fixate on the Hand AOI and subsequently at the Goal AOI. In all studies, gaze fixations were defined as maintaining gaze stationary in an AOI for more than 200 ms (Land, 2006).

The latency of the first saccade was measured by subtracting the time when participants first fixated at the Goal AOI from a relevant time point in the stimulus movie, for example the onset of end-effects. Gaze-arrival times were aggregated and averaged across all valid trials. Participants' mean gaze-arrival times were compared between conditions and against the predefined threshold that divides gaze data into predictive and reactive gaze. The chosen threshold of 0 ms measures gaze-arrival times at a specific location (here the goal of the action) before the onset of a certain event, for instance before the actor begins to lift the goal object. Importantly, this threshold classifies observers' gaze shifts as functionally predictive when gaze shifts occur ahead of time, i.e. before an observed action goal is

achieved. Accordingly, positive numbers refer to gaze arriving at the goal AOI before the goal is completed (classified as anticipation), whereas negative values represent reactive looking, i.e. gaze fixations after the goal is achieved. This criterion was also used in most prior studies on action anticipation (Flanagan & Johansson, 2003; Kanakogi & Itakura, 2011; Kochukhova & Gredebäck, 2010; Falck-Ytter et al., 2006; Gredebäck & Melinder, 2010; Johansson et al., 2001). Here, in Studies I and II, the threshold of 0 ms captured predictive gaze shifts that are based on an online encoding of the observed action before it is completed. In this context, it is important to note that Study III did not measure predictions in line with this operationalization. In the last eye-tracking study, data analyses focused on assessing infants' online observations and their online gaze behavior by comparing differences in gaze latencies between conditions.

All experiments reported in this thesis assessed latencies of goal-directed gaze shifts, except for Experiment 3 and 4 in Study III. In these two preferential looking experiments, infants' looking time in two AOIs (covering the two hand shapes) was measured and averaged over all included trials. The individual proportion of looking time in each AOI in relation to the overall looking time in both AOIs was calculated as a percentage score.

In all three prediction studies, outlier analyses with z -transformations were performed on all data points for each condition separately. Data points with z -scores less than -3 or greater than 3 were classified as statistical outliers and excluded from the analyses. In addition, individual trials were excluded from the analyses if participants did not shift their gaze from the Hand AOI to the Goal AOI during one trial (anticipatory eye movement paradigms), or if infants did not look at either AOI during one trial (looking time analyses).

In all studies, statistical analyses were performed in SPSS. Independent samples t -tests (or analysis of variance, ANOVA) were used to compare mean gaze-arrival times between conditions. Further, one-sample t -tests were conducted to assess if mean latencies differed from the threshold of 0 ms within each condition separately. In the looking time analyses, one-sample t -tests assessed whether percentages of looking time into one AOI was significantly different from chance (tested against 50%).

Study I – Anticipation of biological motion

Study I is motivated by the question of what type of information observers are able to use for action anticipation. As described in the first sections of the introduction, a vast literature on human motion perception has demonstrated humans' sensitivity to biological motion information expressed by PL displays. These studies reveal impressive evidence for how rapidly and reliably observers are able to extract detailed information from biological motion animations. The information humans are able to encode from the kinematics of a PL display range from detection of different walking styles (Montepare & Zebrowitz-McArthur, 1988) to more complex properties, such as social intentions (Manera, Becchio, Cavallo, Sartori, & Castiello, 2011). Although the particular role of human motion for action perception is well established (Blakemore & Decety, 2001), evidence on whether humans are able to use biological motion information for gaze anticipations is still missing. One possibility is that observers detect motion information – low-level kinematic cues – from human actions and use this information to rapidly extrapolate and anticipate the goal of ongoing actions (labeled as biological motion hypothesis of action anticipation). This hypothesis is in line with an embodied account of action anticipation and received further support from numerous eye-tracking studies showing that seeing human actions and our own motor abilities are both important for anticipatory gaze shifts to occur (e.g. Flanagan & Johansson, 2003; Falck-Ytter et al., 2006; see page 22). While this hypothesis predicts that kinematic information from human movements provides sufficient information to elicit predictive eye movements, alternative, non-embodied accounts assume that anticipatory gaze shifts are based on inferential processes, such as inferences about an actor's intentions or higher-level goals (e.g. Csibra & Gergely, 2007; Eshuis et al., 2009). In order to test this hypothesis, it is necessary to isolate “pure” biological motion information, i.e. the kinematics of an observed movement, from other types of information. Otherwise, when observing full vision depictions of human actions, the putative role of kinematic information from biological motion is confounded by other sources of information, such as visual properties normally associated with human actions (e.g. texture, color or contour information). The traditionally used method to isolate motion information are PL displays that allow to present visually reduced human motion (van Kemenade et al., 2012). With respect to the research question of Study I, PL

displays are also suitable stimuli to test whether biological motion provides sufficient information for action anticipation to occur.

As no study has answered this question yet, the first study of this thesis aims to examine to what degree human observers are able to anticipate the goal of a manual reaching action that is represented as a biological or non-biological PL display. An anticipatory eye movement paradigm was used in which participants were presented with a PL representation of a hand reaching for a goal object or with a non-biological version of the same manual PL display while goal-directed eye movements were recorded with near-infrared eye tracking technology. If the biological motion hypothesis of action anticipation is correct, we expected adults to be able to anticipate a biological motion PL display, but not a non-biological version of the same display.

Design

Participants were presented with a PL display recorded from a human reaching action. The stimulus movie contained a PL hand tapping with the fingers, waving toward the observer and subsequently reaching for and interacting with the goal object (a toy bear) partly covered by a barrier (Fig. 1).

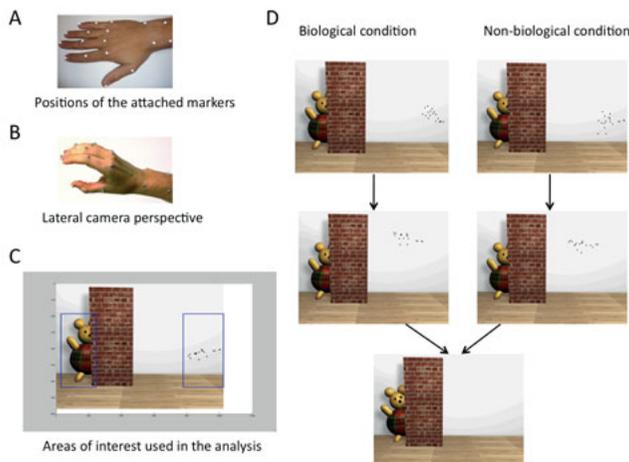


Figure 1. (A) Photo showing the hand with 18 attached markers to create the manual point-light (PL) action by means of a motion capture system. (B) Lateral camera perspective from which the PL reaching action was recorded and presented to the participants. (C) Areas of interest (AOI) used in the analysis: first AOI covers the PL display plus one visual degree at the beginning and end of the PL hand, the goal AOI covers the goal object plus one visual degree in each direction. (D) Snapshots of the stimuli movie during the movement phase, during the reaching phase (both separate for each condition), and after the onset of the end effects (movement of goal object and sound, equal in both conditions).

After the PL representation of the hand disappeared behind the barrier, the goal object was grasped, lifted and replaced on the floor by the PL hand (see Figure 1). Participants watched either 10 trials of a biological motion or non-biological motion version of the PL action (each lasting 12 seconds). In the biological motion condition the velocity and motion profile of the PL markers were consistent with a real reach, including acceleration and deceleration. In the non-biological motion condition the spatiotemporal profile of every PL marker was manipulated to create a linear (constant velocity) and therefore non-biological movement. Throughout the whole manual PL action, biological acceleration and deceleration of the motion was removed in each dimension individually (X, Y, Z) for every movement unit (see Figure 2). Converting the biological motion to a linear movement is not very striking for the naked eye and was not sufficient to prevent that the presented PL display in the non-biological motion condition was perceived as biological motion (as assessed by verbal report). Therefore, the movement direction in the y-dimension was inverted for 50% of the PL markers (for selected movement units only) during the first movement phase (stationary hand, moving fingers). However, to retain maximal similarity between the two conditions, no movement direction was inverted within the second movement phase (reaching phase). The total number of PL markers as well as the timing of the action were identical in both conditions. After stimulus presentation, participants filled out a questionnaire inquiring how they would describe the stimuli and whether they recognized the observed PL display as a familiar object or event.

As a dependent variable, predictive gaze shifts were measured in a time period between the onset of the reaching action and 1000 ms after the onset of end effects. Gaze latency was calculated by subtracting the time when participants fixated at the Goal AOI for the first time from the time when the PL hand first contacted the goal object (onset of end effects). An independent sample *t*-test was used to test differences in gaze latencies between conditions and one-sample *t*-tests assessed if latencies differed significantly from zero within each condition. An additional independent samples *t*-test was performed to examine if gaze performance data in the biological motion condition differed between participants recognizing the PL hand and those that did not. Further, a χ^2 -test was conducted to investigate if the proportion of participants recognizing the PL display differed between conditions.

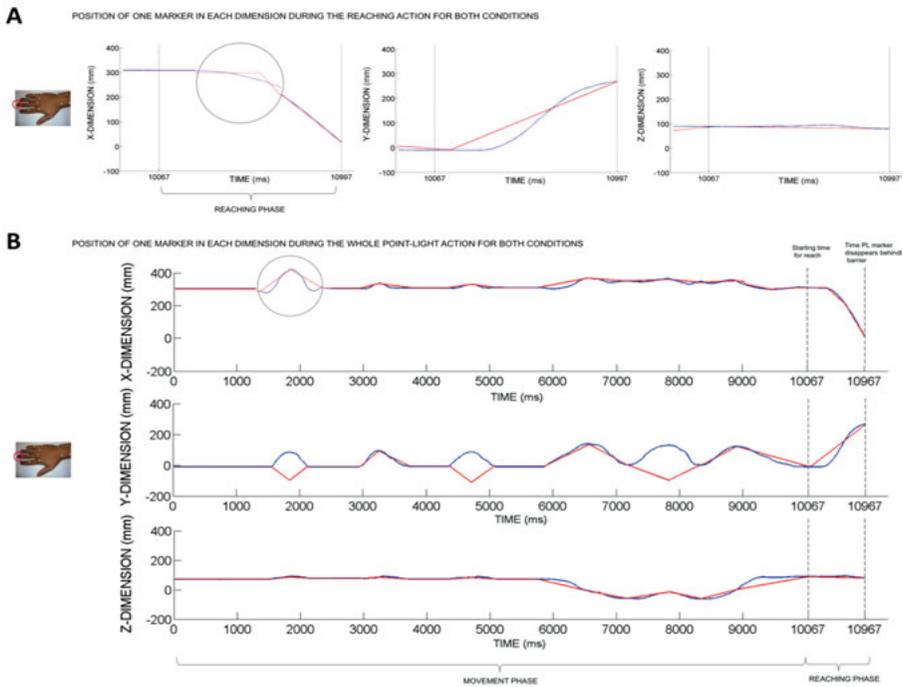


Figure 2. (A) Position of one point-light (PL) marker during the reaching action for the biological motion condition (blue line) and the non-biological motion condition (red line) plotted individually for every dimension X, Y, and Z. The start time for the reach and the points in time when each PL marker disappears behind the barrier are the same in both conditions. The circle represents an enlargement to highlight the different trajectories. (B) Position of one PL marker during the whole action sequence. The linear translations in the non-biological motion condition (red lines) were created by removing biological acceleration and deceleration of the motion in each dimension individually in both the movement and the reaching phase.

