How hands shape the mind

The P400 as an index of manual actions and gesture perception

MARTA BAKKER
Dissertation presented at Uppsala University to be publicly examined in Auditorium Minus, Gustavianum, Akademigatan 3, Uppsala, Friday, 19 October 2018 at 13:00 for the degree of Doctor of Philosophy. The examination will be conducted in English. Faculty examiner: Professor Amy Needham (Vanderbilt University, Department of Psychology and Human Development).

Abstract

Being able to perform and understand actions is crucial for proper functioning in the social world. From birth, we use our bodies to act and to promote learning about ourselves, our environment and other people’s actions and intentions. Our mind is embodied; thus, our actions play a crucial role in cognitive and social development.

This thesis focuses on the close interrelation between action and perception and the role of our hands in this link. Three empirical studies on action processing are presented in a framework of embodied cognition that emphasises the role of bodily experience in social development. All three studies were designed to measure event-related potentials (ERPs) in infants 4 to 9 months old, when they observed manual actions, grasping and the give-me gesture.

Study I demonstrates the neural underpinnings of infants’ action–perception link at the age when their ability to grasp for objects in a functional manner emerges. Neural processing has been found to be influenced by infants’ own manual experience of exactly the same grasping action.

Study II reveals that brief active motor training with goal-directed actions, even before the solid motor plans for grasping are developed, facilitates processing of others’ goal-directed actions.

Study III shows that the same neural correlate that indexes processing of reaching actions is involved in encoding of the give-me gesture, a type of non-verbal communication that conveys a request. This ability was found not to be directly dependent on the infants’ own ability to respond behaviourally to another person’s gesture.

This thesis pinpoints the neural correlate, P400, involved in the processing of goal-directed actions and gestures. The findings highlight the importance of motor experience, as well as the involvement of attentional processes in action processing. Additionally, the data from Study III may suggest a possible involvement of grasping skills in encoding non-verbal communicative gestures.

Keywords: goal-directed actions, action processing, EEG, ERP, P400, gestures, grasping, embodiment, social development, give-me gesture, dynamic system theory

Marta Bakker, Department of Psychology, Box 1225, Uppsala University, SE-75142 Uppsala, Sweden.

© Marta Bakker 2018

ISSN 1652-9030
ISBN 978-91-513-0431-1
urn:nbn:se:uu:diva-358475 (http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-358475)
To my family and all the children that helped in this pursuit
This thesis is based on the following papers, which are referred to in the text by their Roman numerals.


Reprints were made with permission from the respective publishers.
Contribution

The contribution of Marta Bakker to the papers included in this thesis was as follows.

Studies I, II and III: designed and planned the study in collaboration with a supervisor and co-authors. Created the stimuli, collected the data, performed the statistical analysis and was primarily responsible for writing and revising the manuscript.
### Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>EEG</td>
<td>Electroencephalography, electroencephalogram</td>
</tr>
<tr>
<td>STS</td>
<td>Superior temporal sulcus</td>
</tr>
<tr>
<td>ERP</td>
<td>Event-related potential</td>
</tr>
<tr>
<td>MNS</td>
<td>Mirror neuron system</td>
</tr>
<tr>
<td>fMRI</td>
<td>Functional magnetic resonance imaging</td>
</tr>
<tr>
<td>DST</td>
<td>Dynamic systems theory</td>
</tr>
<tr>
<td>TMS</td>
<td>Transcranial magnetic stimulation</td>
</tr>
<tr>
<td>MEG</td>
<td>Magnetoencephalography</td>
</tr>
<tr>
<td>PET</td>
<td>Positron emission tomography</td>
</tr>
</tbody>
</table>
Introduction

"We must perceive in order to move, but we must also move in order to perceive." James Gibson (1979)

Our lives are filled with a diversity of sensations, novel experiences, constant changes and challenges. As part of a social world we move and observe other people’s movements. Movement gives us the ability to explore, manipulate and exchange objects, cooperate and continuously relate to other people and contextual constraints. In fact, it is also through movements that we can infer others’ mental states, thoughts, percepts or emotions expressed in speech, gestures, grimaces and eye movements, for example (Adolph & Berger, 2006).

Newborn babies are already capable of acting on the complex surrounding and they use their bodies to promote new experiences, exploring activities and learning about their social environment through actions (von Hofsten, 2004; von Hofsten, 1993). With embodied cognition from the beginning of our lives, our behaviours are seen not solely as isolated output from the brain. Rather, the body plays a crucial role in shaping the mind (Barsalou, 2008; Clark, 2012; Gallese & Sinigaglia, 2011; Needham & Libertus, 2011; Thelen, 1995; Wilson, 2002). One of the theories of embodied cognition defines cognition as having emerged from, and being dependent on, specific bodily characteristics, and on interactions with the environment, in conjunction with many mental functions, such as reasoning, memory, emotion and language (Thelen, Schöner, Scheier & Smith, 2001). Our motor system, in terms of abilities and constraints, therefore influences our cognition.

Additionally, it is through embodied processes that we experience everything around us, and understand not only ourselves but also others, their actions and intentions. In relation to the embodied account of social cognition, the close interrelation between action and perception and the importance of manual actions in this link have been a recurrent subject in the developmental research field (Campos et al., 2000; Prinz, 1997; Shapiro, 2010; Thelen, 1995; von Hofsten & Lee, 1982). The idea was first explored more than 100 years ago by William James, who pointed out that there is a connection between the mental representation of a movement and the actual movement (James, 1890, p. 293). Jean Piaget also (1953) highlighted the meaningful impact of our sensorimotor abilities on our cognition and developing brain. He asserted that we
gain the ability to understand others through our own constant action production (Piaget, 1977). At the same time, Gibson (1979) pointed out that our perception is connected to our body and environment, and that this coupling promotes rich sensory input (Noe, 2004).

More recently, Prinz has proposed the theoretical framework—common coding—that describes how perceptual representation and motor representations are linked. This notion was documented by a vast literature supporting the idea of action and perception as related processes that greatly influence each other (Prinz, 1990; von Hofsten & Lee, 1982). Additionally, this interrelation was supported by the discovery of the ‘mirror neurons’ that were, it was suggested, a neural basis of action understanding (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). It is proposed that, when observing others, we apply our own action plans to make sense of their actions (Barsalou, 2008; Gallese, Keysers, & Rizzolatti, 2004). That is, we activate the same neural networks when performing an action as when observing the same action performed by others (Rizzolatti & Craighero, 2004).

Several studies have documented that the link between action and perception is already present early in development (Falck-Ytter, Gredebäck & von Hofsten, 2006; Marshall & Meltzoff, 2012; Meltzoff & Moore, 2002) and that our own experience in action production helps us understand other people’s actions (e.g. Cannon, Woodward, Gredebäck, & von Hofsten, 2013; Daum, & Gredebäck, 2011; Kanakogi & Itakura, 2011; Libertus & Needham, 2010; Loucks & Sommerville, 2012; Needham & Libertus, 2011; Skerry, Carey & Spelke, 2013; Sommerville, Woodward, & Needham, 2005).

This thesis promotes the notion that our bodies and experiences are highly significant in our understanding of everything around us. In particular, it focuses on our hands, which seem to play a crucial role in our cognitive and social development since they are used to act, explore, shape our surroundings, and communicate. They may therefore be seen as channels through which we perceive and learn about the world.

An overarching goal is to investigate how manual actions shape the mind. In the set of three empirical studies, the role of infants’ own experience of manual actions and gestures in relation to action–perception coupling is discussed. The findings provide the neural basis for processing of the action–perception link at the onset of reaching actions, as well as gestures.

With respect to the overarching goal, the following questions are discussed. Which neural correlates are evoked when we observe other people’s manual actions early in life? (Study I-III). Does infants’ newly gained experience of manual actions enhance their processing of other people’s actions? (Study I). How is pre-reaching infants’ action processing influenced by brief active training with grasping action? (Study II). Is infants’ understanding of other people’s gestures also driven by their own experience of using gestures? (Study III).
The investigation focuses on infants aged 4 to 9 months. To provide the necessary background and rationale for the above questions, motor development of manual action, organised in the developmental timeline of the reaching action and gestures, is presented. This is followed by an overview of action understanding, with respect to our sensitivity to the goals of actions and gestures. Thereafter, various theoretical views and empirical evidence for the importance of actions for social functioning are described. How infants use embodied processes to learn to perform manual actions and how they begin to understand the surrounding world through their body are discussed.

The introduction ends with an overview of the neural basis for processing social actions. This part provides a background for the methodology used in this work, which has offered scope for insights into the neural underpinning involved in action perception in early life, generated by the child’s own manual actions.

Development of manual actions

Anyone who has ever seen a child grow up and develop knows that their movements undergo a qualitative change in the movements they perform. Based on abundant empirical evidence, in this thesis, motor development is seen as a continuous, lifelong process. Starting before birth, it is a flexible process that undergoes dramatic changes in the motor and nervous system, and is influenced by constant interaction between action, perception and the environment. This process stays flexible and remains amenable to possible refinement even after the movements become fully functional for action and communication (Craighero, Leo, Umiltà & Simion, 2011; Thelen, Anderson & Delp, 2003; Thelen, 1995; von Hofsten, 2004).

One way of explaining motor development is to consider movement as a product of constant interaction between different subsystems, such as personal characteristics (motivation, attention, muscular strength, posture, weight, etc.), task constraints (everything related to action, such as direction, goal, tool use etc.), and environmental constraints (everything that exists outside the individual). This view is expressed in the dynamic systems theory (DST) proposed by Esther Thelen (e.g. Thelen & Smith, 1994; 1998 Thelen, 2005; Thelen & Spencer, 1998). The theory is an attempt to encompass all possible factors that influence and have a bearing on development. It postulates that there are no fixed motor programmes determined by the nervous system alone but, rather, that movement is contingent on the environment. Development is thus highly dynamic, since the state of the system constantly depends on the prior states of the system and determines its future state, as well as interdependencies among different systems (Thelen, 2005). A small shift in one subsystem caused by the constant experience of constraints imposed by the body and
brain alike may affect the whole system, which in turn may affect progress in learning a new motor skill (Colombo-Dougovito, 2017).

As stated in DST, development occurs through self-organising, robust and spontaneous processes that involve multiple interactions within a system that is initially not well-organised, to obtain internal order. This way of looking at development implies that the changes in the system are non-linear and subject to the influence of many other physical and environmental conditions (Thelen & Bates, 2003).

Action production

A presentation of how infants become proficient users of their own hands is given below. How do they learn to reach, and what is necessary for reaching to emerge? Following the developmental trajectory of reaching, how infants start to use their hands as ‘tools’ to communicate, that is, when they learn to gesture, is described.

The path to successful reaching

It has been suggested that motor learning starts in the womb. The evidence for this claim derived from observation of foetal movements by means of real-time ultrasound. In this study, it became clear that hand movements in the womb are already not random but, rather, oriented at specific targets (Castiello et al., 2010; Craighero et al., 2011). Another study using the same technique (Zoia et al., 2007) is particularly interesting, since it captured differences in kinematic patterns between foetal movements performed towards or away from the foetus’s own body. Examinations in the 14th, 18th and 22nd week of gestation showed that movements towards the foetus’s own body, that is the mouth and the eyes, improved over time. At 18 weeks’ gestation, the movements were still jerky. However, a few weeks later (22 weeks’ gestation) they had become straight and better aimed towards targets. In the same study, it was also noticed that phases of acceleration and deceleration were adjusted to the size and properties of the targets (eyes or mouth). This improvement was not noticeable in movements away from the body, that is, without a specific target. These findings suggest that learning to reach is already present in the womb and actually resembles the reaching actions development observed after birth (Zoia et al., 2007). These early intrauterine movements may possibly, provide input to the sensory system that promotes action planning and demonstrates the relation between motor command and sensory consequence (Craighero et al., 2011; von Hofsten, 2009; Sparling & Wilhelm, 1993; Thelen, Corbetta, & Spencer, 1996).
Directly after birth, our movements meet new constraints in the form of gravity and other physical forces such as inertia and centripeta (Bernstein, 1967). Thus, the motor system has to adjust before it can organise its movements in a functional way. This includes gaining control over body changes in terms of size and physical abilities, i.e. the head, trunk, posture, muscles and joints, as well as learning how to navigate one’s own body in relation to a new environment (Savelsberg, van der Kamp, & Wermskerken, 2013; Thelen et al., 1993). Although, at first, the arm movements may look less organised, random and reminiscent of primitive reflexes, several studies have demonstrated that many movements, even before becoming functional and complex, are meaningful, goal-directed and driven by explorative motives (e.g. von Hofsten, 2009; van Der Meer, 1997; von Hofsten & Rönnqvist, 1988).

At the beginning of life, newborns mostly use their hands and arms to explore their own bodies (Rochat, 1993). Soon, however (1–3 months), they start to orient their movements towards objects in their surroundings. Interestingly, at this age, they produce more movement in the presence of objects than when objects are absent (von Hofsten, 1982; von Hofsten & Fazel-Zandy, 1984). The movements are produced with poor control and a jerky trajectory, with multiple segments of acceleration and deceleration (von Hofsten, 1979). Once the object is approached it is explored by a colliding it with a hand rather than being grasped (Piaget, 1952; von Hofsten, 1984). By around 3 months of age, arm movements become more controlled (straighter, with fewer movement units), and are sporadically guided by vision (von Hofsten, 1979; von Hofsten & Rönnqvist, 1993).

Importantly, the progress in movements depends on changes within other systems. In particular, the relationship between movement and visual information is extremely important for functional reaching, since it allows infants not only to detect the goals of their actions, infer their physical properties and spatially locate them, but also to adjust motor control to these multiple constraints (von Hofsten, 1979; McDonnell, 1975). The improvements continue and at around 4 months of age, although infants still have difficulties grasping the objects of their interest, they are more skilled in touching them (von Hofsten, 1979). The child’s desire to interact with the surrounding world, and to explore objects with the mouth, drives repeated performance of reaching actions (Thelen et al., 1993).

In the next few weeks of development, intensive training through repeated cycles of action and perception with respect to environmental constraints (Williams, Corbetta, & Cobb, 2015) improves infants’ performance, enabling them to successfully reach for objects (e.g. von Hofsten, 1979; von Hofsten & Fazel-Zandy, 1984; von Hofsten & Rönnqvist, 1993). Reach itself still involves a primitive form of power grip (Halverson, 1931), but allows intensive
exploration of objects, which in turn provides new visual and haptic information about the surroundings (Ruff, Salterelli, Capozzoli, & Dubliner, 1992). At around the same time, enhanced postural control enlarges infants’ reaching space: they can lean forward to grasp objects that are further away (Yonas & Hartman, 1993). Over time, infants gain more sophisticated reaching ability, such as prospectively controlled movements towards slowly moving objects (Bertenthal, 1996; von Hofsten, 1980; von Hofsten & Lindhagen, 1979).

By around 7–9 months of age, this sophistication extends to the ability to adapt reaching to the properties of objects being reached (Barrett, Traupman, & Needham, 2008; Corbetta & Snapp-Childs, 2009; von Hofsten & Rönnqvist, 1988). The grip also becomes visually, rather than manually, guided. Thus, in reaching for small objects the infant’s power grip is replaced by a more precise grip (pincer/precision grasp), using one or two fingertips and the thumb (McCarty, Clifton, Ashmead, Lee, & Goubet, 2001).

The gradual process of developmental improvements continues and, by the end of the first year of life, the hand has become a fully functional tool for performing countless tasks with several grip patterns. At around the same time, infants start to use two-handed movements, which allow them to hold an object in one hand and manipulate it in another (Bushnell & Boudreau, 1993). The hands also gain a new function: they become tools for communicating with others (Bates, Camaioni, & Volterra, 1975).

**Final note on reaching development**

Finally, it is worth noting that the above timeline for acquisition of reaching skills is merely the average representation of universal stages. Although this timeline is highly informative and fundamental for monitoring typical progress, it provides no clear indication of individual physical and contextual variabilities. In fact, these differences among individual children cannot be dismissed in any discussion of motor performance, since the developmental change is embodied (Bertenthal & Clifton, 1998; Adolph & Hoch, in press). Accordingly, the body has an extensive influence on the course and speed of development. For instance, selection of the proper grip (power or pincer grasp) depends on the child’s cognitive and physical abilities alike.

Cognitively, children need to learn to navigate environmental constraints, solving problems flexibly and adjust their own actions to their current environment, in order to find the best means to achieve the goal (Adolph, Bertenthal, Boker, Goldfield, & Gibson, 1997). Physically, the child needs manual prowess and motor abilities (muscular strength, hand size etc.) to execute the action (Butterworth, Verweij, & Hopkins, 1997; Barrett, Traupman, & Needham, 2008). The constantly changing relationship and continual link between these two factors result in a developmental progression marked by plateau and
regression episodes, that is not linear or independent (Thelen, Corbetta, & Spencer, 1996).

This non-linear approach suggests that motor development, takes place through interactions between a body with particular capabilities and the opportunities allowed by multiple environmental constraints (Adolph, & Robinson, 2013; von Hofsten, 2004). The emergence of successful reaching at around 4–6 months of age therefore affords remarkable opportunities for development, since it allows infants to learn about object properties and the surrounding world in general (Bushnell & Boudreau, 1993; Corbetta, Thelen, & Johnson, 2000; Corbetta & Snapp-Childs, 2009).

**Development of manual actions as tools to communicate**

By developing manual skills, infants not only explore and influence the environment, but also communicate. Communication is the informational exchange among social partners, driven by cooperative and prosocial motives (Carpendale & Carpendale, 2010; Tomasello, 2008) and based on social-cognitive skills, i.e. shared intentionality (Tomasello, 2010).

Before language begins, this exchange between the communicative partners can be expressed through gestures (Goldin-Meadow 2007a; Savage-Rumbaugh & Rumbaugh, 1993; Bates, Benigni, Bretherton, Camaioni, & Volterra, 1977). Gestures are bodily movements (Kendon, 2004) that convey meaning (Crais, Douglas, Cox, & Campbell, 2004; Özçalışkan & Goldin-Meadow, 2005). Gestures allow bond formation and fruitful interactions with other members of society through sharing of thoughts, feelings and intentions. This is crucial for everyone who wants to be fully integrated in a social world. Precise transfer of specific meaning through gestures is possible under several conditions, i.e. joint attention, a common conceptual foundation, shared experience and context, and common cultural knowledge (Tomasello, 1992; Tomasello, & Rakoczy, 2003).

At the end of the first year of life an important socio-communicative skill emerges: fully functional joint attention (Carpenter, Nagell, Tomasello, & Butterworth, 1998). At the same time, infants begin using their hands within a functional referential gesture repertoire that includes, the pointing or give-me gesture to express their needs, convey specific intentions and/or share attention with others (Crais, Douglas, & Campbell, 2004, Carpendale & Carpendale, 2010). It is suggested that through daily experience of gestures, infants learn rules for dialogue and social exchange between social partners that are necessary for their later language communication (Ninio & Bruner, 1978). Subsequently, when spoken language is acquired, gestures are integrated into verbal communication to jointly convey intent (Cassell, 1960). They are particularly suitable for expressing spatial and motor information during conversation (Alibali, 2005).
Much of the developmental literature on gestures in infancy focuses on a pointing gesture (e.g. Bahne, Liszkowski, Carpenter, & Tomasello, 2012; Liebal, Carpenter, & Tomasello, 2010; Tomasello, Carpenter, & Liszkowski, 2007; Carpenter & Tomasello, 2007). This is expressed by extending the arm, hand and index finger, while the remaining fingers are curled under the hand, with the thumb held down and to the side (Butterworth, 2003). Pointing is a social tool that serves to obtain and reorient other people’s attention to focus it on the same object of interest (Bates, Camaioni, and Volterra, 1975; Butterworth, 2003), or specific features of the environment like a location, person or event (Liszkowski, Carpenter, Striano, & Tomasello, 2006). According to some sources, pointing has clear communicative and cooperative motives, since it occurs only in the presence of a social partner (Franco & Butterworth, 1996). Typically, the fully functional pointing gesture emerges at around 12 months of age (Carpenter, Nagell, & Tomasello, 1998; Butterworth & Morissette, 1996).

In contrast to pointing, the give-me gesture has not received much research attention. The give-me gesture is an extended face-up palm hand directed towards the observer to request an object (Mundy et al., 1986). It is not clear why this gesture has been neglected in developmental psychology as back in the 1970s, some literature pointed out that infants’ ritualised exchanges (giving and taking) can be seen as a fundamental basis for communicative and linguistic abilities (Ninio & Bruner, 1978; Ratner & Bruner, 1978). The give-me gesture serves multiple functions. It can refer to a specific object, express a request and communicate a goal of the action (Shwe & Markman, 1997). Production of the give-me gesture emerges at the end of the first year of life. It has been documented that infants start to give others objects to share, and to direct others’ attention at around 9–13 months, and they use giving to influence others’ behaviour from 12–13 months (Bates et al., 1975; Carpenter et al., 1998; Crais, Douglas, Campbell, 2004). Later, when infants start to speak, this gesture complements their speech to express more complex ideas (Özçalışkan & Goldin-Meadow, 2005).

**Action understanding**

Being a proficient partner in social interactions means not only producing actions but also understanding people around us, and especially their actions. Thus, understanding other people’s actions is not a simple task as to make sense of the surrounding world, we need to pay attention to multiple cues that help us to process an ongoing stream of information. It is helpful that immediately after birth infants are, attuned to people’s faces, and their eyes in particular (Langton, Watt, & Bruce, 2000; Hood, Willen, & Driver, 1998). The
ability to follow other people’s gaze facilitates understanding of other people’s goals and intentions (Frith & Frith, 2001; Meltzoff & Brooks, 2001; D’Entremont, Hains, & Muir, 1997; Gredebäck, Theuring, Hauf, & Kenward, 2008; Hood, Willen, & Driver, 1998). In relation to manual actions from the beginning of life, infants are sensitive to the goals of other people’s actions. At the end of the first year, when infants use their hands to convey specific intentions and share attention with others (Crais et al., 2004; Bates et al., 1979; Carpendale & Carpendale, 2010; Mundy et al., 1986), they become skilled at encoding gestures and precisely inferring other people’s intentions. Through daily experience of actions and gestures, infants learn about other people’s actions and social exchange between partners. All the above is necessary for proper functioning in the social world, and for later language communication.

Below, the developmental trajectory of infants’ understanding of goal-directed actions and of gestures is described. This is followed by a paragraph on the role of covert attention in action understanding.

Sensitivity to goal-directed actions
There are many different cues that we need to extract and process when observing others (Thioux, Gazzola, & Keysers, 2008). Such cues include the goals that are fundamental to understanding actions since they imply causation of our movements (Ma & Hommel, 2015). Humans are highly sensitive in detecting goals from a complex information and processing them as meaningful and intentional (Bekkering, Wohlschlager, & Gattis, 2000). Goals of actions have been demonstrated to be critical for social learning, in making predictions and in evaluating of others’ behaviour (e.g. Csibra & Gergely, 1998; Hamlin, Hallinan, & Woodward, 2008; Robson & Kuhlmeier, 2016). This is because they structure our actions (von Hofsten, 2004) and inform observers about other people’s behaviours, minds and intentions behind the behaviours (e.g. Bekkering, Wohlschlager, & Gattis 2000; Grèzes, Frith, & Passingham, 2004). Goals in this thesis, goals are defined as endpoints of an action, an example being a toy or a cup at the end of an ongoing and immediate action.

Sensitivity to goals is noticeable from the beginning of life. Babies just a few days old have been shown to be able to discriminate between goal-directed and non-goal-directed actions. This is evident from their preference for watching hand actions that may result in reaching an object, in comparison with hands performing the same movement but without a clear goal (Craighero, Leo, Umilta, & Simon, 2011). Moreover, at around 6 months of age, infants encode human actions based on the underlying goals and compared with other salient aspects of the action, the goal is most relevant (Woodward, 1998). For instance, in the study by Woodward (1998) infants who had
become habituated to a goal-directed action showed a stronger novelty response (expressed in longer looking time) to the action that altered the goal than to the test event that used new physical properties of the action. That is, infants ignored the change of the path of the reaching hand but reacted selectively to the change of the hand’s goal. Moreover, the goals provide enough information to make even incomplete actions comprehensible (Daum, Prinz, & Aschersleben, 2008).

Our sensitivity to the goals of others’ actions has been found to be enhanced with our own experience of the same action, i.e. people’s own ability to perform the action facilitates their understanding of both their own and other people’s goals (e.g. Cannon, Woodward, Gredebäck, von Hofsten, & Turek, 2012; Sommerville, Woodward, & Needham, 2005; Loucks, & Sommerville, 2012; Libertus & Needham, 2010; Needham, Barrett, & Peterman, 2002; Skerry, Carey, & Spelke, 2013).

Gesture understanding

Some scholars report that from the early age, infants are sensitive to pointing gesture. This sensitivity is at first restricted to dynamic pointing only, but it is suggested to provide information about the functional consequences of pointing (Rohlfing, Longo, & Bertenthal, 2012). At around 6 months, infants are able to follow pointing to the correct side but are unable to precisely determine the pointer’s object of interest (Butterworth & Jarrett, 1991), and comprehend pointing towards close but not distant objects (Morissette, Ricard, & Gouin-Décarie, 1995). By around 12 months, infants are becoming highly skilled in following pointing, so it is suggested that comprehension of pointing is formed at around this time (Brooks & Meltzoff, 2008; Liszkowski, Carpenter, Striano, & Tomasello, 2004; Liszkowski, Carpenter, & Tomasello, 2007; Daum, Ulber, & Gredebäck, 2013; Woodward & Guajardo, 2002).

Much like pointing, the give-me gesture seems to be an important piece of the puzzle in infants’ knowledge about social situations. It is always performed in the presence of another person, implying a communicative function. The give-me gesture can serve as a social cue in observing other people’s interactions, creating an expectation of how the relationship between two infants will unfold. At around the same time (9–12 months of age) as infants start to produce the give-me gesture (see page 16), they become cognizant of the properties of the gesture as a tool to convey communicative meaning, simply by observing it occurring between two people. A study by Elsner et al. (2014) investigated perception of the give-me gesture to convey expectations of ongoing social events. In this study, infants observed an object being transferred from one hand to another. Before the object was passed, the other hand produced either a give-me gesture or inverted hand shape (the give-me gesture presented upside down). It was found that infants shifted their gaze to the give-
me gesture significantly earlier than to the inverted hand shape. This demonstrated that at 12 months, when observing social events from the third-party perspective, infants exhibit the ability to predict the response to the give-me gesture (Elsner, Bakker, Rohlfing, & Gredebäck, 2014).

A similar conclusion has been drawn for 14-month-olds when they observed the interaction between two experimenters from the third-party perspective. In this experiment, infants showed an anticipatory gaze when an experimenter’s hand performed the give-me gesture before the transfer of the object from the other hand. This study demonstrated that by the age of 14 months, infants understand the function of the give-me gesture (the object request). They have an expectation about the ongoing interaction even if they are not involved in this interaction themselves, and they are aware of the social context of gesture (Thorgrimsson, Fawcett & Liszkowski, 2014).

It is highly likely that, with its communicative properties, the give-me gesture is critical for general social skills. It therefore must not be neglected and should be a subject for further investigation.

The role of covert attention in understanding social actions

Attention plays a crucial role in the performance of our own actions and in our perception and interpretation of other people’s actions. Attention can be further reasoned about as two components of our awareness: stimulus-driven and goal-directed attention (Corbetta & Shulman, 2002). The former is automatic (Driver, Davis, Ricciardelli, Kidd, Maxwell, & Baron-Cohen, 1999), depends on nature of the stimuli and is present at birth. The latter reflects the intentional allocation of attention to the predetermined location, and is modulated by the current task and context. The former attentional process is of particular importance to the present set of studies, owing largely to infants’ selective attention only to the critical aspects of visual input from the massive range surrounding us. The selectivity of our attentional processes enables us to prepare and plan our actions.

Additionally, our responses are influenced by previous exposure to specific input (‘action priming’). Specifically, action priming takes place at the moment when various social cues allow us to gain information about subsequent actions. For instance, eye gaze (Senju, Csiabra, & Johnson, 2008) can serve as information about future events. Salient social cues of this kind can automatically shift our covert attention in the direction indicated by these cues, even without our eyes moving. This means that before we overtly, i.e. intentionally, shift attention in the direction of the movement, for example by moving our eyes or head, our attention has already adjusted to its spatial location. It has been demonstrated that this covert shift of attention can be captured by the priming paradigm, introduced by Posner in the 1980s. In these studies, reaction time was measured as a marker for covert attentional shifts.
when a person observes a centrally presented cue followed by a peripheral target (Posner, 1980; Posner, 1994). For instance, when we observe a hand pointing left, followed by the peripheral target appearing on the left, our reaction to the target is faster since the target overlaps the direction previously indicated by the hand (congruent pointing). Consequently, our reaction time is slower when the target appears at a different location (incongruent pointing) than in the direction indicated by a central cue (here, the pointing hand). Those shifts of attention are very rapid, occurring within 300 ms after the central cue in adults and within 500 ms in infants (Gredebäck & Daum, 2015).