Results

In line with the biological motion hypothesis of action anticipation, we found that adults anticipated the goal of the PL action in the biological motion condition ($M = -124$ ms, $SE = 28.5$), $t(18) = 4.36$, $p < .001$, but not in the non-biological motion condition ($M = 21.5$ ms, $SE = 29.4$), $t(18) = .73$, $p = .474$. Further, latencies of goal-directed gaze shifts differed significantly between conditions, $t(36) = 3.56$, $p = .001$, $d = 1.16$, see Figure 3. With regard to recognition of the observed PL action, more participants recognized the hand in the biological motion condition relative to the non-biological motion condition, $\chi^2(1) = 9.87$, $p = .002$. Specifically, 11 out of 19 participants in the biological motion condition reported that the PL display included a human hand. Remaining participants did not recognize the PL display as a hand and made either no suggestion or reported that the PL display

represented a non-human entity, e.g. a swarm of bees or an animal. Within the biological motion condition, no latency differences were observed between those that recognized the hand and those that did not, $t(17) = 1.40, p = .179$. That is, both participants recognizing, $t(10) = 2.57, p = .028$, and participants not recognizing the PL display as a hand, $t(7) = 3.81, p = .007$, exhibited predictive gaze. In the non-biological motion condition, only one participant perceived a hand and this participant did not look at the action in a predictive fashion. No learning effects over the 10 stimulus presentations were observed in the biological motion or the non-biological motion condition. An additional analysis with a differently sized Goal AOI (extended AOI including the edge of the barrier nearest the PL hand) provided the same result as in the presented analysis, demonstrating that a difference in gaze latencies is not restricted to certain AOI sizes.

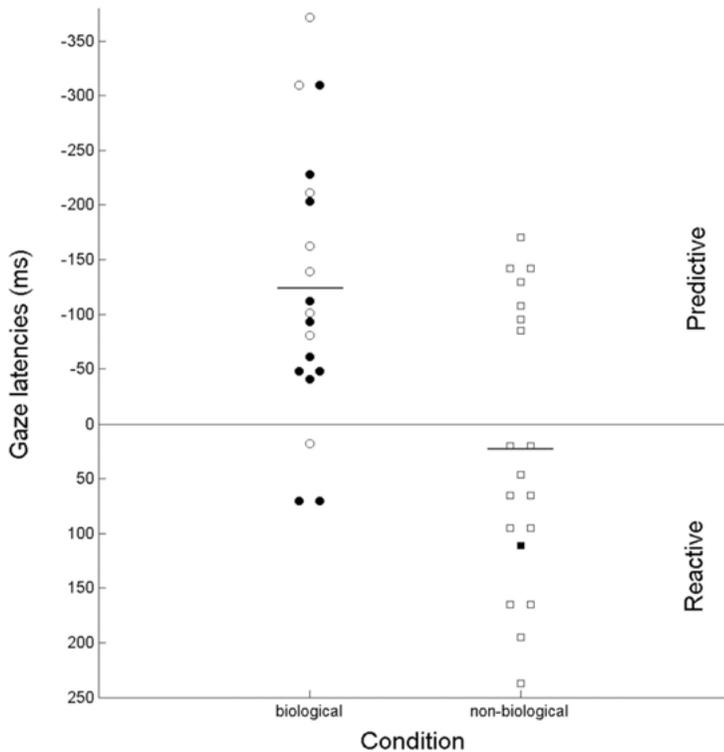


Figure 3. Average gaze latency in the Goal AOI over all 10 trials for each participant, separate for the biological and non-biological motion condition. The horizontal line differentiates anticipatory from reactive gaze shifts. Short horizontal lines mark the group average for each condition. Filled markers represent participants recognizing the PL display; empty markers represent participants not recognizing the PL display as a hand.

Discussion Study I

This eye-tracking study was designed to investigate whether adult observers are able to anticipate the goal of a manual reaching action, represented as a biological or non-biological PL display. The results from Study I show that biological motion PL displays are anticipated to a higher degree than non-biological motion PL displays. More precisely, gaze arrived at the goal of an observed PL reaching action ahead of time only if the presented manual action contained biological motion information. In addition, latencies of goal-directed gaze shifts were unrelated to participants' recognition of the PL display as a reaching hand. Together, these findings indicate that the presence of biological motion is sufficient to elicit anticipatory gaze shifts.

The present study suggests that the fast and effortless processing of biological motion previously documented (for a review see Blake & Shiffrar, 2007) may feed directly into processes for online anticipation of others' actions in human adults. The finding that adults are able to anticipate the goal of others' actions based on kinematic information from biological motion adds to our knowledge about the functional role of biological motion detection in action processing. That is, Study I demonstrates that the brain can make use of kinematic information from human actions to do more than simply detect biological motion. An ultimate function of biological motion processing may be to anticipate the goals of other people's actions. Strikingly, this is done without reliance on visual information that is intrinsically associated with everyday human reaching actions.

In addition, the findings of the current study are in line with an embodied account of action prediction that highlights the contribution of the motor system to anticipatory gaze processes (Ambrosini et al., 2011; Flanagan & Johansson, 2003; Kanakogi & Itakura, 2001). In accordance with findings from Study I, it has been shown that the accuracy of predicting the time-course of temporarily occluded PL actions is influenced by the observed movement kinematics. Specifically, participants were better and faster in predicting occluded actions performed by a human actor or biological motion PL walker compared to robot or non-human PL actions with linearized velocity profiles (Saygin & Stadler, 2012; Stadler, Springer, Parkinson, & Prinz, 2012). Together with Study I, these findings support the assumption that anticipatory processes during action observation of biological motion PL displays could be based on internal simulations and mirroring processes in the MNS.

Another possible explanation for the findings in Study I is that participants first perceived the reaching hand and used this information to anticipate the presented action (Csibra & Gergely, 2007; Eshuis et al., 2009; Southgate, 2013). Although we cannot exclude that lower-level recognition processes preceded action anticipation, this alternative interpretation seems less likely because adults systematically anticipated the action goal even if

they were not able to consciously recognize the action represented by the PL display.

In conclusion, more direct measurements are needed in order to accurately examine the hypothesis that motor representations drive anticipatory eye movements and to fully understand the role of the motor system for online anticipation of goals and actions.

Study II – The role of the motor cortex during online action anticipation

The findings from Study I are in accordance with an embodied account of action prediction that emphasizes the role of the motor system for predictive gaze. However, eye-tracking data do not provide direct evidence with regard to underlying brain processes. Despite plenty of behavioral evidence supporting the idea that the motor system contributes to anticipatory processes during action observation (e.g. Aglioti et al., 2008; Urgesi et al., 2010; Stadler, Springer, et al., 2012), the underlying mechanisms behind anticipatory eye movements are still unknown. Available data are not able to rule out alternative hypotheses, which deemphasize the role of motor brain areas for online gaze anticipations (e.g. Eshuis et al., 2009; Southgate, 2013).

One solution to this debate is the direct measure of brain activities associated with predictive eye movements. In an attempt to directly test the idea that action plans in our motor cortex are functionally related to anticipatory eye movements, Study II used TMS in order to investigate the functional connection between real-time anticipation and activation of the observer's own corresponding action plans. Specifically, online trains of TMS pulses were applied to disrupt activity in the hand primary motor cortex² in order to assess its effect on predictive gaze during observation of PL reaching actions. Previous research efforts have established a link between biological motion perception and the human premotor cortex (Gilaie-Dotan, Kanai, Bahrami, Rees, & Saygin, 2013; Grosbras, Beaton, & Eickhoff, 2012; Saygin, Wilson, Hagler, Bates, & Sereno, 2004) and further demonstrated that TMS over the PMC reduces participants' sensitivity to biological motion stimuli as expressed in PL displays (van Kemenade et al., 2012). Additionally, MNS activation prior to observing an expected action has been interpreted as evidence for anticipatory motor simulation (Borrioni, Montagna, Cerri, & Baldissera, 2005; Fogassi et al., 2005; Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004), suggesting that the MNS plays an important role in anticipatory processes and predictive coding of others' actions (Urgesi et al., 2010, 2006; Wilson & Knoblich, 2005).

² The primary motor cortex has strong reciprocal connections to the MNS and generates MNS-like activity (Borrioni et al., 2005; Dushanova & Donoghue, 2010; Kilner & Frith, 2007; Koski, 2002).

In light of these findings, we expected that TMS over the motor cortex hand area should alter latencies of goal-directed gaze shifts if the observer's own motor representations play a role in guiding anticipatory eye movements to the upcoming action goal. According to inference accounts (e.g. Eshuis et al., 2009; Southgate, Johnson, & Csibra, 2008), TMS over the motor cortex should not affect anticipatory gaze.

Design

In Study II, which was based on the same paradigm as Study I, adult participants were presented with another PL reaching-grasping action. The PL reaching action was shown from the same lateral perspective as in Study I. The PL hand contained of 19 PL markers (\varnothing 4 mm) attached to the joints of the fingers, plus two PL markers attached on the wrist and four additional point-lights that were placed on the arm (two at the elbow, two at the upper arm) (see Figure 4A). After the PL representation of the reaching hand disappeared behind the barrier, the target object was grasped, lifted and replaced on the floor by the PL hand. After gaze calibration, participants were presented with 48 stimulus trials. Since the assessed gaze behavior is subject to quick habituation (Elsner, Falck-Ytter, & Gredebäck, 2012; Henrichs et al., 2012) we altered the stimulus movies (showing reaching from the left or from the right) and presented distractor tasks (counting backwards tasks) as well as various attention-grabbing movies in-between to include more variation.

Participants were randomly assigned to either the TMS-Hand or TMS-Control (Leg) condition. Before stimulus presentation, participants' hand or leg area was marked on a tight tissue cap. The hand area was found by locating the First Dorsal Interosseous (FDI) muscle whereas the control site was set by locating the Anterior Tibialis (AT) muscle representation. Stimulus location and intensity were defined on a subject-by-subject basis. Participants in the TMS-Hand condition received TMS pulses at an intensity of 100% of the FDI resting motor threshold. Participants in the TMS-Leg condition received TMS pulses at an intensity of 100% of the AT active motor threshold. Resting motor threshold and active motor threshold were defined as the intensity of the stimulator output eliciting a MEP of at least 50 mV in half of 10 consecutive stimulations for the resting motor threshold and a MEP of at least 200 mV in half of 10 consecutive stimulations for the active motor threshold (Rossini et al., 1994). This choice was motivated by the fact that the FDI resting motor threshold is always much smaller than the AT resting motor threshold. Therefore, stimulating the leg area at the resting motor threshold would have elicited MEPs also in the FDI muscle, introducing a critical spatial specificity issue. On the other hand, it has to be noted that stimulation intensity for the control site was always higher than

for the hand area, thus excluding the possibility that control stimulation was not able to excite the neural tissue.

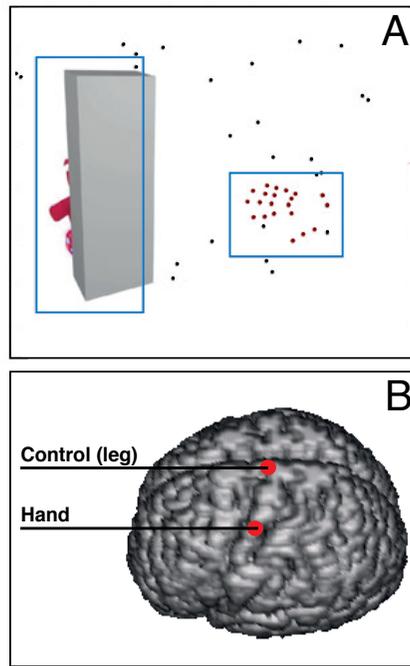


Figure 4. (A) Snapshot from first frame of the stimuli including the target, the barrier, the PL hand and background dots. The areas of interest (AOIs) used in the analysis are shown as blue rectangles: one AOI covered the initial position of the PL hand (plus one visual degree in each direction), the second AOI covered the target object (plus one visual to the right and left side). (B) Location of TMS in the TMS-Hand condition (TMS over hand area) and the TMS-Leg condition (TMS over leg area).