In infants, the priming paradigm was used to assess their perception and understanding of referential actions performed by others, such as gaze shifts (Farroni, Johnson, Brockbank, & Simion, 2000; Senju, Johnson, & Csibra, 2006), grasping (Daum & Gredebäck, 2011) and pointing (Daum, Ulber, & Gredebäck, 2013; Gredebäck, Melinder, & Daum, 2010). Interestingly, the emergence of a priming effect for specific actions relates to infants’ own action repertoires (Gredebäck & Daum, 2015). Reaching ability is, for example, linked to the onset of the priming effect in response to images of hands performing the same action (Daum & Gredebäck, 2011). A similar relationship has been found with respect to the pointing gesture (Daum et al., 2013). Interestingly, these types of priming effect are not evident in an infant population when actions are performed by inanimate objects, such as mechanical claws (Daum & Gredebäck, 2011) or geometric shapes (Wronski & Daum, 2014). The importance of action priming in action processing and its sensitivity to action experience makes it a perfect tool to use in investigation of the action–perception link at the onset of manual actions.

How do infants learn to understand others?

Many theories have attempted to answer the question of how infants start to make sense of the actions they observe in a complex environment. As mentioned above, a number of theoretical approaches emphasise that our understanding of other people’s actions is mediated by our ability to perform those actions (embodied accounts). This includes the action–perception link (e.g. Sommerville & Woodward, 2010), which has a neural basis, known as mirror system theory (Rizzolatti & Craighero, 2004).

Other accounts of action understanding highlight the importance of repeated observational experience (e.g. Kirkham, Slemmer, & Johnson, 2002). More detailed sections related to those theoretical approaches to action understanding are presented below.
Understanding by doing – embodied account

According to the embodied account of action understanding of our developing motor skills (both gross and manual), what we can do not only gives us access to new kinds of information and new learning opportunities about the environment and actions (Bushnell & Boudreau, 1993) but also changes how we perceive and understand the world and other people’s actions (Hauf, 2007). The theoretical framework of embodied theory of the action–perception link has influenced many scholars and yielded ample empirical evidence that action execution is linked to action perception in adults and infants alike (adults: e.g. Casile, & Giese, 2006; infants: e.g. Hauf, Aschersleben, & Prinz, 2007; Sommerville, Woodward, & Needham, 2005; Longo & Bertenthal, 2006; Adolph, 1997).

In infant populations, many studies have captured the relationship between infants’ age and their action perception. This suggests synchrony in infants’ onset of performance of specific actions and their incipient processing of the same actions performed by others (Needham et al., 2002; Sommerville & Woodward, 2005; Sommerville, Woodward, & Needham, 2006; Galles & Goldman, 1998; Hunnius & Bekkering, 2014; Bertenthal, 1996; Woodward & Gersen, 2006; Kanakogi, & Itakura, 2011; Sommerville, Hildebrand, & Crane, 2008). Thus, during the first year of life, as infants’ ability to produce goal-directed actions is increasing in frequency, their ability to understand others also improves.

It is clear that one critical milestone is the onset of reaching action, at around 4–6 months of age (von Hofsten, 1979). This not only changes infants’ interest in objects (Gibson, & Pick, 2000) and other people’s actions (Hauf et al., 2007), but also facilitates their understanding of goal-directed actions performed by others (e.g. Libertus & Needham, 2010; Sommerville, & Woodward, 2005; Woodward & Guajardo, 2002; Kanakogi & Itakura, 2011; Gredebäck and Melinder, 2010; Cannon et al., 2012; Sommerville et al., 2005; Loucks & Sommerville, 2012; Needham et al., 2002; Skerry et al., 2013).

The link between infants’ own reaching performance and their prediction of others’ reaching actions has been captured by several scholars (Kanakogi & Itakura, 2011). For instance, Falck-Ytter and colleagues (2006) measured 6- and 12-month-olds’ ability to predict the goal when an object was transferred in a bucket. They found that the 12-month-old infants (who at this age usually perform such an action spontaneously) were able to predict the goal of an agent’s action, while younger infants were unable to do so. The link between action production and action perception has been demonstrated in relation to actions other than reaching. For instance, infants are better at predicting feeding actions when they have had the experience of being fed. That is, at 6 months they are successful in predicting the goal of the hand bearing food on a spoon to their mouths, but not when the spoon was self-propelled. The action–perception link was also demonstrated for older infants in relation
to playing with puzzles and placing the pieces in the right position (Gredebäck & Kochukhova, 2010).

Regarding gross motor skills, it has been demonstrated that self-produced locomotion changes our ways of perceiving and reacting to the surrounding world (Adolph, 2008). Children who can crawl, or self-locomote using walkers, are more likely to show an increase in heart rate or in avoidance behaviour when they are placed beside the edge of a visual cliff (Bertenthal, Campos, & Barrett, 1984). The onset of self-locomotion also changes infants’ ability to identify self-propelled motion (Cicchino & Rakison, 2008).

The behavioural studies above show a relationship between action and perception, but it was only after the seminal discovery of mirror neurons that the action–perception link gained a very strong foundation at a neural basis (Rizzolatti & Craighero, 2004).

Understanding by simulating action
According to simulation theory (also called ‘mirror neuron theory’), the actions we observe are directly and automatically mapped onto our own motor representation of this action. Observing and producing the actions recruit the same internal representations (Rizzolatti, Fogassi, & Gallese, 2001). This overlap of recruited motor-system neurons facilitates recognition of observed motor actions via internal motor simulation (Gallese & Sinigaglia, 2011; Fogassi et al., 2005). Neurophysiological studies support the involvement of the motor system in action observation, and show that experience or expertise can modulate neural activation within mirror neurons (Southgate, Johnson, Karoui, & Csibra, 2010; Stapel, Hunnius, van Elk, & Bekkering, 2010; Nyström, 2008; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). For instance, in studies on adults, it has been demonstrated that proficiency in dance (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005), piano playing (Haslinger et al., 2005) and basketball (Aglioti, Cesari, Romani, & Urgesi, 2008) correlates with activation during observation of these actions. Data on infants, as on adults, support the link between people’s own experience and motor activation when they observe others’ actions. This relationship has, for example, been found with regard to stronger motor brain activity in 14- to 16-month-old children when they observe walking actions related to their own walking abilities (van Elk et al., 2008).

Understanding by observing
The role of learning from observation in action understanding cannot be neglected. Clearly, infants can also understand actions they cannot yet perform. At 6 months, for example, they can predict food (Kochukhova & Gredeback,

---

1 See page 28 for a description of mirror neurons.
or a cup being brought to the mouth, although at this age they have not performed these actions themselves (Hunnius, & Bekkering, 2010). It is suggested that infants learn and understand the actions of others by observing how the actions are performed and detecting regularities from structured input, which is known as ‘statistical learning’ (e.g. Brass & Heyes, 2005).

**Statistical learning**
According to this view, action understanding is based on goal identification, which in turn is based on various cues. One such cue may be action familiarity, based on the frequency of observed action. From birth, infants are sensitive to statistical regularities among events in the environment that happen in conjunction (Hunnius & Bekkering, 2010; Baldwin, Andersson, Saffran, & Meyer, 2008). When infants repeatedly observe robust social cues (face, eyes, hands, movements), and pay attention to what people around them are doing, they learn about the goals of these actions, the means to achieve the goals, and their action effects (Kirkham et al., 2012). Subsequently, observed and learned regularities facilitate action understanding and prediction of the outcome of actions (e.g. Aslin & Newport, 2012; Cicchino, Aslin, & Rakison, 2011; Henrichs, Elsner, Elsner, Wilkinson, & Gredebäck, 2014).

Originally, this view came mostly from studies on language acquisition that delivered evidence that infants can detect words from fluent speech based on the statistical relationship between neighbouring speech sounds (e.g. Saffran, Aslin, & Newport, 1996). Recently it has been accepted that the segmentation skill that is helpful when learning language seems to be also important and useful for action understanding. More specifically, it is suggested that statistical regularities can facilitate identification of segmental structure of actions that co-occur more frequently than others. The sequential probabilities of small acts are causally related and in turn are more easily understood and predicted (Baldwin et al., 2008). This also suggests that actions that we attend more frequently should be easier to understand. Findings reported by Henrichs et al. (2014) demonstrated that goal anticipation was related to the frequency of visually observed hand movements towards the goal. More specifically, when presented with a choice of three goals, 12-month-old infants expected the hand to move towards the previous most-frequent goal. Green et al. (2016) also found that action understanding is influenced by the cultural context that infants experience visually every day (Green, Li, Lockman, & Gredebäck, 2016).

Together, these findings indicate that the frequency of observed events has a significant bearing on our action understanding. Observed events facilitate our understanding of actions also when they are outside our motor repertoire; that is, we can make sense of actions even if we have not performed them before.
The role of motor experience in linking action and perception

In the previous sections of this thesis, many of the studies presented showed evidence that one’s own action performance is crucial for the development of social perception. Many studies assert the synchronous onset of action and perception, without clearly capturing the causal relationship between the two. In fact, causal evidence is hard to come by. Many studies meet the challenge of disentangling visual from motor experience in order to capture the unique contributions of our own proficiency in our understanding of others. This is because when we perform actions, we also automatically observe them (Flanagan & Johansson, 2003; Rosander & von Hofsten, 2011).

Thus, it is difficult to know whether a change in action processing is due to motor experience or observation, or to general maturation (cognitive and perceptual). The causal relationship between infants’ own performance and understanding can be also challenging to capture when age is used as a function of maturation, because age is often confounded with experience. Accordingly, there are substantial differences in motor skills even among infants of the same age. To minimize this type of confound, some studies attempted to capture the role of self-produced grasping actions through intervention by means of “sticky mittens”.

‘Sticky mittens’ experience

One way to capture the role of experience in perception is to alter the experience of action before its actual onset. To modify reaching experience, some scholars have come up with an ingenious idea: to provide non-reaching infants with specially designed mittens that allow them to obtain the objects. The mittens are equipped with Velcro, enabling the objects to adhere to them on contact (e.g. Libertus & Needham, 2010, 2011; Needham, Barrett, & Peterman, 2002; Sommerville et al., 2005). The study by Needham et al. (2002), for example demonstrates that when infants are provided with early reaching experience, using Velcro-covered mittens, their interest in objects and exploration skills can be enhanced. In gaining experience of grasping with the aid of the mittens, of course, infants not only receive training in manual reaching but they also gain visual experience of this action. This means that the infants’ active experience of using the mittens may also have provided visual information about the action’s goal-directedness. And so, it remains unclear which exact form of experience, visual or active, enhances their understanding of the action the most.

This very question has been tackled in a study by Sommerville et al. (2005) with a similar experimental paradigm. One group of infants had a brief active reaching experience with the aid of mittens while the comparison group was given only the opportunity to observe the same action performance passively.
The authors thereby separated active from passive experience and were able to measure the influence of both on action understanding. For the active experience, they gave pre-reaching infants 200 seconds to interact with the toys placed in front of them. Infants could move the objects by swiping or batting them. When the infant did so, the objects adhered to the mitten so that the infant could raise the object. Infants were then given several seconds with the lifted object before the experimenter removed it and placed it in front of the infant, to make it possible to repeat the task. In the observation-only group, the infants observed the experimenter reaching for the objects but they were unable to explore the objects themselves. Following this procedure, all the infants took part in a visual habituation procedure, during which they watched the hand reaching for one of the two objects. When the infants had become habituated (their time spent watching decreased), the position of the objects was switched so that the children could observe the hand reaching for a new goal, or for the same goal but with a new path towards this goal. The results demonstrated that short active experience, but not passive observation, provided the learning outcome in which infants dishabituated to a new goal structure of action. Further, the findings suggest that rather than general maturation related to infants’ age active experience of self-produced reaching promotes action understanding (Sommerville et al., 2005). Additionally, Gerson and Woodward (2014) demonstrated that even if the amount of observational experience was based on individual infants’ self-produced activity during mittens training, infants that could actively take a part in object exploration showed selective attention to the events with goal-change in other people’s grasping actions which was not the case for the infants that only observed the same action.

Similar findings have been reported in the study examining tool-use training in older infants. Ten-month-old infants who had been actively trained to use a cane to pull a toy closer, and thereby reaching it, showed evidence of representing the means–ends goal structure when they observed another person performing the same action. The group of infants that did not receive the active training but only observed the experimenter using the cane to pull the toy did not show the same ability, suggesting that first-hand experience is critical for action understanding (Sommerville et al., 2008).

Enhanced sensitivity to goal-directed actions after short active training was also found in the study by Hauf and colleagues where active engagement performing actions increased infants’ visual preference and interest in previously produced actions (Hauf et al., 2007).

Most of the above studies assessed only the action processing that took place directly after the training. However, there is one exception, which is the study where the effect of active training was investigated 12 months later and the results demonstrated long-term effects in object exploration (Libertus, Joh, & Needham, 2016). Although the above evidence indicates that self-produced
actions seem to be more powerful in their influence on action understanding, the nature of this effect does not afford insights on the neural correlates involved in this process.

Neural processing of social actions

Despite methodological and technological advances in the past few decades, understanding of the neural mechanisms of social perception is still an extreme challenge. Researching the developing brain is especially difficult because the use of neuroimaging methods that can be applied to healthy children is limited due to ethical and also practical reasons.

Various methodologies (mostly functional magnetic resonance imaging, fMRI) used in adults to investigate neural processing of social perception made it possible to pinpoint the brain areas involved in processing a wide range of social cues, such as social actions, biological motion, goal-directed action, eye gaze. The cortical region implicated in processing social stimuli proved to be fairly extensive, since it includes the ventral premotor cortex (with the inferior frontal gyrus), regions of parietal and temporal cortex with the inferior parietal lobule (IPL), superior temporal sulcus (STS), posterior cingulate cortex (PCC) and temporo-parietal junction (TPJ) (Lloyd-Fox, Wu, Richards, Elwell, & Johansson, 2013). Additionally, it is suggested that the mirror neurons, which are distributed over several cortical regions, are a missing link in our understanding of the neural processing of social cognition, and in our processing of action understanding through a direct matching process (Rizzolatti & Craighero, 2004). The mirror neuron areas that are particularly relevant to this thesis are described below.

Superior temporal sulcus

The STS area has been found to be involved in processing of faces, gaze direction and biological motion. It was found to be activated not only when processing the body parts in movement, dynamic social information but also when presented with static images depicting a face or human body and dynamic social information (Allison, Puce, & McCarthy, 2000; Gobbini & Haxby, 2007; Watson, Latinus, Charest, Crabbe, Belin, 2014). The STS area has been also found to respond preferentially to movements of the hand. The extensive studies with a use of single cell recording on monkeys and positron emission tomography (PET) on humans, showed that STS is very responsive to the grasping action especially when a hand is directed towards a particular object. This sensitivity to the goal could also indicate the involvement of STS in processing intentional actions (Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Pelphrey, Morris, & McCarthy, 2004; Jastrow, Popivanov, Vogels, Vanduffel, & Orban, 2012). Interestingly, the STS area has been also found to be
involved in processing affective speech (Wildgruber, Ackerman, Kreifelts, & Ethofer, 2006) and sign language in deaf participants when producing meaningful signs and sentences in comparison to nonsense gestures (Neville et al., 1998). This activation was only present in participants that could use the sign language themselves (Bonda, Petrides, Ostry, & Evans, 1996), indicating that the STS area is sensitive to communicative and meaningful hand movements.

With regard to action understanding, the STS has been found to exhibit mirror neuron properties related to the mirror neuron system (MNS) (Keysers, & Perrett 2004; van Overwalle & Beatens, 2009). According to Iacoboni et al. (1999), there is a strong association between the STS and the MNS in relation to action understanding. In particular, the STS is responsible for the initial coding of the action in order to subsequently feed the information forward into the primary MNS circuitry for more complex processing (Jellema, Baker, Wicker, & Perrett, 2000).

The involvement of STS in action processing has been further implicated in developmental literature. Research by Lloyd-Fox et al. (2013), who used near-infrared spectroscopy to study the action–perception link in infants found cortical activation of this link in the posterior STS and the temporal-parietal junction region. Although most of the insights on neural origins of social perception are based on adult data, infant population can also deliver important findings about the neural mechanisms involved in processing of socially rich stimuli.

Mirror neuron system

The Mirror Neurons (MNS) are visuomotor neurons that were originally discovered using single-cell recording in macaque monkeys. It was found in ventral premotor cortex, particularly in area F5 (Rizzolatti, Fogassi, & Gallese, 2001b; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). It was demonstrated that these neurons fire not only when the monkeys performed reaching actions, but also when they observed object-related actions performed by others. Mirror neurons have been found to be particularly attuned to goal-directed actions, i.e. they fire when a monkey observes a hand grasping an object, but not when it observes a mimicked grasp. Merely the knowledge that the goal is within reach causes the mirror neurons to fire when monkeys observe a hand reaching for an occluded object (Fadiga & Craighero, 2004).

This discovery had a huge impact on research on social cognition (Gallese, 2009) since it suggested that the mirror neurons could be a neural basis for the relationship between action production and action understanding.

For ethical reasons, single-cell recording is not typically performed when studying humans (an exception is Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). However, thanks to other neurophysiological methods (TMS,
EEG; MEG, fMRI, PET), contemporary literature has collected very strong
evidence for the presence of mirror neurons in the human brain (e.g. Iacoboni & Dapretto, 2006; Gazzola & Keysers, 2008; Rizzolatti & Sinigaglia, 2016).
The human MNS system has been found in the inferior frontal gyrus (e.g. Fadiga et al., 1995); as well as in a broad network of brain regions including
the inferior parietal lobule, the superior temporal sulcus and regions of the
limbic system (Oberman, Pineda, & Ramachandran, 2007; Iacoboni et al.,
2001; Wizker et al., 2003; Molenberghs, Cunnington, & Mattingley, 2012).
Together, these areas form the mirror neuron system (MNS).

The MNS has implications for social cognition, especially action under-
standing (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Rizzolatti et al., 1996b;
Decety et al., 1997; Muthukumaraswamy & Johnson, 2004; Iacoboni & Mazzotta, 2007), imitation (Buccino et al., 2004; Iacoboni, Woods, Brass, & Bekkering, 1999), emotional understanding, empathy and theory of mind
(Iacoboni, 2009 for review).

In contrast to monkey mirror neurons, human mirror neurons fire when we
observe mimicked actions (Fadiga & Craighero, 2004; Warreyn et al., 2013)
and seem to be more strongly activated during processing of social interac-
tions (Oberman et al., 2007). It has therefore been suggested that they may be
involved in processing of gestures and non-verbal communication. Moreover,
the mirror neurons respond selectively to actions that belong to the observer’s
own repertoire (Cross, Hamilton Grafton, 2006). Accordingly, it has been sug-
gested that our own experience of actions facilitates our understanding of oth-
ers, and that this process is mediated by mirror neurons. The evidence for this
view has been found in studies of adults (e.g. Calvo-Merino et al., 2005; Cross
et al., 2006) and of infants (e.g. Nyström, Ljunghammar, Rosander, & von
Southgate, Johnson, Karoui, & Csibra, 2010; Southgate, Johnson, Osborne, &

The MNS activity in infancy is indexed by the $\mu$ frequency band, which
is a marker of motor cortex, and has been found during several motor actions.
Examples are observation of goal-directed versus non-goal-directed actions
(Nyström, Ljunghammar, Rosander, & von Hofsten, 2011), and perception
and production of reaching actions where motor proficiency in grasping is
associated with the $\mu$ response to observed and performed grasping
(Southgate et al., 2010). Another example in the above-mentioned study is
that infants’ individual crawling proficiency was found to be strongly related
to the neural activity measured when infants observed other children crawling,
in contrast to when they watched them walking (van Elk et al., 2008).
Infants’ brain activity for social perception: EEG and ERPs

Most insights into infants’ brain processes come from studies using electroencephalography (EEG), and the same applies to this thesis. This method is particularly valuable for testing a young population because it is non-invasive and relatively easy to use (Hoehl & Striano, 2010). An EEG measures electrical activity in the brain and using multiple sensors (high-density EEG) applied to the child’s scalp, voltage fluctuations allow the signal to be collected from the entire scalp simultaneously (Luck, 2005). Although EEG is suitable for use in infants, testing such young population is not free from challenges when it comes to data collection (Thierry, 2005). In particular, the measurement is highly sensitive to movement, which is unavoidable in a young population, including subtle movements of the face (opening the mouth, blinking) or neck (when infants are not sitting properly), resulting in artefact-contaminated data.

Research applications focus on two types of data: event-related potentials (ERPs) and the spectral content of EEG, i.e. frequencies (event-related oscillations). ERPs can be measured from the beginning of life, which makes them ideal for researching the developmental course of neural processes (DeBoer, Scott, & Nelson, 2007). The big advantage of this method is its excellent temporal resolution, which reflects time-locked changes in electrical activity in response to a specific event, such as the onset of the stimulus. ERPs are recorded from repeated trials that are subsequently averaged to eliminate background noise that is unrelated to the stimulus (Banaschewski & Brandeis, 2007). ERPs can be elicited as a response to sensory, motor or cognitive events, and reflect the evaluation of the presented stimulus. The averaged waveform is assessed in terms of latency, amplitude, polarity and function (Sur & Sinha, 2009; Banaschewski & Brandeis, 2007). ERPs have been found to have variable properties in the course of development: that is, their latency and amplitude change. The ERP components most relevant to the work in this thesis are the P400 and the Nc, which are described in more detail in the following two sections.

**P400**

The P400 is a positive deflection that is most prominent over lateral posterior electrodes (de Haan, Johnson, & Halit, 2003), occurring around 300–600 ms after the stimulus onset. The P400 has been found to index socially relevant stimuli, e.g. biological motion (Reid, Hoehl, Landt, & Striano, 2008), gaze direction (Senju et al., 2008), pointing (Melinder, Konijnenberg, Hermansen, Daum, & Gredebäck, 2015; Gredebäck, Melinder, & Daum 2010), faces, pro-social behaviours (Gredebäck et al., 2015) and chasing (Galazka, Bakker, & Gredebäck, 2015). In these studies, the P400 was found to be larger in amplitude for the functional and goal-directed actions. For example, congruent pointing compared with incongruent pointing (e.g. Gredebäck et al., 2010) or gaze towards rather than directed away from the object (Senju et al., 2008).
This component has been also found to be functionally similar to the adult’s N170 component, which is sensitive to faces. With regard to the analogies to the adult’s N170, the peak of the P400 is sensitive for faces in comparison to objects (de Haan, Nelson, 1999; Taylor, & Baldeweg, 2002; de Haan, Pascalis, & Johnson, 2002) emotional expressions of faces (Leppänen, Moulson, Vogel-Farley, & Nelson, 2007) as well as face directionality (e.g. de Haan et al., 2002; Otsuka, Nakato, Kanazawa, Yamaguchi, Watanabe, & Kakigi, 2006; Balas et al., 2010). In the study by Elsabbagh et al. (2012), the P400 indicated differences in dynamic gaze-shift processing and face processing mechanisms between typically developing children and children at risk for autism within the first year of life. This may suggest the possible application of this ERP component to detect individuals at risk for autism (Elsabbagh et al., 2012).

In sum, the P400 is a neural component that is very sensitive to a range of socially-relevant stimuli. Its characteristics and potential detection early in life make it well suited for the investigation of goal-directed actions and gesture processing in this thesis.

**Negative component – Nc**

The Nc component is one of the most researched infant ERP. This component is a negative deflection, elicited at around 400 ms – 800 ms in the first year of life, mostly prominent in frontal and central electrodes (Csibra, Kushnerenko, & Grossmann, 2008). The temporal characteristic may change during the developmental course, with 1000–1200 at the beginning of life to as fast as 400–500 ms at around 2 years of age (Goldman, Shapiro, & Nelson, 2004). The Nc has been thought of as an attentional component, sensitive to stimulus familiarity (Snyder, Webb, & Nelson, 2002), infrequent or unexpected stimulus (Nikkel & Karrer, 1994) or saliency of the stimulus (Nelson & de Haan, 1996). It has been also suggested that the infant Nc might express recognition processes (Ackles & Cook, 2007) and be involved in processing emotional information (Nelson & de Haan, 1996). Like the P400, the Nc has been found to be sensitive to gaze direction, and when the gaze is away from the object it elicits more negativity and later latencies than the gaze towards the object (Hoehl, Reid, Mooney, & Striano, 2008). In sum, the Nc component reflects infants’ allocation of attention (Richards, 2003). This characteristic makes it particularly interesting for Study II in this thesis, since infants’ attentional processes can be modulated by their experience of a newly-learnt action. Thus, this component may possibly be involved in encoding of goal-directed actions following brief experience of such actions.
Aim of the thesis

The overarching aim of this thesis is to gain deeper insights into how manual actions shape the way we perceive actions of others. More specifically, I investigate which neural correlates reflect understanding of manual actions and gestures. As reviewed in the introduction, several scholars have demonstrated a mutual relationship between action and perception. However, the neural mechanisms involved in the processing of this link at the onset of the grasping action and the give-me gesture are still unknown. Additionally, the causal effects between infants’ own active experience and their observational experience of manual actions, and perception of the same action, are still not fully understood. To address those issues, EEG methodology is used to measure event-related potentials in the three empirical studies comprising this thesis.

The objective of Study I was to investigate neural correlates involved in the perception of manual goal-directed actions. This investigation aimed to capture neural changes linked to experience of the grasping action during the most critical period, i.e. when infants start to engage in functional grasping actions. Additionally, Study I investigated whether newly gained experience of grasping action using a power grasp could be generalised to an understanding of other types of goal-directed grasping action, such as a pincer grasp, that is not normally part of 6-month-olds’ motor repertoire.

Deriving from findings in Study I, as well as behavioural evidence that short training with grasping in pre-reaching infants facilitates actions and objects processing (e.g. Libertus & Needham, 2010; Needham et al., 2002), Study II focused on capturing ERPs for action perception time-locked to infants’ onset of grasping experience. To access changes in neural processing that are tightly linked to action experience, infants that do not grasp yet (4 months old) underwent training sessions involving either passive observation or active performance. Study II also investigated which type of experience (active or observational) is more powerful to alert the change in neural processing of goal-directed actions. Its design allowed discussion of the causal relationship between active versus passive experience and understanding of goal-directed actions.

Human manual actions are essential for social cognition and, with developmental advances, start to serve a communicative purpose. The aim of Study
III was to investigate the neural underpinnings of manual gestures. The findings are discussed in relation to the importance of infants’ own experience of gesture production in their understanding of and compliance with gestures.
Methods

Participants
All subjects were recruited from the existing participant listing of the Uppsala Child and Baby Lab (UCBL). The list includes all the families who have voluntarily indicated their interest in taking part in research projects, with their child, after receiving an informational letter from the UCBL at the time when the child turns 5 months. From these registries, children are selected according to their age and study selection criteria. In all three studies described here, the inclusion criteria included no history of pre- and perinatal complications, full-term gestation period (>37 weeks), and no indications of neurological abnormalities or atypical development. When the child fulfilled these criteria, and matched the age required in the study, the parents were contacted by phone and informed of their child’s eligibility for the study. During the phone conversation, the purpose and procedure of the study were explained to the parents. Following their agreement to take part in the study, the appointment for the lab visit was made. On arrival at the lab, the parents were once more given the description of the study, the procedure was clarified and, before it started, they were asked to sign the consent form. At any time before or during the experimental session, parents could opt not to participate in the study.

The infants participating in the study were excluded from the final analysis if they did not provide the data owing to fussiness, crying or a general lack of attention to the stimuli. Every participating family received a voucher to a value of approximately EUR 10 for their participation. All the studies were approved by the Regional Ethical Committee and conducted according to ethical standards specified in the 1964 Declaration of Helsinki.

Study I
Eighty-three infants were tested, of whom 23 were excluded from the final analysis owing to fussiness or having fewer than 15 artefact-free trials per condition. The final sample, comprising 66 children, was divided into three experimental groups. Experiment 1 included 14 4-month-olds (8 girls, mean age 128 days, SD = 6 days), and 14 6-month-olds (7 girls, mean age 186 days, SD = 3 days). For Experiment 2, there were 24 subjects (12 girls, mean age 154 days, SD = 6 days), and these 5-month-olds were divided into two subgroups, depending on their grasping ability (low grasping score: 12 infants, 5 girls, mean age 152 days, SD = 6 days; high grasping score: 12 infants, 7 girls,
mean age 150 days, SD = 6 days). The two groups did not differ in age, \( t(11)=0.79, p=0.444 \). Experiment 3 included 14 (9 girls, mean age 181 days, SD = 4 days) 6-month-old children.

**Study II**

In Study II, 59 infants were tested, of whom 29 were excluded from the final analysis because they did not meet the minimum criteria for artefact-free trials (\( n < 10 \) trials/condition) owing to fussiness or excessive movements. The remaining 30 (16 girls) 4-month-old infants were included in the final sample. In Experiment 1, 15 infants (9 girls, mean age 129 days, SD = 5 days), and in Experiment 2, 15 infants (7 girls, mean age 126 days, SD = 7 days) were included.

**Study III**

In total, 29 9-month-old infants were included (15 girls, mean age 8 months and 28 days, SD = 6 days). An additional 30 infants participated in the study but were not included in the final analysis because they did not meet the minimum criteria for artefact-free trials (\( n < 10 \) trials/condition) owing to fussiness, intense movement or technical problems.