During half of the PL stimulus presentations and in a randomized order, a train of TMS biphasic pulses over either participant's hand or leg area of the left primary motor cortex was delivered (see Figure 4B). The train was applied at the beginning of the reaching trajectory, when the maximal acceleration is located in time, and consisted of three pulses spaced 100 ms between them. The TMS sequence was decided to stimulate the motor cortex long enough to disrupt the underlying contribution of motor cortices to others' action simulation. Short burst or trains of pulses are often used in online TMS protocols, especially when a strong temporal hypothesis cannot be formulated (Sandrini, Umiltà, & Rusconi, 2011; Siebner, Hartwigsen, Kassuba, & Rothwell, 2009). The onset and timing of TMS pulses during stimulus presentation were the same in the Hand and the Leg condition. All participants were also presented with 24 trials with no TMS, randomly

mixed with the TMS trials. After the first block (24 PL stimulus presentations), participants filled out a questionnaire and were asked to describe the presented PL stimuli.

During data analyses, *a priori* one-sample *t*-tests on latencies from all trials were conducted to assess if participants' average gaze behavior was significantly predictive or reactive. Thus, latencies of all valid goal-directed gaze shifts were compared to the threshold of 0 ms, expecting that all latencies should be significantly different from 0. Furthermore, an independent-sample *t*-test was used to compare mean latencies in No-TMS trials between the Hand and the Leg condition to test for baseline differences in participants' gaze behavior. Due to the inherent inter-individual variability in gaze behavior, individual difference scores between mean latency in TMS trials and mean latency in No-TMS trials were calculated. These difference scores were used as dependent variable to evaluate only the TMS-induced modulation by removing baseline differences. In order to test the predictions, one-sample *t*-tests comparing difference scores with 0 were performed to assess if gaze behavior differed between TMS and No-TMS trials within the Hand condition and within the Leg condition (two-tailed probabilities corrected for multiple comparisons with $\alpha = 0.025$). Further, an independent samples *t*-test examined if difference scores between TMS and No-TMS trials differed between the two conditions.

Results

Ninety-five percent of all participants detected the PL display as a hand (assessed by questionnaire, see Study I) and all but one participant showed anticipatory gaze during PL action observation (TMS trials: $M = 645.0$ ms, $SE = 67.8$; No-TMS trials: $M = 603.3$ ms, $SE = 74.8$). Further, an independent-sample *t*-test revealed that there was no significant baseline difference in participants' gaze behavior between the Hand and the Leg condition in No-TMS trials, $t(19) = 1.44$, $p = .166$.

With regard to the TMS-induced modulation in the Hand condition, participants' difference scores between TMS and No-TMS trials differed significantly from zero, $M_{(TMS-No\ TMS)} = -137.6$ ms, $SE = 50.3$, $t(9) = 2.73$, $p = .023$ (Fig. 5). That is, TMS over the hand area significantly delayed latencies of goal-directed gaze-shifts (TMS trials: $M = 575.8$ ms, $SE = 98.5$) compared to trials without TMS (No-TMS trials: $M = 713.4$ ms, $SE = 98.6$). In the Leg condition, difference scores were also significantly different from zero, $M_{(TMS-No\ TMS)} = 204.6$ ms, $SE = 48.0$, $t(10) = 4.26$, $p = .002$. In this condition, we found the reverse effect, i.e. TMS trials: $M = 707.8$ ms, $SE = 93.8$, No-TMS trials: $M = 503.2$ ms, $SE = 106.4$. Difference scores between the TMS-Hand condition and the TMS-Leg condition differed significantly from each other, $t(19) = 4.92$, $p < .001$, $d = -2.25$, see Figure 5.

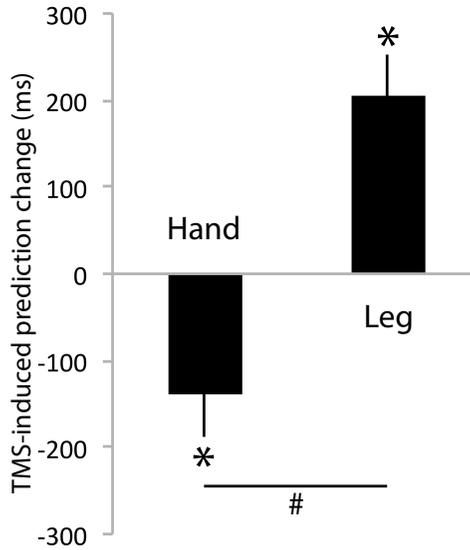


Figure 5. Mean difference scores between TMS and No-TMS trials in the TMS-Hand condition (TMS over hand area, left panel) and in the TMS-Leg condition (TMS over leg area, right panel). Significant effects are represented by # for the between-group comparison and * for one sample *t*-tests ($p < .05$). Error bars equal 1 SE.

Discussion Study II

In the original paper on gaze prediction (Flanagan & Johansson, 2003), it was suggested that the presence of strong eye-hand coordination programs allows humans to predict the goal of other people’s manual actions. However, the claim that these tight links enable action prediction when observing others’ actions was based on behavioral measures alone and subsequent studies (Eshuis et al., 2009; Southgate et al., 2008) suggested that other non-motor inferential strategies could account for the same effects. Although the findings from Study I were in line with the idea that predictive gaze shifts are guided by embodied simulation processes in the MNS, eye-tracking data do not allow conclusions with regard to underlying brain processes. Despite a large number of TMS studies examining the role of the motor system for visual processing, goal recognition and simulation of future actions (e.g. Aglioti et al., 2008; Stadler, Ott, et al., 2012; van Kemenade et al., 2012), the specific contribution to anticipatory gaze processes remained unresolved. That is, prior to Study II, no neuroimaging or neurophysiological study has yet been conducted to assess the role of the motor system for predictive gaze shifts. In an attempt to address this open question, Study II aimed to examine the underlying mechanisms of predictive gaze by directly

measuring the effect of TMS over brain areas associated to predictive eye movements. In this experiment, we used online trains of TMS pulses to modify activity in the hand primary motor cortex in order to test the effect on gaze prediction during observation of hand actions. The results showed that stimulation of the motor hand area, but not of the leg area, significantly delayed latencies of goal-directed gaze shifts (compared to no TMS). The findings speak in favor of a functional connection between real-time goal anticipation and activation of the observer's own corresponding action plans.

This is the first study describing the neural markers of anticipatory gaze behavior during an action prediction task. Prior studies have shown that measuring activity of the cortico-spinal tract (via TMS stimulation of the primary motor cortex) was a good proxy for the MNS as a whole (D'Ausilio et al., 2009; Stadler, Ott, et al., 2012). Since the primary motor cortex enables the differential stimulation of two body effectors due to its clear and large somatotopy, we were able to target different sections of it by means of TMS. Thus, based on the findings in the Study II, we argue that stimulation of the motor cortex directly impacts a direct-matching process guiding predictions of other people's action goals. Together with findings from Study I, our data suggest that humans anticipate the goal of others' actions in the following manner: (1) biological motion is encoded by the STS, (2) fed forward to the MNS, (3) where kinematic information from perceived human actions is mapped onto the observer's own motor representations. This direct-matching process allows the observer to (4) simulate future action goals based on his/her own motor plans, and through connections with oculomotor control systems, (5) to initiate an anticipatory gaze shift to the future goal of others' ongoing actions.

It is important to consider whether our results could reflect a differential effect on an adjacent brain area, in particular the frontal eye fields (FEF), which are known to be important for saccadic eye movements. Although Study II did not include a stimulation of the FEF as a control site, it is unlikely that the results are linked to the FEF since the distance from any of the experimental sites to the FEF is more than 4 cm, and at this scalp distance TMS effects drop to below 30% of the actual pulse strength (Siebner et al., 2009).

In Study II, we found a reversal effect in predictive gaze behavior when stimulating the leg primary motor representation. This may be due to several reasons. In fact, a reversal of effects is frequently reported (Kapur, 1996; Najib & Pascual-Leone, 2011), e.g. when stimulating competing cortical representations (Walsh, Ellison, Battelli, & Cowey, 1998). Stimulating the leg area might release the hand cortex from lateral inhibition, resulting in a net facilitation (Kobayashi & Pascual-Leone, 2003). Stimulation on the control site was stronger (due to the inherent lower excitability of the leg area) and thus more likely to elicit sub-threshold spreading to the adjacent

hand area. The exact nature of the reversal effect, although interesting, goes beyond the scope of Study II.

In summary, the underlying mechanisms of anticipatory eye movements have never been tested in a neurophysiological study and, thus, this is the first one providing direct support for the view that a direct-matching process implemented in the mirror-neuron system plays a functional role for real-time goal prediction. This study demonstrates that predictive eye movements during observation of PL reaching-grasping actions could be based on a matching process onto the observer's corresponding motor plans, as originally suggested by Johansson & Flanagan's seminal paper.

Study III – Infants’ online perception of give-and-take interactions

Whereas Studies I and II looked at the role of biological motion information and the contribution of motor brain areas for online gaze anticipations, both studies focused on manual actions performed by a single individual. The third eye-tracking study of this thesis aimed to increase our knowledge about anticipations of social actions between two individuals. Specifically, information about infants’ ability to anticipate observed social interactions from a third-party perspective is limited. Study III addressed this gap by examining infants’ online perception of a simple give-and-take interaction. In this study, the social interaction consists of an exchange of an object between two individuals.

While we know from prior research that infants’ predictive gaze is influenced by properties of action goals (Ambrosini et al., 2011; Gredebäck et al., 2009; Henrichs et al., 2012), Study III investigated whether the properties of a give-me gesture as a social goal of an observed give-and-take interaction affect online gaze behavior in 12-month-old infants. Specifically, the first experiment of Study III examined differences in latency of goal-directed gaze shifts toward a receiving hand forming either a meaningful and functional gesture (a give-me gesture) or a non-functional hand shape (an inverted hand shape). Finding faster gaze shifts to the give-me gesture would be consistent with the hypothesis that infants are sensitive to the social properties of the gesture as a part of the give-and-take interaction.

However, an alternative explanation would be that infants do not perceive the social interaction but rather react to the give-me gesture as a more likely place to put an object given that the palm-up hand shape has a higher affordance (Ellis & Tucker, 2000; Gibson, 1979). According to this hypothesis, infants might match the transferred object to the form of the give-me gesture due to its shape, leading to in earlier gaze arrival times in the upright “matching” condition compared with the inverted “non-matching” condition. Therefore, Experiment 2 was designed to test whether differences in affordances rather than infants’ sensitivity toward social goals and actions could account for differences in gaze latencies as measured in Experiment 1.

Another possibility is that give-me gestures attract more of infants' attention than the inverted hand shape and that this increase of attention facilitates goal-directed gaze shifts through priming (Daum & Gredebäck, 2011). The purpose of the two subsequent preferential looking time experiments (Experiment 3 and 4) was to investigate whether infants have an attentional preference toward the give-me gesture, which could lead to shorter latencies of goal-directed gaze shifts as measured in Experiment 1. Specifically, Experiment 3 addressed this potential alternative explanation by presenting 12-month-olds with the two hand postures from Experiment 1 simultaneously, together with a moving ball, while measuring looking times at the give-me gesture and at the inverted hand shape. If infants generally pay more attention to the give-me gesture, they should look more at this gesture than at the inverted hand shape. In addition, Experiment 4 examined if an attentional preference toward give-me gestures is present only in even more complex social situations, i.e. when there is another human agent holding an object that could be transferred.

Design

In Experiment 1, 12-month-olds were presented with movies of a manual give-and-take transaction between two people. The stimulus presentation started with a still frame showing an actor's hand forming a fist that was positioned on the right or left side of the screen and an object (ball) that was placed in the middle of the scene. Then, another actor's hand entered the scene from the side (opposite to the first hand) and grasped and lifted the ball. After squeezing the ball accompanied by a sound, the other hand subsequently formed either a give-me gesture or an inverted hand shape. After the ball was squeezed a second time, the ball was passed to the receiving hand on the other side of the screen. The stimulus movie ended with a still frame (1 s) showing the ball touching the receiving hand (Fig. 6). In both conditions, infants viewed in total 10 trials of two different stimuli versions, i.e. reaching from the right and from the left side. All reaching actions of the four different stimuli versions (alternating reaching from right or left side with either a give-me gesture or an inverted hand shape as the goal) had approximately the same length. As a dependent variable, the latency of infants' goal-directed gaze shifts was measured, i.e. how fast infants shifted their gaze from the passing hand to the receiving hand (shaped as a give-me gesture or an inverted hand shape).

In Experiment 2, another group of 12-month-olds observed the same action sequence as in Experiment 1, but the hand was replaced with a three-dimensional object shape. We chose an unfamiliar object shape to avoid potential confounds of the object's familiarity with its affordance and their respective effects on the latency of goal-directed gaze shifts. Affordance was

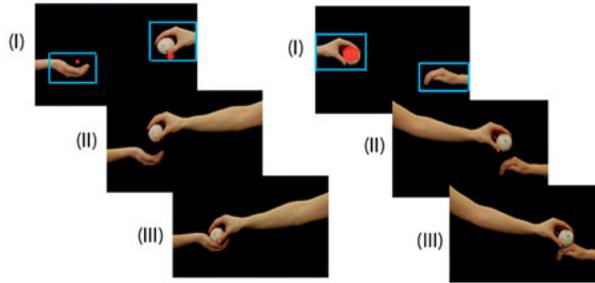
varied by the orientation of the goal object, i.e. the final position of the object shape was upright in the High Affordance condition (similar shape and orientation as a give-me gesture) and was inverted in the Low Affordance condition (similar shape and orientation as the inverted hand shape, Fig. 6). All four versions of the stimulus movie (upright vs. inverted object shape, reaching from right or left side) lasted 14.1 s in total. Both the upright object shape in the High Affordance condition and the inverted object shape in the Low Affordance condition represent goal objects without apparent social properties. Thus, if infants' gaze latencies are mediated by affordances, goal-directed gaze shifts should occur earlier during observation of the upright object shape as the goal object (High Affordance condition) compared with when the ball is passed toward the inverted object shape (Low Affordance condition). Alternatively, if the social properties of the give-me gesture rather than its affordance mediate differences in the latency of infants' goal-directed gaze shifts, latencies of goal-directed gaze shifts should not differ during observation of passing actions toward goal objects with high or low affordances, as presented in Experiment 2.

In the first two experiments of Study III, one AOI covered the position of the "giving" hand holding the ball and the other AOI covered the area around the receiving hand shape (Experiment 1) or object shape (Experiment 2) in its final position (i.e. Goal AOI, Fig. 6). Goal-directed gaze shifts were measured during a time period between the end of the second ball squeezing and 1 s after the ball touched the receiving hand shape or object shape, respectively. The duration of the reaching action, from the onset of the hand movement until the hand entered the Goal AOI, was approximately the same amount of time between conditions and across the two experiments (Experiment 1: average duration in the Give-Me Gesture condition = 1440 ms; average duration in the Inverted Hand Shape condition = 1380 ms; Experiment 2: average duration in the High and in the Low Affordance condition: 1534 ms). Latencies of goal-directed gaze shifts were assessed to be anticipatory if infants fixated on the Goal AOI before the first part of the hand entered the Goal AOI. Importantly, analyses of predictive gaze shifts in Experiment 1 and 2 did not test whether infants' gaze was predictive or reactive, but concentrated on comparing latencies of goal-directed gaze shifts between conditions.

Experiment 1

Give-me gesture

Inverted hand shape



Experiment 2

Upright object shape

Inverted object shape

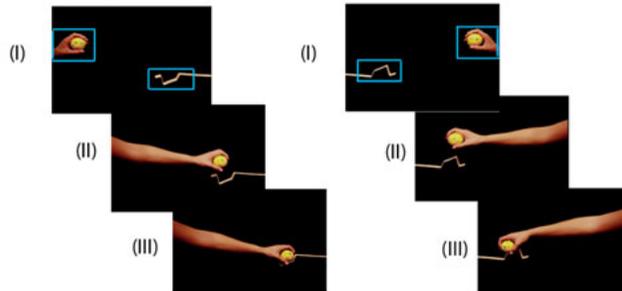


Figure 6. Snapshots of the action sequences presented in Experiments 1 and 2 separately for the different conditions showing either a give-me gesture or an inverted hand shape (Experiment 1), or an upright or inverted object shape (Experiment 2). Depicted for both experiments are the time points when the hand/object postures are formed (I), of the passing action toward the receiving hand/object shape (II), and when the ball was placed (III). Note that the object shape in Experiment 2 is three-dimensional and, thus, allows a ball to be physically placed on it in both conditions. AOIs (covering the passing hand and the action goal) used in the analyses are marked by blue rectangles, and recorded gaze is plotted in red.

In Experiment 3, the stimulus movies showed a ball, together with a stick that was hanging in the top middle of a black screen (see Figure 7A), moving like a pendulum back and forth for approximately the same amount of time as the reaching-grasping action presented in Experiment 1. However, no action of receiving the ball was presented. Subsequently, one hand formed a give-me gesture and the other one formed an inverted hand shape (same hand postures as in Experiment 1). Both hand shapes were matched in their size as well as in their respective distance to the ball. At the end of the movie clips, a still frame of the two hand postures and the pendulum in the middle of the screen were presented (Fig. 7A). All versions of the stimulus movies lasted 14.48 s.

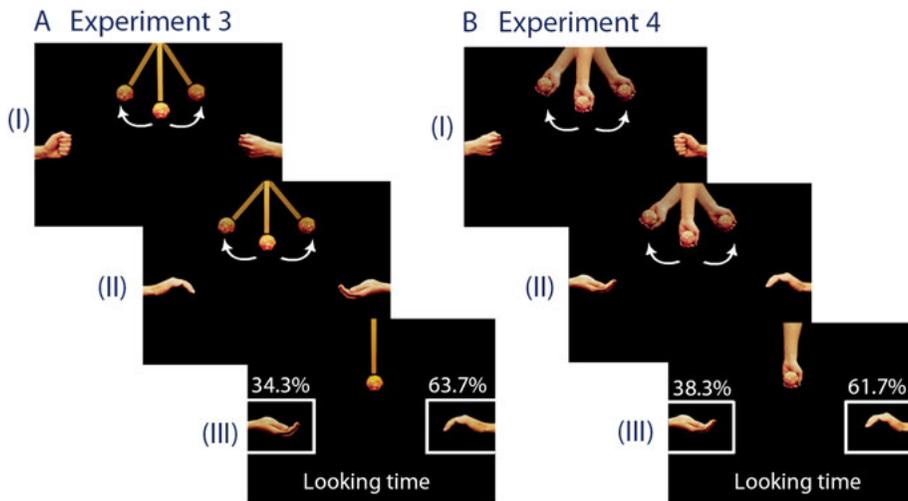


Figure 7. Snapshots of the action sequences presented in Experiment 3 (A) and Experiment 4 (B) depicting the fistened hands at the beginning of the movie (I), the two hand positions after the hand postures were formed (II), and the pendulum motion from the ball either attached to a stick (A) or held by a human hand (B), with motion directions indicated by arrows (I + II). AOIs (covering the two hand postures) used in the looking time analysis are marked by white rectangles (III).

In Experiment 4, the presented stimuli were identical to those used in Experiment 3 except that instead of a wooden stick, a human hand held the ball and the visible arm moved like a pendulum (see Figure 7B). All versions of the stimulus movies had a total length of 14.4 s. Both in Experiments 3 and 4, looking times at the two hand shapes were the dependent variables. Looking time was included in the analysis if infants fixated on an AOI for at least 200 ms during the time period when the hands started to form the hand posture until the end of the movies. Overall looking times around each hand shape were measured to assess whether infants prefer to look at one of the two hand postures.

Results

In Experiment 1, infants fixated on average on the area around the give-me gesture before the passing hand entered the Goal AOI ($M = 73.71$ ms, $SE = 52.52$, 95% confidence interval [CI] [-38, 185]). In the control condition, on average, 12-month-olds fixated on the Goal AOI after the hand had entered it ($M = -278.77$ ms, $SE = 57.58$, CI [-401, -157]). Mean gaze-arrival times were significantly earlier during observation of the give-me gesture than

when infants were presented with the inverted hand shape, $t(32) = 4.523$, $p < .001$, $d = 1.60$ (see Figure 8). Moreover, mean gaze-arrival times differed significantly between the two conditions even on the first trial ($M_{\text{Give-Me Gesture}} = -97.75$ ms, $SE = 71.09$, $M_{\text{Inverted Hand Shape}} = -317.33$ ms, $SE = 59.29$), $t(29) = 2.36$, $p = .025$, $d = 0.87$.

In Experiment 2, 12-month-olds in both the High Affordance condition ($M = -131.51$ ms, $SE = 40.91$, 95% CI [-218, -45]) and the Low Affordance condition ($M = -164.85$ ms, $SE = 74.17$, CI [-322, -8]) fixated on the goal on average after the passing hand entered the Goal AOI (see Figure 8). A corrected t -test (Welch-test for heterogeneous variances) revealed that there was no significant difference in mean gaze latencies between the two conditions, $t(24.91) = 0.394$, $p = .697$, $d = 0.14$. Further, no evidence of learning effects was found in the High Affordance condition; that is, infants did not show an improvement of performance over the course of trials.

Additionally, a 2×2 ANOVA with the factors Goal Object (Hand vs. Object shape) and Affordance (High vs. Low) as independent variables was conducted to examine differences in gaze latencies between the different goal objects across experiments. The analysis showed a significant main effect for Affordance, $F(1,67) = 11.24$, $p = .001$, $\eta_p^2 = .15$, no significant main effect for Goal Object, $F(1,67) = 0.63$, $p = .431$, $\eta_p^2 = .01$, but a significant Goal Object \times Affordance interaction, $F(1,67) = 7.69$, $p = .007$, $\eta_p^2 = .11$. Post-hoc comparisons (Fisher's LSD) indicated that infants fixated on the Goal AOI significantly earlier when they observed the give-me gesture compared with the other High Affordance condition showing the upright object shape (mean difference [MD] = 205.22, $SE = 81.39$, $p = .014$). However, there was no significant difference between the inverted hand shape and the inverted object shape in the Low Affordance condition ($MD = 113.91$, $SE = 81.4$, $p = .166$).