In all three studies the attrition rate was high (41%), but it was comparable among the studies. This high dropout rate has been found to be typical in studies on ERP responses at a very early age (Stets, Stahl, & Reid, 2012). This is due to infants’ short attention span, movement artefacts, possible tiredness from performing the experimental procedure and fussiness for different reasons that cannot be clearly communicated.

**Stimuli**

In all three studies, the stimuli were presented using the E-Prime 2.0, E-Studio software (Psychology Software Tools, Inc., Pittsburgh, PA).

**Studies I and II**

Infants watched the stimulus material on a 17-inch computer screen that was rotated 90°. Every child observed two conditions: congruent (a hand directed towards an object) and incongruent (a hand directed away from the object). The trials were presented in randomised order. In both conditions, each trial began with 100 ms of two rectangles (6 horizontal times 5 vertical visual degrees) that appeared at the upper and lower part of the screen, 13 vertical degrees apart. Subsequently, a fixation cross was presented at the centre of the screen and remained there for the next 1300–1750 ms. When the fixation cross disappeared, a target appeared inside one of the rectangles for 240 ms. The trial ended with the 1000 ms presentation of the picture of the hand, formed a
power grasp, directed towards (congruent condition) or away from (incongruent condition) the rectangle where the target had previously been depicted (Figure 1). In Experiment 3 of Study I, ERP responses were measured for the congruent and incongruent hands formed in a precision grasp (unlike Experiments 1 and 2, where the power grasp was examined). The picture of the grasping hand was changed and the object size was adjusted to the distance between the thumb and the index finger. For all the experiments in Studies I and II, the order of the pictures in the stimuli was the same: rectangles – fixation cross – target – hand.

Figure 1. Stimulus sequence in the congruent condition for Study 1, Experiments 1 and 2. The times in the top left corner of each picture indicate the duration of presentation.

Note on the spatial cueing paradigm
Deriving from the idea that covert attention plays an important role in online encoding of action goals, the design for the stimuli in Studies I and II was based on the Posner paradigm (Posner, 1980), which measures reaction time to presented cues. The reaction time thus serves as a marker for covert attentional shifts when the infant is observing a centrally presented cue followed by a peripheral target. Unlike the typical Posner paradigm, in the stimuli of Studies I and II the order of the presented cue and the target is reversed. That is, a ball (peripheral target) is presented prior to the appearance of the hand (centrally located cue). The hand specifies the direction of the action as it relates to the ball, in either a congruent (graspable) or an incongruent (non-
graspable) manner. As in our study, this switch was used in other infant EEG studies examining gaze direction (Senju, Johnson, & Csibra, 2006) and pointing actions (Gredebäck & Melinder, 2010), as well as eye tracking and grasping (Bertenthal et al., 2014; Daum & Gredebäck, 2011; Daum et al., 2013). This specific order of presentation was implemented to access the neural response to the hand that, depending on the direction (congruent or incongruent), indicates the goal of the action.

We believe that independently of the order of the stimuli, attentional processes play an important part in processing the presented action, and presenting the ball as a context for the hand highlights infants’ attention to the location of the cue. Once the ball (peripheral target) disappears, the infant’s attention is modulated by the direction of the hand. Unlike Studies I and II, Study III, did not use the attentional paradigm. This is because the give-me gesture is a manual action that does not need closeness to the object and, even without this proximity, conveys meaning. Since we were interested in neural correlates for the give-me gesture itself, the gestures were directed towards the observing infant.

Study III

The infants were presented with the stimulus (20.7 x 16.5 visual degrees) on the 17-inch computer screen. The stimulus (Figure 2) consisted of the hand appearing in the middle of a grey background for 1000 ms, followed by the fixation cross presented for 100–300 ms. The hand was 5 x 16 visual degrees in size, and was rotated differently depending on the condition. In the experimental condition the hand was presented with a palm facing upward, that is, expressing a give-me gesture. A control condition depicted the same hand rotated 90 degrees, effectively eliminating the gesture’s communicative intention. Each child watched both conditions in randomised order, subject to the constraint of a maximum of three repetitions of the same stimulus.

*Figure 2. Stimulus for the give-me gesture condition (left) and a control hand (right).*
General procedure

All three studies were conducted in the Uppsala Child and Baby Lab at the Department of Psychology at Uppsala University, Sweden. Every infant was accompanied by a parent throughout the time in the lab. Before the experimental procedure began, the parent was given an explanation about the purpose of the study and received instructions about the procedure, focusing on what was expected of him or her during the testing. In the event that the caregivers had additional questions about the scientific purpose of the study that had occurred to them during the testing, they were allowed to ask them at the end of the procedure. The testing began after the parent signed the consent form. The infant was then given a short warm-up with the experimenter, to enable him or her to start feeling comfortable and safe in the lab environment.

In all three studies, EEG was used to record the infants’ ERPs. Before the EEG recording, the geodesic net was applied to the infant’s head and the electrodes were checked for proper contact with the scalp. In Study I, Experiment 2, and also in Studies II and III, additional tests besides the EEG were performed. A detailed description of these tests is presented below.

During the EEG recording, the infants were placed on the parent’s lap in a way that gave them maximum comfort and posture stability. After application of the net, the infants were placed in front of the computer screen, at a distance of 60 cm. To minimise visual distraction, light conditions were kept constant. The amount of light was restricted and a curtain separated the experimenter and EEG equipment from the child and parent. The experimenter monitored the infant’s attention to the stimuli on an additional computer screen used to display the infant’s face. If the child was not paying attention to the presentation, an attention-grabbing picture, with accompanying sounds, was presented until the infant became interested again in looking at the screen. If a longer break was necessary, the presentation was paused and the infant was turned away from the computer screen to encourage brief playing with toys or to be comforted by the parent. The experiment was run as long as the child’s attention to the stimuli was retained. The tests before and after the EEG recording are presented below.

Study I

In all three Experiments the EEG net was applied before infants were presented with sequences of pictures of a human hand and an object (see page 35 - 36 for a detailed description). Additionally, in Experiments 2 and 3, prior to EEG recording, infants’ grasping skills were assessed. In Experiment 2, the grasping test was designed to divide the sample into two groups of infants – those who were already advanced in their grasping ability (‘proficient graspers’) and those who were still developing the functional grasping skill (‘non-proficient graspers’). The total duration of the grasping test did not exceed 5 min. During this time, we video-recorded the performance of up to three
grasps. The test started when the child was presented with three rubber toys (all measuring 5 x 5 cm, the size that allows a comfortable grasp). The experimenter offered the child one toy at a time, on the palm of the hand, with an outstretched arm. The experimenter’s hand stopped in front of the child at a distance that enabled the child to grasp the toy. The experimenter remained in this position until the child initiated a grasping motion, but not longer than 10 s. The time was measured from the moment when the child’s attention was directed to the object. If the child did not commence the grasp within the maximum time frame, the experimenter withdrew the toy and started the procedure again with a new object. After three trials, the procedure was terminated.

The videos were coded afterwards with a focus on three components: the extension of the infant’s arm towards the object, the grip of the object and the ability to hold the object. The components were scored with 0, 0.5 or 1 point. Score 0 indicated that the child did not perform any movement that would help to achieve the goal. The 0.5-point score was granted when the child initiated the movement towards the toy, touched it or even grasped it, but the incorrect hand aperture did not allow lifting of the toy. Finally, the child received 1 point when the action was performed successfully, that is, when the child moved a hand towards the object, used the correct hand aperture and successfully lifted up the toy. The maximum attainable score was therefore 3 points for this subscale. In order to gain the information on grasping skills of each child in their daily behaviour, the caregivers were asked to score their child’s grasping performance before the visit in the lab. The child could obtain additional 0–3 points from the parent, which result in a total of 6 points. According to the final score, the children were divided into two groups. Infants who scored a total of 0–3 points were assigned to the ‘non-proficient graspers’ group and those with 3.5–6 points were allocated to the ‘proficient graspers’ group. The rational for such division was motivated by possible underperformance in the lab condition but also by protecting the possibility to be allocated in the ‘proficient group’ based solely on the parental report.

In Experiment 3, infants were screened for their reaching skills in order to validate the previous findings that indicated that infants cannot perform the precision grasp before the age of 9 months (Butterworth, Verweij, and Hopkins, 1997). Infants performed three power grasps and three precision grasps with the same procedure as in Experiment 2. In the precision grasp tasks, infants were supposed to grasp small objects that force the use of precision grasp in order to lift them up.

**Study II**

Prior to the EEG recording, infants participated in the Active experience task (Experiment 1) or passive observation task (Experiment 2) (Figure 3). During the active task, the infants were encouraged to actively reach for the objects while they were seated on their caregiver’s lap, positioned in front of the table.
Before the start of the procedure, a pair of custom-made mittens, equipped with Velcro on the palm side, were put on the infants’ hands. The mittens had previously been used in other studies (Needham, Barrett, & Peterman, 2002; Sommerville et al., 2005). Infants were then presented with nine custom-made balls (3 x 3 cm) covered with the corresponding Velcro side, which allowed them to stick to the mittens when touched. To give an opportunity to experience the grasping action, one ball at a time was placed on the table in front of the infant, who was encouraged to reach for it. Once the ball was touched, the child was able to lift it.

The session was video-recorded and coded for the number of goal-directed actions. The goal-directed action was coded when the infant’s action resulted in contact with the object, which was subsequently lifted from the table, and when the infant’s visual fixation on the object preceding the action had not exceeded 3 seconds. We computed the average number of goal-directed actions in order to use the same number of goal-directed actions in Experiment 2. In total, each infant had 240 seconds to interact with the balls and, and during this time, performed an average of 9.7 goal-directed actions. In Experiment 2, the infants did not engage in any reaching activity; instead, they observed goal-directed actions performed by the experimenter, who performed the number of grasps that matched the average of successful grasps previously captured in Experiment 1.

![Figure 3](image-url)

*Figure 3.* The left-hand section denotes the type of training used in Experiments 1 and 2. In both instances, infants were presented with the same stimulus set during EEG recording, demonstrated in the right-hand section of the figure. The numbers mark the duration of each image in the stimulus sequence (in milliseconds).
Study III
The Behavioural Request Procedure from the Early Social and Communicative Scale (Mundy et al., 2003) was used to assess infants’ behavioural responses to the give-me gesture after the EEG recording. The procedure began with the experimenter presenting three rubber toys (5x5 cm) to the infant one at a time. Subsequently, the toy was placed on the table in front of the child and after 3 seconds the experimenter verbally requested the toys with the phrase “Give it to me.” The experimenter waited 3 seconds and, if the child did not initiate any action, repeated the verbal request while performing the non-verbal gesture (the palm up, directed to the child, indicating the give-me request). This procedure was repeated for each toy. The whole task did not exceed 5 min and was performed after the EEG recording. The performance was coded for the number of times the child handed over a requested toy.

Additionally, parents were asked if they have observed their child producing or responding to the give-me gesture outside of the laboratory.

Apparatus
In all studies, the ERP signals were measured. We used 128-channel HydroCel Geodesic Sensor Net with net size appropriate for the infants’ age. The signal was vertex-referenced and amplified (EGI Net Amps 300 amplifier, Electric Geodesic, Eugene, OR), with a low-pass filter of 100 Hz sampled at 250 Hz and stored for offline analysis. The EEG signal was digitally filtered (0.5–25 Hz) and segmented around tagged events. The electrodes from the most anterior and posterior areas were not included in the final analysis because of general high noise caused by poor contact with the scalp.

Data analysis
In all three studies, after recording, the data were segmented (see below for the specification for each study) and inspected manually. The electrodes contaminated with artefacts were rejected and the data from the missing channels were interpolated from the surrounding electrodes. If trials contained more than 10% of the artefact-contaminated electrodes, they were rejected from the final analysis (standard procedure in infant ERP work; see Hoehl & Wahl, 2012). The criteria for inclusion, in the final analysis, were a minimum of 15 trials per condition in Study I, and a minimum of 10 trials per condition in Study II and III. The data were baseline-corrected and the individual data were averaged to finally create the grand average, that is, the average from all the individual subjects who met the criteria for inclusion.
Study I

Data were segmented from 550 ms before the appearance of the hand (including the last 160 ms of the empty rectangles with the fixation cross and 240 ms of the target with the fixation cross) until 900 ms after the hand was presented.

Further analyses were performed on five areas: lower occipital, electrode numbers 74, 75 (Oz), 82; left posterior temporal, electrode numbers 65, 66, 67, 69, 70 (01), 71; right posterior temporal, electrode numbers 76, 77, 83 (02), 84, 89, 90; left central, electrode numbers 35, 29, 30, 36, 41, 42, 37; and right central, electrode numbers 87, 93, 103, 104 (C4), 105, 110, 111; with a time interval ranging from 300 to 600 ms (labelled P400) after the onset of the stimulus. The choice of electrodes was based on a similar procedure used in the study by Gredebäck et al. (2010).

In Experiment 1, the average amplitudes within the selected time window were statistically compared in a 2x2x2 repeated measures analysis of variance (ANOVA), with condition (congruent, incongruent) and lateralisation (left, right) as within-subject factors and age (4 and 6 months) as the between-subject factor.

In Experiment 2, the average amplitudes within the selected time window were statistically compared in a 2x2x2 repeated measures ANOVA, with condition (congruent, incongruent) and lateralisation (left, right) as within-subject factors and grasping proficiency (good graspers, non-graspers) as the between-subject factor.

In Experiment 3, the average amplitudes within the selected time window were statistically compared in a 2x2 repeated measures ANOVA, with condition (congruent, incongruent) and lateralisation (left, right) as within-subject factors.

Study II

The data were segmented from 550 ms before the appearance of the hand (including the last 160 ms of the empty rectangles with the fixation cross and the 240-ms presentation of the object) until 900 ms after the hand was presented. As in Study I, the analyses were performed on six channel areas: lower occipital, electrode numbers 74, 75 (Oz), 82; left posterior temporal, electrode numbers 65, 66, 67, 69, 70 (01), 71; right posterior temporal, electrode numbers 76, 77, 83 (02), 84, 89, 90; left central, electrode numbers 47, 42, 37, 31, 51, 52, 53 (P3), 54; and right central, electrode numbers 87, 93, 98, 79, 80, 86, 92 (P4), 97; with a time interval ranging from 90 to 150 (labelled P100), 300 to 400 (labelled N290), and 400 to 600 (labelled P400) ms after the onset of the stimulus. Based on visual inspection of the data, additional analyses were performed on the frontal area, electrode numbers 5, 6, 7, 12, 13, 20, 29, 30, 36, 104, 105 (C4), 106, 111, 112, 118; with a time window of 300–700 ms (labelled Ne) after the onset of the stimulus. The average amplitudes for the P100, N290 and P400 components for the posterior temporal and central areas
were statistically compared in a 2x2 repeated-measures ANOVA, with condition (congruent, incongruent) and lateralisation (left, right) as within-subject factors. The average amplitude within the time window used to assess the lower occipital P100, the P400 and the frontal Nc was compared using a repeated-measure t-test with averaged amplitude over channels as the dependent variable and condition as the independent variable.