In Experiment 3, on average, infants spent 19.4 s ($SD = 9.0$) looking in both of the AOIs over all included trials (average number of valid trials = 10.86, $SD = 1.6$). Of the aggregated overall looking time, infants spent 63.7% ($SD = 10.7$) of the time looking at the AOI around the inverted hand shape (see Figure 7A). This average percentage of looking to the inverted hand shape was significantly different from chance, $t(13) = 4.82$, $p < .001$. In Experiment 4, infants looked on average 21.3 s ($SD = 9.6$) in the two AOIs covering the two hand postures (average number of valid trials = 10.92, $SD = 1.3$). This experiment replicated the attentional preference for the inverted hand shape. Here, 12-month-olds spent 61.7% ($SD = 7.2$) of the time looking at the AOI covering the inverted hand shape (Fig. 7B). Infants' preferential looking to the inverted hand shape was significantly different from chance level, $t(13) = 6.11$, $p < .001$.

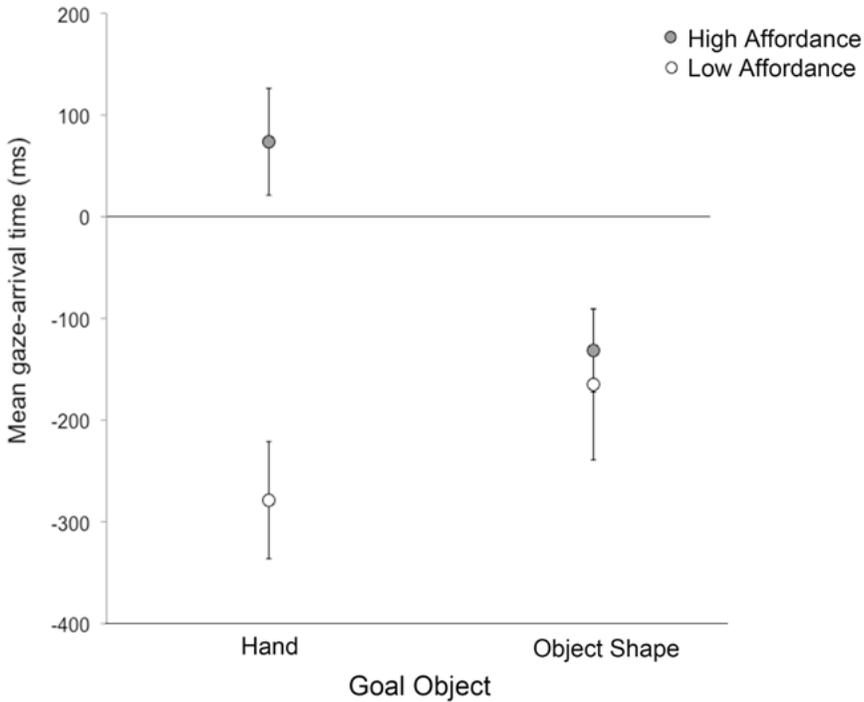


Figure 8. Aggregated mean gaze-arrival time of trials 1 to 10 for each of the four conditions presented in Experiments 1 and 2 (Goal Object: Hand vs. Object shape; Affordance: Low vs. High). Error bars depict standard errors. Values above 0 ms correspond to earlier arrival of gaze at the goal area relative to the arrival of the hand.

Discussion Study III

The overarching aim of Study III was to assess how 12-month-olds perceive a give-me gesture in the context of a give-and-take interaction between two individuals. In Experiment 1, we found that 12-month-olds' gaze shifts from a passing hand to a receiving hand are significantly faster when the receiving hand forms a give-me gesture relative to when it forms an inverted hand shape. The objective of Experiment 2 was to test the alternative explanation that a higher affordance of the give-me gesture rather than its relatedness to social action may account for shorter latencies of goal-directed gaze shifts. However, based on the findings from Experiment 2, this possibility seems less plausible. That is, latencies of goal-directed gaze shifts observed in Experiment 1 are unlikely to be driven by different affordances of the two goals because affordances did not influence goal-directed gaze shifts when the action was directed to objects. In addition, infants' preference for the inverted hand shape found in the two preferential looking experiments rules

out the alternative interpretation that differences in anticipatory gaze shifts in Experiment 1 might be mediated by a general attentional preference for the give-me gesture in the absence of the social action of receiving.

Together, the experiments from Study III provide evidence that 12-month-olds perceive an object transfer action between two social agents that includes a give-me gesture as a more well-formed goal-directed action than when the same action is completed with an inverted hand shape. This set of studies extends prior research, which has shown that properties of physical goals affect latencies of infants' goal-directed gaze shifts during action observation (e.g., Gredebäck et al., 2009; Henrichs et al., 2012). Study III suggests that 1-year-olds are sensitive to the properties of social action goals (e.g., of a give-me gesture) and that these social properties influence infants' goal-directed gaze shifts during observation of a give-and-take interaction.

However, it needs to be noted that in Study III, infants' latencies of goal-directed gaze shifts were not significantly different from 0 ms, also not in the condition showing the give-me gesture. That is, infants did not fixate on the goal of the action ahead of time and their gaze was not functionally predictive. The lack of predictions could be based on the fact that 12-month-olds' own experience with collaborative actions (Brownell, 2011) and in producing imperative gives to request objects (Carpenter et al., 2009; Crais et al., 2004) is still limited. Another reason could be that a social interaction including a give-me gesture is a more complex action sequence compared to single-person reaching actions toward one object, which were presented in most prior prediction studies. In line with this assumption, previous infant studies with more complex goal structures have used a more liberal criterion of -200 ms that incorporates a 200 ms reaction time to overcome the internal processing lag of the oculomotor system (e.g. Cannon et al., 2012; Daum et al., 2012; Gredebäck et al., 2009). In Study III, mean gaze-arrival times of anticipatory gaze shifts were significantly above the threshold of -200 ms in the give-me gesture condition. This indicates that 12-month-olds shifted their gaze on average faster to the goal (give-me gesture) than what would be expected if gaze shifts were driven by a visual reaction to the hand-goal-interaction. Yet, of most importance for our research question was the difference between conditions.

Another possibility that needs to be considered is that infants' gaze behavior observed in Experiment 2 could be influenced by action familiarity (Southgate, 2013). Indeed, prior studies have shown that infants' understanding of goal-directed actions performed by an unfamiliar agent, such as a mechanical claw, improves after a brief familiarization (Boyer, Pan, & Bertenthal, 2011; Hofer et al., 2005). The influence of novel agents could potentially apply to novel goal objects as well. Thus, it is possible that infants exhibited later gaze shifts to the unfamiliar object shape, especially in the High Affordance condition, only due to its novelty. Although most prior studies dealt with the potential effect of novelty by including a brief training

period, Experiment 2 did not include a pre-test familiarization. Nonetheless, both goal objects were novel, and yet there was no evidence of learning for the upright goal object in the High Affordance condition. This does not support the assumption that infants needed to learn about the new goal object in order to exhibit goal-directed gaze shifts.

In addition, it needs to be acknowledged that the current set of studies cannot unravel whether infants perceived the presented object transfer event as an action or as a segment of a social interaction. One possibility is that infants were faster in exhibiting online goal-directed gaze shifts to a palm-up hand without necessarily encoding the give-me gesture as an integral part of the observed social interaction. Another richer interpretation of infants' gaze behavior would suggest that infants are sensitive to the communicative information of the give-me gesture (i.e., the conveyed request), the compliant reaction to pass the object to the recipient's hand forming the give-me gesture, and the give-me gesture as an appropriate gesture to receive the object. However, the current data do not permit inferences about how much infants' goal-directed gaze shifts were based on encoding the social context of the give-and-take interaction such as that the passing hand provides some benefit for the receiving hand. Future research needs to further examine whether infants are able to encode the social nature of the give-me gesture during a third-party interaction.

In summary, Study III aimed to provide insight into infants' very early online perception of give-and-take actions between two individuals. Together, the experiments showed that already by 12 months of age, infants' goal-directed gaze behavior differs between observed object transfer actions that involve a give-me gesture and those that involve an inverted hand shape. These findings are consistent with the interpretation that infants, by their first year of life, are sensitive to the communicative properties of a give-me gesture in the context of a give-and-take social interaction and that, therefore, these properties are likely to play an important role in infants' action understanding from a third-party perspective.

General discussion

The overarching aim of the thesis was twofold. The first two studies aimed to examine the role of the motor system for anticipatory gaze processes. Deriving from embodied simulation theories (e.g. direct-matching theory), Study I and II investigated whether observers use their own motor knowledge to predict other people's actions. Both studies used PL displays as stimuli to isolate human motion information and measured observer's action prediction abilities by means of eye-tracking techniques. In addition, Study II used TMS as a neurophysiological method to directly modify motor cortex activity in order to test the functional role of motor-simulation during action observation. Study I revealed that kinematic information from biological motion can be used to anticipate the goal of other people's PL actions and that the presence of biological motion is sufficient for anticipation to occur. The main finding of Study II was that TMS-induced temporary lesions in the primary motor cortex selectively affected observers' gaze latencies. In summary, the reported results from these two studies on adults provide compelling evidence for an embodied account of action prediction, suggesting that sensory input from perceived object-directed actions is automatically translated into corresponding action plans in the observer. The reported findings in this thesis support the interpretation that a recruitment of observers' own action plans during observation of others' motor actions is causally related to predictive eye movements.

The second aim of this thesis was to extend our understanding about action prediction in the context of third-party interactions. Motivated by the lack of insight into infants' gaze behavior during observation of social interactions, Study III examined infants' online gaze while 12-month-olds were presented with a give-and-take interaction between two individuals. Study III demonstrated that already at one year of age, infants shift their gaze from a passing hand to a receiving hand faster when the receiving hand forms a give-me gesture compared to an inverted hand shape. Three control experiments were conducted to rule out alternative explanations of gaze shift differences, such as affordance- and attention-based explanations. Together, Study III indicates that 12-month-olds are sensitive to the social functionality of action goals, here the communicative properties of a give-me gesture, within the context of give-and-take interactions while observing from a third-party perspective.

In the following sections, I will discuss the findings from the reported studies in more detail and with respect to recent empirical findings on the topic.

An embodied account of action prediction

As reviewed in the introduction of this thesis, a vast number of infant studies highlight the close correspondence between infants' motor abilities and their action prediction abilities (Cannon et al., 2012; Kanakogi & Itakura, 2011). Similarly, studies on adults indicated that predictive gaze during action production and action observation might rely on the same underlying processes (Flanagan & Johansson, 2003), and that the motor system seems to play an important role for anticipatory gaze processes during action observation (Butterfill & Sinigaglia, 2014; Costantini et al., 2012a; Stadler, Springer, et al., 2012). Together, these studies suggest that observers deploy embodied action representations for predicting other people's actions (Kilner et al., 2004; Wilson & Knoblich, 2005). Specifically, as action production and control rely on prospective processes (von Hofsten, 2004), it has been suggested that embodied representations may also account for anticipatory looking at others' actions. According to this hypothesis, predictive eye movements reflect motor activation and an engagement of embodied action representations in the observer. In sum, a large body of research has provided support for the idea that the motor system selectively contributes to predictive gaze shifts. At the same time, alternative theories have criticized action-resonance theories. Prior to the work presented in this thesis direct evidence for an embodied account of action prediction had been missing.

In an effort to augment current knowledge, Study I assessed whether motion information from observed manual PL actions provides sufficient information to elicit anticipatory gaze shifts. The finding that human observers can use biological motion information for action prediction provides further support for the idea that the motor system plays an important role for predictive eye movements. An interesting finding of Study I was that in the biological motion condition participants' ability to predict the PL reaching action was unrelated to their ability to recognize the PL display as a hand. These findings indicate that explicit recognition is not required for anticipation to occur and corroborate direct-matching theories suggesting that embodied simulation processes account for participants' prospective gaze shifts in the biological motion condition.

However, more direct evidence was needed to support this hypothesis. In an attempt to fill this gap and to go beyond correlational studies, Study II of this thesis induced motor-interferences by means of TMS to directly test the causal relation between motor processes and action prediction. By demonstrating that stimulation of the motor hand area, but not of the leg

area, slowed predictive gaze behavior, Study II contributes an important piece of the puzzle in the discussion about the mechanisms underpinning action prediction.

The revealed evidence that the motor system is causally related to predictive eye movements during action observation was validated by a subsequent TMS study (Costantini, Ambrosini, Cardellicchio, & Sinigaglia, 2014). In accordance with the results from Study II, Costantini and colleagues provided further support the distinctive role of the motor cortex in guiding goal-specific anticipatory gaze shifts. Temporary alterations of activity in motor and non-motor cortical areas were induced by means of repetitive TMS (rTMS) in order to test the effect on anticipatory eye movements, respectively. The study showed that during observation of manual reaching-grasping actions transient inactivation of the left PMCV delayed observers' gaze-arrival times compared to gaze latencies recorded before delivering rTMS. Interestingly, this temporal interference effect on participants' gaze performance was only evident when the grasping action included a pre-shaping of the actor's hand, but not during trials where they viewed an actor performing simple touching actions with a closed fist posture. The authors suggested the interpretation that the temporal suppression of the PMCV impeded participants from exploiting motor cues and information with respect to the hand pre-shaping or the corresponding goal object. As in Study II, the rTMS-induced effects were selective with regard to the stimulated brain area. That is, no TMS effects on anticipatory gaze were found after applying rTMS to control sites, i.e. the posterior part of the left STS or the left FEF. This study is of particular importance with respect to the stimulated FEF as Study II did not include this area as a control site. Specifically, their finding that temporary lesions in the FEF did not affect predictive gaze supports the suggested interpretation of Study II.

With regard to predictive eye movements, the existing evidence prior to Study II and the subsequent paper by Costantini et al. (2014) had not been able to answer the question whether the motor system plays a causal role for action prediction. By means of TMS-induced 'virtual lesions', the two studies provide converging evidence for a direct link between anticipatory eye movements and motor cortex activity. The finding that the motor system is involved in predictive gaze shifts constitutes a significant contribution toward unraveling the processes behind predictive gaze. Specifically, the revealed findings corroborate action resonance theories and implicate that a recruitment of embodied action representations plays a crucial role for implementing predictive eye movements during action observation. Together, the reported studies in this thesis (i.e., Studies I and II) have added new insights into the processes behind action prediction and Study II was the first one describing the neural markers of anticipatory gaze behavior.

In the following sections, I will discuss several open questions that remain to be answered.

How is the motor system causally involved?

The findings from Study I, II and Costantini et al. (2014) provide compelling evidence for the involvement of the motor system in anticipating other people's actions on the basis of perceptual-motor mapping. However, the exact processes of how observed actions are transformed into the motor plans of ones' own actions are complicated and not yet fully understood. In addition to brain stimulation studies, brain lesion studies aimed to specify the causal relation between brain lesions and behavioral deficits in action perception and understanding (Urgesi, Candidi, & Avenanti, 2014). While these demonstrate that lesions in certain regions of the putative MNS are associated with deficits in perceiving and understanding other people's actions, they cannot denote the exact nature of the neural mechanisms, such as the directionality of the underlying processes mediating predictive eye movements. In recent years, granger causality method (applied to fMRI data) aimed to explain the dominant directionality of information flows within different regions of the MNS. This method revealed that the MNS functions as a dynamic feedback control system with both forward and reverse directions of information flows, for instance during observation of communicative hand gestures (Schippers & Keysers, 2011). Based on Study II, we know that the motor system plays a causal role for anticipatory gaze processes, however, we are still not able to fully answer questions regarding the specificity of activation or the exact temporal relation between action observation and neural simulation.

What is being predicted?

The reported results from Studies I and II point toward a causal role of the motor system for action prediction. At the same time, the presented experiments contribute to research in the larger framework of embodied simulation theories and action understanding. In addition to the presented evidence illuminating the neural underpinnings of predictive gaze, one open question worthy of further discussion is what is being predicted in action prediction studies. Specifically, this point concerns the extent to which predictions involve an ascription and understanding of the goal of an action (Steinhorst & Funke, 2014; Woodward & Cannon, 2013). In general, predictive gaze could potentially involve movement-based or goal-based anticipations, and they are not necessarily mutually exclusive. What posits a challenge is to determine if the goal of an action is included in a prediction (Hunnus & Bekkering, 2014). Yet, as reviewed at the beginning of the thesis, it is fundamental to perceive an action as directed toward future action outcomes and goals in order to generate predictions (Butterfill & Sinigaglia, 2014; Woodward & Gerson, 2014). Thus, the predicament of action prediction studies lies in the difficulty to ensure that observers' action predictions also incorporate information about the goal of an observed action

(Krogh-Jespersen & Woodward, 2014; Uithol & Paulus, 2013). This issue is related to a general disadvantage of most action prediction studies in which the final location of the observed movement trajectories and the goal of an action are confounded (Cannon & Woodward, 2008). That is, when measuring gaze shifts from a reaching hand toward the end state of an action, it is difficult to distinguish whether participants predict the final location of the observed movements or if they also rely on goal-relevant aspects of an observed action (Hunnius & Bekkering, 2014). Uithol and Paulus (2013) emphasized that this issue does not only concern experimental stimuli, but also predictions in real-life situations where the goal and the end of a movement are often in the same location and, additionally, the goal often matches with the actor's intention.

Ample evidence for the influence of goal information on action understanding comes from neurophysiological studies demonstrating that both information about the kinematics and the action goal are involved in direct-matching processes (e.g. Bonini & Ferrari, 2011; Cattaneo, Caruana, Jezzini, & Rizzolatti, 2009; Rizzolatti & Sinigaglia, 2010; Umiltà et al., 2001). For instance, similar mirror neuron responses to actions performed by different effectors or agents have been interpreted as goal encoding and matching (Gazzola & Keysers, 2009). Moreover, recorded activity in macaques' inferior-posterior area and ventral premotor area F5 during observation of grasping motor acts revealed that mirror neuron responses were unrelated to target locations, but depended on the goal of different actions, such as grasping for eating versus grasping for placing (Bonini et al., 2010; Fogassi et al., 2005). Similarly, it has been shown that pantomimed or intransitive actions did not lead to responses in macaques' MNS (di Pellegrino et al., 1992; Gallese et al., 1996). Jointly, these studies suggest that MNS activity is independent from observed effectors, relates to object-directed actions and shows sensitivity to the goal in which observed actions are embedded.

In support of the notion that observers integrate goal information when generating action predictions, prior research has demonstrated that the overarching goal of an action affects gaze latencies (Gredebäck et al., 2009) and that goal saliency influences predictive gaze behavior (Ambrosini et al., 2011; Henrichs et al., 2013). Further, a recent study demonstrated that infants recruit goal analyses during action predictions, although these goal-based gaze predictions are more cognitively taxing and require longer processing times (Krogh-Jespersen & Woodward, 2014). Moreover, Study III shows that infants' gaze performance also relies on social information from observed gestures as the goal of social interactions. In this context, Study III adds to the knowledge about infants' online goal understanding by demonstrating that communicative properties of social goals affect their online gaze behavior.

In light of these findings, it seems likely that predictive gaze shifts as measured in Studies I and II did not only reflect specific movement-based anticipations, but also captured goal-based predictions of the PL reaching action.

What is the function of embodied simulation for action prediction and understanding?

The presented evidence showing that MS activity is selectively related to action goals has important implications for the ascribed function of embodied simulation processes in the MNS. The above-mentioned neurophysiological studies imply that mirroring activity entails and fosters action understanding. However, despite more than two decades of research on the MNS, our knowledge about the exact functional role of embodied simulation for action understanding is still limited. As humans are able to derive and infer others' intentions based on their behavior, the question arises whether embodied simulation processes can also result in a higher-level understanding - or if inferences about intentionality recruit primarily other routes and cortical areas outside of the MNS. Due to the fact that our environments as well as the constrained experimental settings always contain both lower-level and more abstract goal information, it is challenging to distinguish the different forms of action understanding (Hamilton & Grafton, 2008; Michael et al., 2014). It has been suggested that mirroring processes yield to an understanding on multiple levels (de Lange et al., 2008; Hamilton & Grafton, 2008), but it has been a matter of debate whether MS activity is generally involved in the detection of underlying intentions, beliefs and abstract goals of observed actions (Cattaneo et al., 2009; Iacoboni et al., 2005; Jacob & Jeannerod, 2005; Steinhorst & Funke, 2014). Brain imaging studies attempting to clarify the sensitivity of the MNS to the intentionality of others' actions have assessed the activation of mirror neuron circuits in response to stimuli and tasks that require mentalizing processes. On the one hand, researchers found that the MNS is activated when participants were explicitly asked to reason about others' intentions (de Lange et al., 2008; Liepelt, Von Cramon, & Brass, 2008a), demonstrating that not only the frontal but also the parietal cortex is involved in higher-level action representations of action outcomes and goals (Hamilton & Grafton, 2008). On the other hand, studies revealed activity in cortical areas outside the classical MNS³ during mentalizing tasks in which participants had to encode higher-level action intentions (Brass et al., 2007; Van Overwalle & Baetens, 2009). In conclusion, fMRI studies and meta-analyses provide converging evidence that not all forms of action understanding are related to mirror

³ The activated cortical areas were assumed to be part of a so-called mentalizing system, comprising the anterior cingulate cortex, the medial anterior frontal cortex and the temporo-parietal junction (Saxe, 2005; Van Overwalle & Baetens, 2009).

neuron activity, but that the MNS is primarily recruited when observers represent the goal and infer the final outcome of object-directed motor actions (Bonini et al., 2010; de Lange et al., 2008; Fogassi et al., 2005; Hamilton & Grafton, 2008; Liepelt, Von Cramon, & Brass, 2008b). Jointly, these results lead to the conclusion that observers are able to encode proximate motor goals and infer what another person is doing by recruiting one's own action representations, without relying on higher-order processing. The findings of Study II provide strong support for this conclusion by highlighting the role of the motor cortex for action prediction. At the same time, more complex intentional inferences are unlikely to be solely achieved by direct-matching processes (de Lange et al., 2008; Van Overwalle & Baetens, 2009). However, the direct-matching theory does not claim that the activation of embodied action representations is a necessity for all forms of action understanding.

In an attempt to isolate different components of action understanding, a recent TMS study tested the causal role of the PMC for understanding hand and mouth actions with varying levels of complexity (simple, intermediate and complex) by manipulating the degree to which participants had to recruit contextual information during an action understanding task (Michael et al., 2014). In relation to Study II, this experiment provides further evidence that somatotopically organized areas in the PMC causally contribute to action understanding, but, unfortunately, the authors could not draw conclusions with respect to the hierarchical level at which the PMC supports action understanding.⁴ Future work should address this gap by exploring the relative contribution of embodied simulation for different levels of action understanding further.

What are other processes involved in action prediction?