**Study III**

The data were segmented from 200 ms before the appearance of the hand to 1000 ms after the onset of the stimulus. Based on the visual inspection of the individual averages and the grand average, 11 channels in the posterior area (62, 67, 70, 71, 72, 74, 75, 76, 77, 82, 83) were selected for the statistical analyses, with three different time windows – P1 (80–140 ms), N200 (150–250 ms) and P400 (300–600 ms) – to compare the mean amplitude between conditions (the give-me gesture and control condition). On all three mean amplitude ERP components (P1, N2, P400), analysis of variance 2x2 repeated measures ANOVA, with the condition as a within-subject factor and gender as a between-subject factor, was performed. Additionally, the effect of gender on ERP amplitude was statistically inspected.

*Note on channel selection for Studies I, II, and III*

To obtain the most reliable data outcome, the choices of channels and time windows used in the final analysis were based on the previous literature selection as well as on visual inspection of each dataset for each of the studies separately. Overall, based on the previous literature that investigated neural correlates of social perception in infants, the main focus of investigation for all three studies was the area of the posterior electrodes (e.g. Gredebaek et al., 2010; Senju et al., 2006). There were similarities as well as some differences in the final selections of channels and time windows of analysed components. The channels selected for the posterior areas were the same for Studies I and II, but in Study III we used a channel cluster containing 9 out of 11 electrodes. These were the same as those selected in Studies I and II, but without being divided into the left and right areas; instead, they were analysed together. This adjustment derives from visual inspection of the data, and the most pronounced neural activity detected in the area of interest was centrally located. Additionally, in Study II, the frontal channels were selected for final analysis because of the prominent activity of the Nc component.
Study I – Neural correlates of action perception at the onset of functional grasping

Study I was a response to growing interest in finding early developmental evidence for neural underpinnings of action perception and an action-production link. Action performance and action understanding are essential for proper functioning in the social world. Thus, the synchronous emergence of both in specific actions attracted many scholars’ attention and resulted in a wide range of empirical evidence for action–perception interrelation in the developing brain (e.g. Flack-Ytter et al., 2006; Needham et al., 2002; Sommerville et al., 2005; van Elk et al., 2008). As reviewed in the introduction, at around 5 months of age infants start to grasp objects with visually guided, object-directed and smooth reaching trajectories (e.g. von Hofsten, 1980; von Hofsten, 1982). By about the same time, infants are also able to encode the grasping actions of others (Kanakogi & Itakura, 2011; Kochukhova & Gredebäck, 2010; Woodward, 1998).

The overarching aim of Study I was to investigate the neural correlates of grasping perception at the age when grasping first develops. More precisely, the study explored which neural ERP component indexes observed grasping actions, and how this component is modulated by infants’ own experience of grasping. By inspecting different age groups, Study I had the potential to capture the exact point in infants’ development when they start to process the goal-directed actions of others and check how these relate to the infants’ own experience of grasping. We hypothesised to find the P400 component, because of its sensitivity to socially relevant stimuli, such as pointing congruency, gaze direction and facial expression (see page 30-31).

The three experiments had the following goals. That of Experiment 1 was to pinpoint the event-related potential that would be more pronounced in the group of infants who had experience of grasping action, compared with those who did not yet grasp. In Experiment 2, the experimental design served to capture the neural correlates of action perception, independently from the participants’ age and, instead, closely linked to their individual differences in grasping ability. The goal of Experiment 3 was to investigate whether the P400 is specific for the action that is part of children’s manual repertoire, or whether it expresses the overall functional relationship between hand and object. The question was thus whether the proficient 6-month-old graspers
would elicit P400 when they observed a precision grasp – an ability that typically emerges a few months later.

Design

For a description of the core procedure for all three experiments, see the methods section on pages 37 – 39.

In Experiment 1, 4- and 6- month-old infants were presented with sequences of pictures of a human hand and an object while their ERPs were recorded (see page 34-35 for detailed description).

In Experiment 2, 5-month-old infants’ grasping skills were tested. This enabled them to be divided into two groups: proficient and non-proficient graspers. Additionally, the ERPs were recorded while infants were presented with the very same stimuli as in Experiment 1.

In Experiment 3, 6-month-old infants were tested for their ability to use a precision grasp to lift small objects. Subsequently, ERPs were recorded while infants observed the same stimuli as in Experiments 1 and 2, with two exceptions: (1) the grasping hand changed the hand aperture from power grasp to precision grasp and (2) the objects that preceded the hand were adjusted in size to fit between the thumb and index finger of the presented hand.

In all three studies, we used a within-subject design to compare the neural activity between the conditions at group level.

Results

Experiment 1

On average, 88 trials (both conditions) were presented to the 4-month-olds and 78 trials to the 6-month-olds. The average number of artefact-free trials for 4-month-olds was 60. The group of 6-month-olds contributed an average of 58 artefact-free trials.

The analysis revealed a significant interaction between condition and age, $F(1, 26)=5.60, p=0.026, \eta^2=0.17$. For the 6-month-old infants, the post hoc analysis showed a significant P400 amplitude difference between congruent and incongruent trials in the posterior temporal area. That is, the amplitude was higher in the congruent (12.3 µV) than in the incongruent (8.3 µV) condition, $t(13)=2.32, p=0.037, d=0.61$. The difference between the conditions was significant only in the group of 6-month-olds, and not in the 4-month-olds, $t(13)=0.70, p=0.491$. The spatial distribution of grand average ERPs for posterior temporal channels for 4- and 6-month-olds is presented in Figure 4.
Experiment 2
On average, we presented 63 trials (both conditions) to the group of proficient graspers and 71 trials to non-proficient graspers. On average, the proficient graspers provided 49 artefact-free trials, while the group of non-proficient graspers contributed 51 artefact-free trials. The analysis revealed a significant interaction between conditions and grasping performance, $F(1, 22)=8.65$, $p=0.008$, $\eta^2=0.282$. Post-hoc analysis showed that, for the group of proficient graspers, there was a significant difference in P400 amplitude between the congruent (4.95 $\mu$V) and incongruent (1.40 $\mu$V) trials over posterior temporal sites, $t(11)=2.93$, $p=0.014$, $d=0.84$, but not for the non-proficient graspers $t(11)=1.38$, $p=0.194$. Differences between congruent and incongruent conditions were only observed in the posterior temporal region, and there were no significant differences between the hemispheres in this brain area, $F(1, 22)=0.04$, $p=0.83$. For the averaged P400 amplitude difference between conditions for Experiment 1 and 2, see Figure 5.
Experiment 3

On average, 52 trials were presented in both conditions. After the manual inspection of the data, the children provided 42 artefact-free trials on average. The analysis revealed no significant differences between conditions in the region of interest, that is, neither in the posterior temporal sites \(t(13) = 0.19, p=0.86\), nor in the other areas investigated (lower occipital, left central and right central regions; \(p>0.05\)).

Conclusions – Study I

In Study I, we demonstrated the neural correlate – P400 – that indexes the link between action production and action perception at the age when the ability to grasp for objects in a functional manner emerges. Moreover, the changes in neural processing were evidently enhanced when the infants themselves had experience of the grasping action. Furthermore, we demonstrated that the difference in conditions in the P400 ERP was not significant when infants were presented with a pincer grasp instead of a power grasp. This indicates that the enhanced P400 ERP found in Experiments 1 and 2 is not only involved in the processing of visually similar actions or caused by general maturation. Instead, it reflects sensitivity actions in the infants’ own motor repertoire.

The developmental approach used in Study I is crucial for such investigation, since it allows examination of the link from the perspective of emerging experience. Additionally, it provides scope for investigating the role of experience in perceptual processes. This is the first study to address the most critical period, when functional motor skills are emerging.
Study II – Enhanced neural processing of goal-directed actions after active training in 4-month-old infants

Based on findings from Study I, as well as behavioural evidence supporting the notion that short training with grasping in pre-reaching infants facilitates the processing of actions and objects (e.g. Libertus & Needham, 2010; Needham et al., 2002; Skerry et al., 2013), Study II aimed to explore this relation on a neural level. To ascertain the directionality of a causal relationship between action production and action perception, 4-month-old infants were given brief training before their EEG data were recorded. A similar design had previously been used in a habituation study by Sommerville et al. (2005), in which active training was found to be powerful in learning about others’ actions. However, knowledge of the neural correlates for this process in a young population were still lacking.

The goal of Study II was to capture the difference in neural processing of goal-directed action between infants with different grasping experience (active versus passive observation). The study has potential to capture the causal relation between motor experience and neural processing of action perception at a very early age. Moreover, since the stimuli used to present goal-directed actions after training session were based on Posner paradigm, the study allowed investigation of the changes within attentional processes in relation to different nature of experience.

To this end, we ran two experiments to address two consecutive questions. Experiment 1 was designed to answer the question of whether brief active experience can activate neural processing of the goal-directed action indexed by P400. For Experiment 2, the question was whether a comparable amount of visual experience is sufficient, and as powerful as active experience, to facilitate processing of others’ actions.

Design

Each subject participated in a behavioural training session (240 sec) followed by an EEG recording while they observed congruent and incongru-
ent trials of hands in relation to objects (Figure 3, page 40). During the behavioural training session, infants were seated in front of the table, on their parents’ laps.

The behavioural task was different for the two experimental groups. That is, in Experiment 1 infants received active training, using custom-made mittens. In Experiment 2, instead of active training with mittens, infants observed goal-directed actions performed by the experimenter (see page 39 for a detailed description).

Results

Experiment 1:
Active training session: Infants on average performed 9.7 goal-directed actions (range 5–16, SD = 3).

EEG recording: on average, we presented 85 trials for both conditions, with 35 trials free of artefacts (16 for congruent condition and 18 for incongruent condition). We found a significant difference between congruent and incongruent trials in the P400 amplitudes (Figure 6), in the posterior temporal area ($p = .006$, $\eta^2 = 0.426$), with higher amplitude for the congruent condition (4.5 $\mu$V) than the incongruent condition (0.45 $\mu$V). No other effects in this area were found. ERP amplitudes for the lower central occipital P400 demonstrate higher amplitudes for congruent (2.6 $\mu$V) than for incongruent ($-2.6 $\mu$V) trials, $t(14) = 3.68$, $p = .002$, $d = 0.77$. No other effects in this area were found.

In addition to the P400 effect, we found neural activity in the Nc component, located in the frontal area, with more negatively pronounced congruent trials ($-3 $\mu$V) than incongruent trials, 1.34 $\mu$V, $t(14) = -3.696$, $p = .002$, $d = 0.48$, Figure 7).

Experiment 2:
EEG recording: on average, we presented 87 trials for both conditions, with 26 trials free of artefacts (12 for the congruent condition and 14 for the incongruent condition). The analysis over the posterior temporal area for the P400 component revealed no significant difference between the congruent (0.23 $\mu$V) and incongruent trials (1.12 $\mu$V). The analysis for the P400 component over the lower occipital area (mean amplitudes of 3.15 $\mu$V for the congruent trials and 1.10 $\mu$V for the incongruent trials) revealed no significant difference between the conditions, $t(14) = 0.836$, $p = .417$. Additional analysis for the P400 component in the central (left, right) area indicated no significant difference between the congruent ($-1.73 $\mu$V) and incongruent conditions ($-1.46 $\mu$V)
Analysis of the Nc component demonstrated no significant differences in neural activity between the congruent (−0.2 μV) and incongruent (−0.6 μV) trials, $t(14) = 0.355$, $p = .309$.

**Statistical comparison between Experiments 1 and 2 – effect of training**

Analysis of the amplitude difference in score between conditions in the P400 component located over the posterior temporal area revealed a significant difference as a function of experience. We found a larger relative P400 amplitude for the active training (3.9 μV) than for the passive training (−1.1 μV) condition, $F(1, 28) = 6.381$, $p = .017$, $\eta^2 = 0.18$. Additional analyses on the amplitude difference score between conditions for the two components that were found significant after active training experience revealed no significant effects.

**Figure 6.** Illustration of P400 ERP waveforms for the two experiments (active training: Experiment 1; passive observation: Experiment 2) separated for occipital and posterior temporal sites (with channels marked with black included in the analysis). The solid black lines represent the congruent and dotted grey lines the incongruent condition.
Conclusions – Study II

The study revealed the neural correlate, P400, to be involved in processing other people’s actions after brief active training with goal-directed actions. This effect was present even before the solid action plans for grasping were developed. Finally, we learnt that there is a causal relation between infants’ manual performance of grasping and their improved understanding of other people’s grasping actions.

Taking into consideration the specificity of our EEG paradigm, it is possible that the P400 captured in Study II originates from enhanced attentional processes that result from the first-person experience with a specific action. This speculation is supported by the visible Nc component, located in the frontal ERP area, which is known to reflect selective attention or sensitivity to unexpected events (Richards, 2003). The presence of the Nc seems to be directly related to the active training, since it has not been found before in similar infant studies (e.g. pointing, grasping, goal-directed animate agents). The negativity of the Nc captured in Study II is boosted by congruent actions, which may indicate that, after active training, infants perceive the congruent actions as more interesting because they give a potential accomplishment of the goal. Another explanation is that active training facilitates encoding of goal-directed actions in posterior temporal P400, which in turn modulates attentional processes in the frontal area. It is possible that later in life, when infants become proficient in performing goal-directed actions, the Nc is no longer as prominent because attentional processes play a less important role than at the beginning of the learning process. This speculation clearly needs
more in-depth examination that would tackle observation of goal-directed actions with respect to the priming effects and general attentional processes.

It is important to add that although the short training seems to be very powerful, we do not think it is sufficient to build up a strong motor representation that would be necessary for, for example, predictions of other people’s actions. For this, regular motor training and general motor development seem to be necessary (Adolph et al., 2013; Gredebäck & Falck-Ytter, 2015; Gredebäck & Melinder, 2010).
Study III – The neural basis of non-verbal communication

Study III aimed to deliver the neural underpinning of gesture understanding directed towards the child. Deriving from the idea that understanding manual actions is linked to one’s experience with the same action, Study III examined to what degree gestures are also experience dependent. Nine-month-old infants were tested, since the behavioural data indicate that at this age infants begin to understand other people’s gestures (Gredebäck & Melinder, 2010; Woodward and Guajardo, 2002) and some may possibly begin to produce the give-me gesture. The data from the previous two studies suggest a relationship between manual action production and understanding. However, since the give-me gesture has no inherent function outside its communicative aspects, the link between action production and perception may not be entirely clear.

As it stands in the introduction, current developmental literature is replete with research focusing on the pointing gesture. Much less attention has been paid to other types of gesture, such as the ‘give-me’ gesture. Study III is therefore an attempt to shift the scientific focus towards a gesture that seems to also serve an important function in our social development, since it allows exchange among social agents, as well as informing them about specific needs.