In relation to action prediction, it is evident that eye movements can also be based upon other neural processes and routes during tasks that require inferences about higher-level social intentions of others' actions (Schneider, Bayliss, Becker, & Dux, 2012; Senju et al., 2009). However, these evaluations certainly also require longer processing times. Importantly, predictions relying on embodied simulations are likely to play a crucial role in real-life situations where observers need to generate fast and on-line predictions about what is going to happen next. In light of humans' sensitivity to biological motion and in comparison to other more complex or less notable facets of an observed action, biological motion information from observed actions may constitute a rich source of information for achieving

⁴ Inferences with regard to the level of action understanding (i.e. whether the PMC supports the understanding of low-level kinematics, proximate or distal goals) were not possible as this study did not reveal a significant interaction between complexity level, TMS sites and action type. One possible explanation for that might be that kinematic information was part of the presented actions at each level of complexity.

these rapid predictions. The findings from Study I suggest that the observed kinematics from an unfolding action (here in form of a PL display) provide sufficient information for predicting other people's actions ahead of time. Study II sheds light on the neural underpinnings of humans' action prediction abilities and provides direct evidence for the notion that these predictive gaze shifts reflect embodied simulations in the observer's motor system. In addition, the ability to predict others' actions as they unfold may constitute a foundational social competence in order to produce contingent responses in social interactions. Already infants need to be "fast social thinkers" in the context of any interactive learning situation (Krogh-Jespersen & Woodward, 2014). Being able to rapidly predict the behavior of other social partners allows infants to perform timely behavioral responses, which in turn might enhance the chance that social interactions will continue. In line with this reasoning, Study III indicates that already at one year of age infants' online gaze behavior is influenced by the social information conveyed by a give-me gesture in the context of a simple social interaction.

Anticipatory eye movement paradigms seem to provide a particularly suitable method for capturing humans' ability to generate these rapid predictions of other people's actions. Interestingly, not many prediction studies have demonstrated predictive gaze for self-propelled objects moving toward goal objects⁵. Additionally, most evidence against direct-matching theory and in favor of the inference account has been provided by habituation studies measuring looking times. Available data, together with findings from Study I and II, support the interpretation that fast online predictions are mediated by embodied simulation processes. Specifically, neurophysiological evidence from other TMS studies validated the notion that premotor activation during action observation reflects anticipatory motor simulations (Borroni et al., 2005; Kilner et al., 2004; Michael et al., 2014). Further support comes from single-cell recording studies demonstrating that certain mirror neurons discharge before an action is completed, for instance during the initial reaching phase (Fogassi et al., 2005). In light of the anticipatory properties of motor resonance, it seems unlikely that MNS activity is only subsequent to action understanding, i.e. encompasses action reconstruction processes. Hence, these findings, together with Study II, contradict opposing accounts claiming that goals are inferred and identified outside of the MNS (Csibra, 2007). For instance, the findings from Study II would be difficult to explain if activation in the motor system was only a side-product of action prediction.

Additionally, it is likely that inferential processes, such as teleological reasoning, come into play when observers need to retrospectively evaluate

⁵ So far, only two studies have reported predictions of self-propelled objects: Eshuis et al. (2009) and Bíró (2013). However, the interpretations of their findings have been criticized as well (Falck-Ytter, 2012; Gredebäck & Melinder, 2010).

changes and consequences of observed actions (Gredebäck & Melinder, 2010). Consequently, these retroactive judgments, which are typically measured in looking time and habituation studies, serve a different function than predictive gaze shifts (Daum et al., 2012). Thus, the reported evidence for the different accounts of action prediction implicate that inferential and simulation processes, although not mutually exclusive, may play an important role at different time points in the course of an action and may also match different task requirements. Moreover, these processes can be influenced by statistical regularities in the environment, depending on prior action or visual experience (Brandone, Horwitz, Aslin, & Wellman, 2014; Gredebäck & Kochukhova, 2010; Green et al., submitted; Henrichs et al., 2014).

What is matched in direct-matching?

While the studies discussed in the section above target the question of how goals and intentions are incorporated in gaze predictions, a related point concerns the input that feeds into direct-matching processes (Barresi & Moore, 1996; Liepelt et al., 2008a). That is, a puzzling question deriving from the cardinal matching properties of mirror neurons is what exactly is matched. There are several possibilities, e.g. a matching of kinematics from observed movements, object-actor relations, or perceivable action effects⁶ (Knoblich & Jordan, 2002). Along this line, the question arises how the same goal can be inferred when the observed kinematic information differs, for example when grasping a cup with contra or ipsilateral reaches. From a strictly direct-matching perspective, it is difficult to explain how simulation processes in the MNS can result in the same goal inference when the observed kinematics to attain a specific goal differ, for instance when reaching with the right or left hand. One possible explanation for this discrepancy comes from the predictive coding framework of simulation theory. Proponents of this Bayesian account have suggested that that observers use the same generative model (e.g. how they would produce the reaching action with their dominant hand) to simulate observed actions with varying kinematics. Importantly, their prior predictions are modulated by the observed kinematics (Neal & Kilner, 2010). That is, by comparing previously viewed input with current visual input, the likelihood of the prior

⁶ The common coding theory suggests that actions are coded, matched and represented in terms of their perceivable effects (Hommel et al., 2001; Prinz, 2010). When performing a movement, a bi-directional association between the generated motor patterns and the produced sensory implications is established. As a consequence, during observation of a certain event, the associated action becomes activated, and vice versa, i.e. performing an action also activates the associated perceptual representations with that event. Advocates of this account propose that actions are controlled and predicted by these bi-directional action-effect associations (e.g. Elsner & Hommel, 2001; Hommel et al., 2001).

can be estimated and predictions are updated on a kinematic, goal and intention level (Kilner, 2011; Miall, 2003, see page 34). Hence, this approach resolves how a unique goal is inferred when the observed movements to achieve this goal differ (Kilner et al., 2007). In line with the idea of a generative model for action prediction, other recent accounts proposed that mirror neurons are shaped by associative (Catmur & Heyes, 2011; Cook et al., 2014) or Hebbian learning⁷ (Keysers, Gazzola, et al., 2014). According to these models, the learned associations between actions and their sensory effects could form the basis for “priors” (i.e. prior predictions), assuming stronger associations for more frequently occurring events (e.g. Keysers & Gazzola, 2014). Jointly, in contrast to the classical direct-matching theory, these accounts do not suppose a direct mapping of observed kinematic information onto the same motor plan. Moreover, by emphasizing the associative relation between actions and their effects, these models could also explain more directly how the goal is encoded when observing and predicting others’ actions (Press et al., 2011). Based on these recent models, one could speculate that participants could have relied on a generative model for reaching actions to predict the presented manual PL actions in Studies I and II.

So far, the discussion has concentrated on research about prediction and action understanding of manual actions performed by a single person. However, in our social world, we frequently observe actions performed by more than one person. Consequently, it is important to extend our understanding about action prediction from single-person actions to social interactions. In an effort to fill this void within the action prediction literature, Study III examined infants’ online gaze behavior during observation of social interactions. The following sections discuss the role of embodied simulation and other processes during anticipation of social interactions.

Prediction of social interactions

Although infants’ ability to actively participate in coordinated joint interactions develops gradually during the first two years, they passively observe social interactions, such as interactive exchanges between social partners, from the beginning of their lives. Recent research efforts have been paying more attention to infants’ perception of social interactions, for instance how infants look at actions that are performed by more than one

⁷ The associative sequence learning (ASL) account has been focusing on the origin of the MNS, suggesting that mirror neurons are shaped by sensorimotor associative learning (Catmur, Walsh, & Heyes, 2007; Heyes, 2010). The Hebbian Learning account provides a similar explanation for the emergence of mirror neurons, but concentrates more on a neural level (Keysers, Perrett, & Gazzola, 2014).

individual. Study III was one of the first to address this widely unexplored question by examining how infants at one year of age look at a give-and-take interaction between two individuals. The results denote that 12-month-olds' online gaze is influenced by the social information of a give-me gesture as the goal of the observed exchange.

Does social context influence infants' online gaze behavior?

The findings from Study III raise the question whether infants' goal-directed gaze shifts were based on encoding the social context of the give-and-take interaction, such as that the passing hand provides some benefit for the receiving hand. Other infant eye tracking studies provide more detailed information about whether infants' online gaze behavior is influenced by the social context of an observed interaction. For instance, an eye tracking study by Fawcett and Gredebäck (2013) demonstrated that at 18 months infants make predictions based on the goal of an observed joint or individual action. Infants viewing two socially engaged actors performing an action sequence were more likely to predict them pursuing a joint goal compared with infants who observed the same sequence of actions but in which the actors displayed less social engagement. Similarly, the findings from another recent eye-tracking study indicate that at 14 months infants are able to recognize the communicative intent of requesting or pointing gestures during observation of social interactions (Thorgrímsson, Fawcett, & Liszkowski, 2014). Detailed examination of infants' gaze behavior revealed that when observing an interaction between two people 14-month-olds form expectations about communicative gestures, such as an addressee's reaction in response to requesting or pointing gestures. While infants participating in these studies were a few months older, two other studies have examined how infants comparable in age with those in Study III look at social interactions from a third-party perspective. The first one investigated infants' action prediction abilities at 6 and 12 months of age while infants observed the actions of two adult actors feeding each other (Gredebäck & Melinder, 2010). With regard to the context of the presented interaction, this study found that 12-month-olds were faster at shifting their gaze toward the recipient of the food when the feeding action was executed in a rational than in an irrational manner. Additionally, a recent eye-tracking study examined 9- and 12-month-olds' and adults' gaze behavior during observation of a block-stacking task that was performed by either a single person⁸ or as a joint action between two individuals (Keitel, Prinz, & Daum, 2014). While adults anticipated both individual and joint actions to the same degree, infants of both age groups initiated gaze shifts in general later than adults. More importantly, 9-month-olds showed faster predictions when viewing the individual compared to the

⁸ Similar to the block-stacking action presented in the eye-tracking study by Flanagan and Johansson (2003).

joint action, while this difference was only marginally significant in 12-month-olds. The authors suggested that the difference between individual and joint action condition was especially prominent in 9-month-olds because they were not able to represent the overarching joint goal of the observed action⁹ and, thus, their gaze behavior relied to a larger degree on observable lower-level visual information.

In summary, these studies suggest that from one year of age infants become gradually more sensitive to the social context and common goal structure of observed joint actions. In line with this reasoning, Experiments 3 and 4 from Study III show that in the absence of a social context (i.e., a give-and-take interaction in which one person receives an object from another person), infants did not show a preference for the give-me gesture compared to the inverted hand shape when both were presented side by side. Additionally, the ability to predict and encode social action goals seems to emerge at around 12 months of age. In light of the present evidence, it is possible that Study III captured the onset of infants' sensitivity to the communicative properties, and thus to the social functionality, of joint action goals.

Are infants' predictions of social interactions related to their own motor experience?

As mentioned in the introduction, several infant prediction studies have argued that infants' predictive gaze corresponds with their own motor experiences (Falck-Ytter et al., 2006; Kanakogi & Itakura, 2011). Accordingly, it has been suggested that the different developmental trajectories of infants' ability to predict individual or joint actions may be explained by the earlier onset of their ability to perform individual manual actions compared to when they start to engage in more complex social interactions (Keitel et al., 2014; Schmitow & Kochukhova, 2013). This notion is in line with the studies mentioned above, showing that 14-month-old infants with increased experience in joint actions are able to form expectations about collaborative gestures in social interactions (Thorgrimsson et al., 2014) and encode joint action goals (Henderson & Woodward, 2011).

The idea that infants' anticipatory gaze processes during social interactions depend on their own active experience with joint actions provides one possible explanation for the findings from Study III. While Study III reveals a large difference in gaze latency between the conditions showing either the give-me gesture or the inverted hand shape as the goal of the social interaction, infants in this study failed to initiate predictions ahead

⁹ The authors provide evidence that the increased visual complexity in the joint action condition did not result in increased visual distraction and, thus, is unlikely to account for later gaze latencies.

of time. Thus, these findings may reflect a developmental trend that infants at 12 months of age begin to show sensitivity to the social properties of action goals, but still lack sufficient experience with collaborative actions (Brownell, 2011) and in producing imperative giving to request objects (Carpenter et al., 2004; Crais et al., 2004). According to the direct-matching hypothesis, the abilities to successfully engage in social interactions and to efficiently produce imperative give-me gestures would in turn allow infants to generate predictions before an observed interaction is completed.