Based on Studies I and II, as well as other empirical findings for neural correlates of social perception, we hypothesised that the P400 component, which previously indexed pointing, goal-directed actions and gaze direction understanding, will be evoked when processing a socially relevant, communicative hand in the configuration of give-me gesture. Additionally, we expected to find the relationship between infants’ neural responses to the give-me gesture and their ability to respond to the same gesture behaviourally.

Regarding the stimuli design, the hand in Study III, is not directed to any objects (as in Studies I and II). This change is based on the assumption that the gesture itself conveys the meaning even in the absence of objects. Instead, the hand is directed towards the baby, who should see the hand as directed towards him- or herself in a form of request. Consequently, this should elicit the possible neural underpinnings for the communicative intent of the hand.
Design
All the subjects participated in two tasks. First, we recorded infants’ neural responses to the hand stimuli. Subsequently, they took part in behavioural tasks in which we checked their behavioural responses to the give-me gesture request.

EEG recording
The infants were presented with the hand forming the give-me gesture and the control hand (Figure 2). Rather than being directed to any objects, the hand was instead directed towards the child. This should make the child see the hand as directed towards him- or herself in a form of request, based on the assumption that the absence of objects conveys the non-verbal meaning. Consequently, it should elicit the possible neural underpinnings for the communicative intent of the hand.

Behavioural task
Infants’ behavioural response to the give-me gesture performed by the experimenter were assessed using the Responding to Behavioural Request procedure from Early Social and Communicative Scale (ESCS; Mundy et al., 2003) (see page 40 for detailed description). Additionally, the parent was asked whether the infant reacted to the give-me gesture request in the home setting.

Results
On average, infants saw 90 trials across both conditions, with 32 trails free of artefacts (15 for the give-me gesture, and 17 for the control hand). To test differences in neural responses for the give-me gesture hand and control hand, within the P400 component, as well as the effect of sex on the modulation of the neural component amplitude, we conducted a 2(sex) x 2(condition) mixed repeated measures ANOVA. The results revealed a main effect of condition, $F(1, 27)=40.12, p<0.001, \eta^2=0.598$; mean amplitude in P400 was 15 µV in response to the give-me gesture and 9 µV to the control hand configuration (Figure 8). Only 3 out of 28 infants did not show the higher amplitude for the give-me gesture than for the non-communicative hand configuration. Additionally, there was a significant interaction between condition and sex $F(1, 27)=5.384, p=0.028, \eta^2=0.166$. Further analysis revealed significant differences between the conditions, both for girls, $t(27)=4.750, p<0.001$, and for boys $t(27) =4.360, p<0.001$, with more positive mean amplitude for the give-me gesture. Moreover, an independent sample t-test with amplitude difference as a dependent variable and sex as a grouping variable revealed a significant amplitude difference between the sexes, $t(27) =2.320, p=0.028$, with a larger
difference in conditions for girls ($M=8 \mu V, SD=6 \mu V$) than for boys ($M=4 \mu V, SD=3$). No other effects in P1 and N200 ERPs were found.

No statistical analysis was performed in relation to behavioural data as none of the infants responded to the give-me gesture as determined by the ESCS. In response to the give-me gesture, four infants extended the arm towards the experimenter but did not release the object. Additionally, two infants after seeing the gesture performed by the experimenter moved their hand that was holding the toy away. The parents did not report that their infant was producing or responding to the give-me gesture outside the laboratory.

![Image](image_url)

**Figure 8.** Grand average of ERP of the posterior area (channels of interest are marked in black). The black line represents the give-me gesture condition and the grey line the control hand.

**Conclusions: Study III**

With these findings, we have extended knowledge about give-me gesture processing. This study was the first to pinpoint the P400 neural correlate to be sensitive to hand configuration with socially rich content – the give-me gesture, which conveys a request from another person. In Study I and II, the link between action production and action perception was found, however in Study III this link could not be directly tested due to the lack of variability in the behavioural data. That is none of the infants responded to the gesture even though most of the infants showed the sensitivity to presented gesture on the neural level. It is possible that by 9 months of age, infants use experience gained from other actions, such as grasping, as a foundation for processing other people’s actions. An understanding of grasping affords the opportunity to learn about other people’s goals and intentions that can be developed outside one’s own motor abilities.

It is also worth mentioning that there is a difference between Study III and Study I in terms of testing infants’ own action performance. In the grasping experience task (Study I), the child’s performance of the actual grasping action was tested. In Study III, on the other hand, we tested responses to the
give-me gesture. These may possibly require a higher level of action processing, since the child not only has to understand the action but also has to be ready to respond to it appropriately. It is possible that such a response is dependent on many other factors, such as understanding of the turn-taking aspects of the action, as well as on individual differences in temperament and personality. This conclusion clearly needs more research to examine developmental trajectories of perception and production of give-me gestures, as well as other, later cooperative actions, such as helping or sharing.

Additionally, the findings demonstrated gender differences in neural responses to the give-me gesture, with more pronounced differences in amplitude among girls. This result may reflect previously demonstrated gender differences in processing of non-verbal cues (Hall, 1978), as well as joint attention (Olafsen et al., 2006) or the onset of gesture and sentence production (Özçalışkan & Goldin-Meadow, 2010), captured with behavioural measures.
General discussion

Deriving from dynamic systems theory and the embodied account of action perception, the present studies were designed to explore the neural basis of manual actions and gestures as well as the relationship between infants’ own experience with these actions and neural processing when they observe them being performed by others. Additionally, the influence of active versus passive experience on action perception was investigated. All the studies used ERPs to examine the neural underpinnings of action understanding in infants between 4 and 6 months old for reaching actions, and aged 9 months for gestures.

The main findings from Study I revealed a neural correlate of the link between action production and action perception at the age when the ability to grasp for objects in a functional manner emerges. This study was the first of its kind to capture the P400 in relationship to the action – perception link at such an early age.

Study II focused on the directionality of the relationship between action and perception, and demonstrated that brief active training in goal-directed actions, even before solid motor plans for grasping are developed, facilitates processing of others’ goal-directed actions. In Study II, active experience and observational experience were compared, and this provided evidence that active experience is more powerful in enhancing the social networks involved in processing goal-directed actions. Very brief active, but not observational, training was sufficient to enhance neural processing in response to the functional action cues. That is, in participants who had received grasping training by means of “sticky mittens”, the P400 and the Nc component both showed higher amplitude in response to grasping hands oriented towards the object. This indicates that bodily, first-person, self-produced experiences influence observers’ sensitivity to observed actions.

Finally, Study III focused on investigating gesture processing at the age when infants begin to use non-verbal communication to express their needs. This study was the first to demonstrate the involvement of the P400 neural correlate in encoding socially rich hand actions, such as the give-me gesture. Nine-month-olds who showed the enhanced P400 when observing give-me gestures did not yet respond behaviourally to this gesture, nor produce it on a daily basis, as reported by their parents. Thus, it is possible that for more complex actions, such as social interactions involving non-verbal communication,
infants’ understanding is not directly based on simulation processes. Rather, it may be a combination of embodied experience with more basic actions, as well as with learning from observation of social events.

In sum, the data in this thesis demonstrated that the P400 is a valid measure of the action processing at an early age, and is enhanced by functional grasping actions and meaningful gestures.

P400 a key ERP marker for research on early-life neural underpinnings

The findings from all three studies highlight the sensitivity of the P400 to functional reaching actions and gestures. This is in line with prior ERP studies on infant populations indicating the involvement of the P400 in processing socially rich stimuli (see p. 30). Additionally, Studies I and II show that the P400 is a valid marker for capturing experience-dependent processes in early life. Furthermore, the data from Study III indicate that the P400 is sensitive to communicative intent of gestures that are not directed towards specific objects (as in Studies I and II).

Although infancy research has provided evidence for a link between action and perception, the central assumptions were based on data from older age groups and on changes within event-related oscillations, in particular the mu rhythm. This frequency is known to be altered when we observe and perform motor actions, and has been previously linked to MNS activity (e.g. Cannon et al., 2015; de Klerk et al., 2014; Gerson, Bekkering, & Hunnius, 2016; Lloyd-Fox et al., 2015; Nyström 2008; Paulus et al., 2012; Staple et al., 2010; van Elk et al., 2008). Measuring oscillations was shown to be beneficial for investigating action understanding, but this method is not the best suited to the study of very young populations. One reason for this is that in infant populations, the mu rhythm is typically detectable at between 6 and 8 months of age (Stroganova, Orekhova, & Posikera, 1999), and its properties continue to change over time, from 6–8 Hz at around 8 months to 7–9 Hz at 11 months of age (Berchicci et al., 2011). This indicates a possible risk of large individual differences in the presence and salience of the mu rhythm in the infant EEG at younger ages (Shimada & Hiraki, 2006; Marshall & Meltzoff, 2011).

For the purposes of this thesis, studying young populations was essential to capture the underpinnings of an action–perception link for grasping actions at its’ onset. The behavioural data suggest that the coupling between reaching actions and perception emerges at roughly 6 months of age, and measuring oscillations of the mu rhythm would therefore not be optimal. Accordingly, measuring the action–perception link using ERPs, creates opportunities for gaining new insights and allows significant contributions to the developmental EEG literature. Additionally, the findings from Study III demonstrate that
the P400 can also be used as a valuable measure for investigating neural processing of socially functional stimuli in general. Since it was also found to be sensitive to sex differences in processing of the give-me gesture, it may possibly serve as a means of gauging individual differences in processing of social stimuli.

What are the possible origins of the P400?

Unfortunately, the EEG data provide no information about source location or connectivity within neural networks. This thesis therefore does not allow clear identification of the source of the P400. However, as presented in the introduction (p. 30), it is suggested that the infant P400 is functionally related to the adult N170 (de Haan et al., 2003; Nelson et al., 2006). In turn, because the N170 is linked to activation in the superior temporal sulcus (STS) (Dalrymple et al., 2011; Itier et al., 2004; Puce, Allison, Bentin, Gore, & McCarthy, 1998), it is highly probable that the P400 also originates from this area.

The exact function of the STS in processing of the actions performed is unclear, but two possible scenarios may be proposed. First, the STS may provide the input to the MNS located around the inferior frontal and superior parietal cortex (Iacoboni et al., 1999). This implies that the P400 found in the current data may be enhanced by initial perceptual processes. The second possibility is that action processing may occur through a MNS feedback loop from the inferior frontal and/or superior parietal areas. This way, the STS would have a double function – receiving information from the MNS but also feeding it forward, thus allowing a comparison between action observation and action execution (Rizzolatti et al., 2014). This view implies that the P400 is generated by a MNS feedback loop in which mapped information is sent back to the STS. The premotor cortex is not usually associated with attentional orienting networks; rather, it is known to receive the input from the STS in order to involve matching processes for action processing (for review see Atkinson, Simpson, and Cole, 2017; Corbetta & Shulman, 2002; Van Overwalle & Baetens, 2009). Because of the specificity of the paradigm used in Studies I and II (i.e. the attentional paradigm), an initial involvement of the STS in processing the directionality of the hands is also highly probable. Literature on adults delivers further evidence that such attentional and initial processing takes place in the STS (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000).

Whether the P400 found in Study III also derives from the STS is hard to ascertain. It is, of course, possible that encoding of gestures is supported by the STS, since it has been found to be sensitive to intentional human actions that are socially meaningful (Bahnemann, Dziobek, Prehn, Wolf, & Heekeren, 2010). However, it is also possible that in order to encode the communicative intent of the give-me gesture, more mentalising processes are necessary. In
this case, an alternative source of the P400 could be the temporo-parietal junction (TPJ), which was previously found to be associated with processing other people’s mental states and, in particular, with adopting a third-person perspective (Carter, Bowling, Reeck, Huettel, 2012). However, because of their close position both structures are very difficult to distinguish (Yang, Rosenblau, Keifer, & Pelphery, 2015).

In sum, based on the data from all three studies, I demonstrate that the P400 component is enhanced by processing of functional actions. I highlight the possible involvement of the STS and TPJ in these processes, on the assumption that they allow the initial detection of goal-directed actions, i.e. from processing visual inputs to subsequently feeding forward the information for more advanced processing. Moreover, the findings from Studies I and II indicate that this initial process in the STS may be facilitated through enhanced attentional processes that, in turn, are modulated by infants’ own experience of grasping actions.

How does covert attention modulate the P400 and facilitate action processing?

The stimuli in Studies I and II were based on the Posner cueing paradigm (Posner, 1978, 1980) with centrally located hands that cued direction towards objects previously presented, in either a congruent or incongruent relationship. The paradigm was used to investigate the effect of action production on action perception through action priming. According to the theoretical model of the action–perception timeline proposed by Gredebäck and Daum (2015), the shift of covert attention is an important step in action processing. This is because it facilitates estimation of the future goal of an ongoing action and is an initial stage in action processing that takes place within the first 500 ms.

According to this model, there are three processes that are sequential, mutually dependent and critical for social perception. These are (a) action priming, (b) action perception and (c) action evaluation. That is, first, we detect the agent; the covert attention is then allocated to the future state of the agent – priming. This subsequently leads to overt gaze shifts that allow for prediction of the action goal and, finally, evaluation of the outcome (Gredebäck & Falck-Ytter, 2015).

The P400 captured in Studies I and II seems to reflect the first step in action processing, that is, action priming for congruent actions. The data from Studies I and II suggest that the P400 is heightened by attentional shifts between the central cue and the targets. More specifically, when infants looked at the object that was presented at the top or bottom of the screen, their attention to

---

2 The order of the pictures in the stimuli is reversed in comparison to the original Posner paradigm. See page 36 for detailed description.
the location where the object appeared (see Figure 1, p. 35) was heightened. Subsequently, their attention shifted to the central cue, the hand, which again directed the infants’ attention along the reaching axis. This happened only in the congruent trials, where the infant’s attention shifted from the object and the direction of the hand overlapped, and the summation of these shifts resulted in an enhanced P400.

Both Studies I and II demonstrated that infants’ own ability to perform grasping actions facilitated their action perception. Thus, only infants that were able to grasp by themselves showed an enhanced P400, which may be the result of overlapped attentional shifts. Additionally, the presence of the Nc component in the group that received active training in Study II suggest that there is an enhancement of attentional processes involved in action understanding that result from the training. The Nc component, which is known to index selective attention (Richards, 2003), appeared frontally and was more strongly elicited for congruent actions. The Nc effect is most likely directly connected to the mittens training, since it was not found in either Study I or Study III, nor in other studies that have investigated the P400 in pointing gestures with similar stimuli (Melinder et al., 2015; Gredebäck et al., 2015). It is possible that because the Nc component was found only in the youngest group of tested infants, the attentional processes are mostly recruited at the time when the link between action and perception emerges. This suggests that, at the time when more solid motor plans are already available, they are no longer needed and thus not pronounced.