In conjunction with this view, a recent study demonstrated that 18-month-olds, but not 10-month-olds, are faster in shifting their gaze to the goal of an action when observing a turn-taking event in which two actors jointly built a tower of blocks or exchanged objects in a give-and-take interaction (Schmitow & Kochukhova, 2013). Accordingly, 18-month-olds might be faster in initiating gaze shifts due to 1) greater manual experience or 2) greater visual experience with these types of actions. Thus, an increased experience with manual actions may have facilitated goal-directed eye movements in the group of 18-month-olds. At the same time, the older infants in this case could have benefitted from their more extensive visual experience in joint actions. Similarly, Henderson et al. (2013) showed that already 10-month-olds are able to represent common goals of two collaborating partners if infants received active experience with the same collaborative action.

In addition, Study III highlights that not only the action toward a goal, but also the goal of the observed action affects gaze latencies. As the revealed correspondence between infants' active experiences and their action prediction abilities has primarily focused on the action to attain a specific goal, the findings from Study III shed new light on the complexity of the processes behind action prediction. If the ability to perform an action is important (for direct-matching processes) and if goal information also influences predictive gaze, an open question is what part of a social interaction is matched. In Study III, it could either be the transporting hand or the recipient, or both. If both, then this could be one part of the explanation of why there is a delay in latency when observing a social interaction compared to single-person actions, as the properties of a give-me gesture as the social goal are more complex.

In conclusion, more research is needed to clarify whether infants' understanding and predictions of third-party interactions builds on their own experience with collaborative actions or is primarily based on visual experience deriving from passive observation of others' interactions. In relation to Study III, the developmental trajectories of infants' engagement in give-and-take interactions in conjunction with their action prediction abilities could be investigated in future longitudinal studies.

To what degree do predictions of social interactions rely on embodied simulation?

On a more general level, an interesting but open question concerns the degree to which embodied simulation processes can account for action prediction and action understanding in social interactions. As action understanding is closely connected to the ability to predict and encode the behavior of social partners in joint actions, prior research attempted to assess the extent to which mirroring processes contribute to making sense of others' actions during social interactions (Sebanz & Knoblich, 2009). For instance, Knoblich and Jordan (2002) proposed that matching others' actions to one's own motor repertoire could form the basis for action coordination in conjunction with other people's actions. With regard to the role of movement information for action prediction, it has been shown that adults are able to predict and discriminate between different social and non-social intentions already during the initial phase of an observed grasping action (Sartori, Becchio, & Castiello, 2011). Specifically, in the absence of contextual cues and solely on the basis of kinematic information, observers were able to predict at the beginning of the movement if an object will be grasped with the social intent to compete or cooperate or with the intention to perform an individual action.

In further support of the idea that a common neural system for action and perception fosters the processing of social interactions, it has been shown that the MNS is sensitive to social cues in the context of joint actions (Doerrfeld, Sebanz, & Shiffrar, 2012) and involved in the processing of stimuli with social relevance. For instance, Oberman, Pineda and Ramachandran (2007) showed that modulations in mu rhythm suppression are related to the extent of social content and degree of interaction when participants observed 3 individuals tossing a ball up in the air to themselves (non-interacting condition), to each other (observed social action condition), or in some occasions also seemingly to the observing participant (interactive social action condition). They found that observation of the latter condition resulted in the highest mu suppression, followed by the observed social action condition. In a similar vein, another EEG study demonstrated that social relations between an observer and an actor modulate action simulations during action anticipation (Kourtis, Sebanz, & Knoblich, 2010). In detail, they found that anticipatory activation in the areas of the motor cortex is enhanced when participants anticipated the action of an interaction partner compared with predicting the same action executed by a 'loner', i.e. an actor that always acts alone.

Proponents of embodied accounts have further suggested that mirror mechanisms may also be involved in comprehension of communicative hand gestures (Montgomery, Isenberg, & Haxby, 2007; Möttönen, Farmer, & Watkins, 2010) and other manual communication (Rizzolatti et al. 1996). In

line with the idea that the motor system facilitates communication, they also demonstrated that the MNS is activated during language perception (Glenberg et al., 2008; Rizzolatti & Arbib, 1998)¹⁰. Advocates of an embodied approach to language have ascribed gestures a relevant role in language evolution (Corballis, 2003, 2010) and emphasized that production and comprehension of language are interwoven (Pickering & Garrod, 2013). Further evidence comes from neurophysiological studies investigating the modulation of the motor system during speech perception (D'Ausilio et al., 2009; Fadiga, Craighero, Buccino, & Rizzolatti, 2002). Along this line, the notion of embodied semantics has received support from studies revealing corresponding activation patterns in the premotor cortex during action observation and when listening to action sentences describing the same actions (Aziz-Zadeh et al., 2006).¹¹

In sum, the available evidence implicates that mirror mechanisms are not only beneficial for representing and rapidly predicting others' motor intentions during object-directed actions, but that they also contribute to the perception and prediction of social interactions. In the context of the give-and-take interaction presented in Study III, resonance-based processes could have played an important role for infants' online gaze. It is possible that observing an actor expressing a request by forming a give-me gesture activated infants' corresponding action representations. Consequently, embodied simulation processes could have facilitated infants' goal-directed gaze shifts in the give-me gesture condition. At the same time, as infants' ability to produce give-me gestures has emerged just recently, 12-month-olds might only be able to overcome their internal processing lag of the oculomotor system, but could not yet generate predictions ahead of time.

In relation to more sophisticated social interactions, additional processes are likely to contribute to humans' ability to infer and represent social and communicative intentions (Knoblich & Sebanz, 2008). As joint and collaborative actions are often based on more complex overarching goals, e.g. the desire to jointly achieve a common goal, these types of actions require observers to represent and infer action goals on a higher cognitive level (Knoblich & Sebanz, 2008). In this case, goal representations need to go beyond the level of proximate goals when generating predictions about future action outcomes. Consequently, it has been argued that a more complex understanding of joint actions cannot be accomplished on the sole

¹⁰ This notion has its origin in the *motor theory of speech perception* by A. Liberman (e.g. Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967), suggesting that the motor system is not only involved in speech production but also in speech detection and that language has evolved through an evolutionary ancient communication system based on non-verbal gestures (Gentilucci & Corballis, 2006).

¹¹ Despite the evident relationship between communicative hand movements, speech perception and the motor system, opponents of embodied semantics have argued that the revealed motor activity does neither entail phonetic processing nor constitute a necessity for speech perception (Scott, McGettigan, & Eisner, 2009).

basis of mirroring processes. Observers may rely to a larger degree on conceptual knowledge and higher-level representations of joint tasks and goals when observing and encoding social interactions directed toward conspecifics (Jacob & Jeannerod, 2005). As inferences about higher-level social intentions require a more complex social understanding, it is not surprising that the ability to encode joint action goals develops later compared to infants' ability to understand and predict single-person actions. Thus, it is very likely that infants' action prediction abilities relate not only to their own motor repertoire but also to their cognitive abilities, such as their ability to represent others' higher-level goals and social intentions.

To date, it is yet not fully understood to which extent lower-level processes (e.g. action simulation) or higher-level processes account for humans' striking ability to infer and predict others' behaviors in observed interactions. On a related note, it remains unspecified to which degree the processes underlying predictions of interactions between social partners differ from the mechanisms for predictions of individual actions directed toward objects. The reported studies identify differences between infants' predictions of individual actions and social interactions, but more research is needed to explore and understand the ontogeny of humans' prediction abilities during observation of social interactions.

Future directions

In general, one major challenge for future research seems to be to unravel how embodied simulation processes may interact with higher-level cognitive processes, such as mental belief and intention attributions in various contexts. Further, as it became evident in the reviewed literature by the focus on studies investigating the role of embodied simulation for action prediction, future research would benefit from testing more directly the contribution of inferential or mentalizing processes on anticipatory gaze. In the same vein, it is of particular relevance to assess the scope of the mirroring and mentalizing system, respectively, in order to dissociate which processes dominate and override others under which conditions. Along this line, it remains an unsolved question at which goal level direct-matching processes entail and support action prediction and understanding.

Based on the empirical findings and theoretical aspects discussed in this thesis, one important future direction for this research would be to examine in more detail to which degree embodied simulation processes can account for predictions of social interactions and what other mechanisms may mediate action predictions in social contexts.

In relation to Studies I and II, more detailed information about the perceptual processes during observation of PL displays would increase our knowledge about the functional role of biological motion for action

prediction. For instance, it would be interesting to assess and compare the distribution of looking times at different specific areas of a PL display showing either a biological or non-biological reaching action during an action prediction task. Another open question concerns the degree to which humans can anticipate action goals of non-human animal agents from biological motion information. Additionally, future work should further explore the relation between action prediction and recognition of the observed PL animation. Another way is to target the developmental trajectories of infants' and children's ability to anticipate other people's PL actions. At the same time, more neurophysiological studies are needed to corroborate the findings from Study II, for instance by targeting other control stimulation sites or by extending this TMS protocol to other actions.

Related to Study III, future studies should expand recent research efforts with respect to infants' perception and prediction of social interactions. For instance, it remains unexplored how infants look at social interactions within richer social contexts that include faces, verbal communication or multiple social partners. At the same, another open question concerns the developmental trajectories of how the social context affects infants' action understanding, i.e. when social information supports or impedes infants' comprehension of others' actions.

With regard to gesticulation, further research is needed to specify the circumstances under which infants perceive communicative gestures as meaningful or ambiguous and when the social functionality of gestures, especially of give-me gestures, begins to influence infants' gaze behavior during observation of social interactions. Along this line, finding neural correlates of infants' perception of give-me gestures and various social interactions might shed some light on the underlying processes.

Last but not least, more research is needed to understand the developmental trajectories of the degree to which embodied simulation processes account for and foster infants' action prediction abilities in social contexts. So far, little research has addressed how exactly infants' own active experience in social interactions relates to their understanding of joint actions. At the same time, as the ability to represent others' higher-level goals and intentions evolves gradually with increasing age, one open question concerns the consequences of this development for the mechanisms underpinning prediction and understanding of social interactions. For example, future work could address the relative contribution and interaction of mirroring and higher-level inferential processes during infants' perception of actions performed jointly between individuals. Additionally, future studies should examine the extent to which cultural factors and visual experience in general affect infants' action prediction and action understanding abilities. In this context, more information about short- and long-term learning effects on infants' action predictions would be very valuable.

Final conclusions

In summary, this thesis establishes a direct connection between anticipatory eye movements and motor cortex activity. Along with prior demonstrations of real-time action anticipation across species, the findings reported here suggest that we are tapping a phylogenetically ancient mechanism at the core of social cognition. As the ability to anticipate others' actions has been demonstrated in both infants and chimpanzees (Myowa-Yamakoshi, Scola, & Hirata, 2012), this mechanism might bootstrap social cognition at large. Nevertheless, the full extent to which the MNS plays a causal role for action prediction and action understanding in various contexts remains to be explored further.

In addition, the thesis extends prior action prediction studies by exploring anticipatory gaze processes during observation of social interactions. Thereby, it highlights the role of action goals for action prediction and captures infants' ability to form expectations about others' actions in the context of simple social interactions. Importantly, Study III implicates that at one year of age infants begin to show sensitivity to the communicative properties, and thus to the social functionality of action goals. In this context, more research is needed to unravel how direct-matching or other processes may contribute to infants' predictive gaze during observation of social interactions.

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