Studies I and II clearly demonstrated that the priming effect is linked to own action proficiency. Previous literature on eye tracking also reported the synchrony between the emergence of action priming in relation to observer’s own ability to perform the same action (Daum & Gredebäck, 2011; Daum, Ulber, & Gredebäck, 2013). Additionally, to the clear effect of training Study II shows that the priming effect can be highly plastic as only a few minutes of active reaching training was sufficient to facilitate action processing in pre-reaching children.

How does experience boost development?

An article by Campos et al. (2000) reviews how the onset of self-produced locomotion changes the whole set of infants’ abilities within the social, emotional, and cognitive domain. The title of this article is simply “Travel Broadens the Mind”. Here, paraphrasing, it is no exaggeration to assert that manual actions broaden the mind.

Manual actions, such as reaching and gesturing, open new perspectives on the self, the environment and their mutual interactions. They help to com-
municate and are valid cues for action processing. Additionally, manual actions lead to infants’ sensitivity to actions’ goals (Sommerville et al., 2005) and more advanced object segregation abilities (Needham, 2000), and even boost their preference for faces (Libertus & Needham, 2014).

**Active versus observational experience**

Different ways of experiencing the world seem to have distinct influences on emerging skills (Bushnell & Boudreau, 1993; Campos et al., 2000). Study II compared two different ways of experiencing grasping actions and revealed a substantial difference between active and passive training. The active group were given the opportunity to grasp and lift objects at a time when such an ability was not yet part of the infants’ motor repertoire. In the passive training, the infants observed the grasping actions performed by an experimenter.

Although the training sessions were matched in terms of duration and number of goal-directed actions performed, their impact on subsequent action encoding evidently differed. Passive observation generated no comparable enhancement in neural activity, while significantly higher amplitudes of the P400 were visible after active training for congruent than for incongruent actions. Much as in Study II, several studies directly compared active and passive experience. Corroborating with our findings, these studies found that active experience (compared with passive experience) facilitates different ranges of behaviours to a higher degree. For instance, in the study by Libertus and Needham (2010), active and not passive experience of reaching (with sticky mittens) before the onset of reaching facilitated this behaviour and enhanced infants’ attention to objects and others’ goal-directed actions.

Varying effects may, of course, reflect the varied duration of active training. For instance, just a few minutes’ training can speed up visual predictions (Ambrosini, Reddy, Looper, Costantini, Lopez, & Sinigaglia, 2013; Cannon et al., 2012; Filipi & Woodward, 2016; Kochukhova & Gredebäck, 2010) or, as in Study II, modulate attention to functional actions. Longer experience has been found to enhance object exploration (Libertus & Needham, 2010; 2011; 2014; Needham et al., 2002) as well as to promote earlier reaching onsets in infants born preterm (Heathcock, Lobo, & Galloway, 2008). Moreover, two-week-long training has been found to result in lasting effects (evident from retesting 12 months later) on object exploration, and seems to have an impact in other respects, such as face preference (Libertus & Needham, 2011; Libertus & Needham 2014). Thus, all the above-mentioned studies highlight the evident importance of our motor experience, however, the intensity of effects and their functionality may depend on training duration.

Despite the overwhelming evidence for the power of active experience on the developing brain, questions remain. What is so special about self-produced actions, and why does passive observation not have the same effect?
Answering these questions would necessitate precise investigation of how infants learn and what exactly they learn when given opportunities to perform actions. It is possible that performance of an action provides the requisite information about the effects of the performer’s movements and goal-directedness in general. Active training also most likely provides richer sensorimotor information, since it entails visual information along with proprioceptive input from experiencing an object’s weight in one’s own hand.

It is thus suggested that experiencing associations between actions and their sensory input, when both occur often and in rapid succession, results in development of motor representation of these actions. This representation may be activated later, when the same action is being performed by others (Heyes, 2001; Keysers & Perrett, 2004; Paulus et al., 2012). When infants repeatedly grasp for an object, they visually pay attention to their own actions and their sensory consequences. Additionally, Libertus and Needham (2010) suggest that active training boosts motivation because infants can then observe the immediate contingency between their own movements and their consequences in relation to objects. This in turn may invite repeated performance of actions. Moreover, the findings from Study II indicate that motor experience most likely enhances attentional processes that are involved in the very first step of action processing. Altogether, it seems that motor experience may simply provide more input, resulting in more in-depth processing of other people’s actions. Moreover, it also provides motor representations that can be used to map other people’s actions, thereby allowing more precise predictions and interpretations of observed actions to be performed.

Motor experience is crucial for development and action understanding. However, as reviewed in the introduction, action processing cannot be based solely on active experience: what we experience visually must also matter. Previous literature demonstrated that infants can encode goal-directedness in actions that are not yet in their motor repertoire (Southgate & Begus, 2013) or when they are performed by non-human agents (Gergely et al., 1995). It is suggested that infants’ sensitivity to goal-directedness is based on inborn principles based on statistical regularities learnt from multiple observations. Indeed, the study by Daum et al. (2016) emphasises that observational experience has its own important function in action processing. They found that action priming significantly modulates infants’ overt attention after only brief observational training of counter-intuitive grasping actions. Although the infants tested were already able to perform and encode reaching, their covert attention remained flexible in response to changes, according to observed regularities. Additionally, the associations formed on the basis of daily observations are not only tied to the visual domain, but can create the link between different modalities through action–effect associations (Kuhn, Elsner, Prinz, & Brass, 2009; Paulus, van Dam, Hunnius, Lindemann, Bekkering, 2011). For instance, Paulus et al. (2013) demonstrated that 9-month-old infants showed
increased motor activation in response to the sound of a rattle they had previously heard, but only while observing their parents shaking the rattle and hearing this specific sound simultaneously.

All above points suggest that although action experience has been found to be more powerful in facilitating action encoding and possibly speeding up an action–perception linkage, it is through multiple types of experience that infants build optimal mechanisms for functional, fast and, at the same time, flexible action processing. Thus, learning from statistical regularities does not necessarily reject motor system involvement in action processing. Instead, it is possible that different mechanisms are recruited during different phases of action understanding. Additionally, there may be a crucial difference in how much experience is needed for various action-processing stages, where context-related rationality and action simulation may be involved, but in different parts of this process. This means that not all processes conflict; rather, they complement one another in helping infants make sense of other people’s actions.

Can infants’ own action experience be generalised and assist understanding of similar actions performed by others?

In Study I, proficient graspers did not encode the directionality of the hand when it formed a precision grasp. The conclusion of this study was that the lack of difference in the P400 amplitudes between the congruent and incongruent trials was due to inexperience in using such a grip when grasping for objects (this ability typically emerges at around 9 months of age). In Study III, however infants were able to encode the give-me gesture although their parents did not clearly notice that they are able to perform it. This is very puzzling and raises questions about the exact mechanisms that are involved in action perception.

Studies that support an action–perception link imply that the relationship between the action and perception is highly specific. In other words, some study designs similar to Study I suggest that, in order to encode or predict goals of other people’s actions, we need this particular skill in our motor repertoire. For instance, Ambrosini et al. (2013) found that although all the infants tested in their study showed an anticipatory gaze to the whole-hand grasp, only those who could perform pincer grasps could anticipate the action by using pincer grasps. Moreover, infants’ manual skills were found to be related to the ability to use the cues from the shape of the actor’s hand to differentially predict the goal of the observed action. Such precise encoding of actions would directly promote the action simulation theory. However, in-
ability to transfer experience from one skill to another appears to be not functional. Thus, there must be mechanisms that allow not only learning but also translation of learnt actions into understanding of similar actions. It is possible that motor experience plays a crucial role, and acquired skills through active experience may serve as a basis for similar, but more complex actions. This would imply that once basic actions are fully integrated in people’s own motor repertoire, they can serve as a fundament for observational experience that provide input for novel actions, and plays an important role in our learning and building of knowledge about other, often more complex, actions.

Along these lines, richer experience may provide a basis for more flexible action processing and sensitivity to various action consequences, like in the study by Young et al. (2015), in which 15-month-olds were found to be able to generalise their trained behaviour of pushing a button on one toy and apply the same skill to novel toys. Regarding gestures, it was also found that experience in producing gestures facilitates infants’ understanding of gestures’ referential functions, which in turn leads to an understanding of the communicative and intentional motives of other people’s gestures (Sodian & Thoermer, 2004). Thus, the ability to generalise one’s own experience to other actions comes from more basic skills, and is based on the transfer of knowledge about the goals of those actions. Most likely, this is based on extensive motor practice, further supported by regularities learnt through observation. In Study III, the infants showed sensitivity to the give-me gesture before demonstrating the ability to produce it or respond to it. Since the infants lacked stable action plans for the give-me gesture, the enhanced processing of observed gesture may derive from the infants’ ability to perform more basic actions, for instance reaching. Similar reasoning has been proposed by Bertenthal, Harding, & Boyer (2014). That is, we may possibly see complex actions as a set of simple subsidiary actions. Thus, the infant’s own skills in performing these subsidiary actions may facilitate the processing of more complex events. According to Arbib (2012), this is how we process novel and more complex actions (i.e. manual dexterity), even without the communicative intent. It is important to point here that even if the use of basic actions i.e. reaching action for the processing of the give-me gesture in Study III is not empirically supported, the recognition of the gesture does not appear to be based on the low-level processing. A study by Juvrud et al. (2018) found a direct link between P400 activation and pupil dilation measured in action evaluation when two actors used the give-me gesture while they were interacting with each. The infants with higher amplitude for the give-me gesture were found to have greater pupil dilation when attending inappropriate actor’s response to the give-me gesture at the age of 9 months. Additionally, the amplitude of the P400 could predict the giving behaviour later in life.

In sum, our action processing and action production skills seem to be a result of complex relationships among developing systems, and in multiple
domains that change through constant interactions between one another. Moreover, generalising from one ability to other actions may depend on the amount of experience, but it seems to be possible and most functional in order to become a proficient member of society.

To train or not to train?

Development is a process and, as dynamic system theory perspective suggests, one influenced by many factors: everyday activities, experiences, neural maturation, environmental changes, physical characteristics, amongst others. All these factors play a part in infants’ advancing motor skills. Importantly, these multidimensional factors may either facilitate or delay developmental progress. This is because our development never takes place in isolation; instead, before a new skill emerges, many factors need to achieve a functional level of performance or receive satisfactory input. For example, several factors play a crucial role in indicating a child’s readiness for walking (Adolph & Robinson, 2013; Thelen, 1995). Examples are development of specific brain regions responsible for coordination, motor control, sensitivity to visual flow, motivation for locomotion, changing body dimensions, muscular strength and postural control. The child will be unable to walk if the postural control is underdeveloped, but postural control alone, without the other factors, will not be sufficient for the child to walk. Thus, the first steps the child takes are actually based on a highly complex foundation of multiple skills, including experience derived from maternal routines or paediatric advice (Adolph & Robinson, 2013). This also means that a healthy child will begin to walk when all these factors are “ready” for walking behaviour. The way the child is taken care of in early life can make a difference when this ‘readiness’ emerges (for the skill of walking, it may vary by a few months). This is because the child’s brain is plastic and can be trained in the same way as the body.

For instance, children’s musical education in the form of playing a musical instrument causes structural changes in the right precentral gyrus, corpus callosum and primary auditory region (Hyde et al., 2009). The extent of this change is highly dependent on the amount of experience (Schlaug, Marchina, & Norton, 2009). The mittens training that was used in the Study II lasted only a few minutes but resulted in evident differences in action processing tested directly afterwards. The same but longer training resulted in longer-lasting effects in terms of object exploration and attention-focusing skills (Libertus et al., 2016). Altogether, by providing training we can undoubtedly change and, in many cases, speed up the onset of motor skills. However, the question remains whether we should do so with no medical indication. In fact, the acquisition of new motor skills may not only speed up the development but also
cause a reorganisation of infants’ existing motor, perceptual, and cognitive skills. For instance, according to Corbetta and Bojczyk (2002), the onset of walking may cause a temporary plateau or even regression in development of bimanual reaching. The decrease in reaching ability has been demonstrated independently from the position in which the child was tested. This indicates that the brain is constantly changing and that even skills that are already functional may undergo modification due to reorganisation. Moreover, the tools used sometimes to help kids to speed up learning process do not always meet the right goals. For instance, popular walkers used to give pre-walking children the possibility to move around the room have been found to give different kinds of experience and training than needed for proper walking milestones and as a result delayed the walking onset. Thus, the training with sticky mittens used in this work, despite showing clear effects for action perception in relation to the infants’ own manual experience, mostly served to gain fundamental knowledge on action processing, but should not be used as everyday tool to boost developmental trajectory. For this, we would need more in-depth investigations that would permit precise knowledge of the exact changes that emerge during the training. The training with sticky mittens is, of course, potentially beneficial for populations with possible motor delays. For example, a positive outcome of training was found for use of a treadmill, which promoted earlier walking in children with Down Syndrome (Angulo-Barroso, Burghardt, Lloyd, & Ulrich, 2008). A more longitudinal approach in studying training mechanisms, as in Libertus et al. (2016), could potentially achieve long-term positive effects and also capture potential side effects in using this tool in therapeutic use. However, for typically developing children, caregivers should keep in mind that normal development has its own speed, and parental scaffolding should be sufficient to support it at its own pace. Meeting infants’ needs of active exploration and providing creative environments should result in healthy development that takes place in a spontaneous, robust and self-organising manner.

**Future directions**

One major direction for research is to further explore the interrelationship between body and mind. Children’s development should be approached from the idea that our body and the environment we experience through it are crucial for our cognitive development and social functioning. The investigation should include both behavioural and neural data, in order to gain a full grasp of the complexity of relations between body, environment and brain. Regarding the action–perception link, more studies are needed that would tap into the exact processes that take place in the body during motor experience of actions. Here, I highlight the importance of attentional processes in action processing.
I suggest that more studies need to target the Nc component in relation to action observation and action production. Understanding how attention is influenced by our own actions, but also how our attention helps to connect our action performance and action processing, would most likely result in a better understanding of our brain and behaviour as a whole.

Further, more infant studies need to target the P400 component to pinpoint its origins. Obviously, such investigations call for use of advanced technology, that has the potential to detect and pinpoint the pathways between the P400 area of origin and MNS in very young population.

Another direction that the work in this thesis brings to the fore is a more in-depth investigation of the ‘sticky mittens’ effect. This powerful tool to enhance action processing and object perception is still not well understood. Specifically, a detailed examination of the impact of different types and amount of experience on the developing brain and neural plasticity, as well as learning processes, would be highly beneficial for fundamental science and could possibly be used in a therapeutic approach for children with developmental delays.

Additionally, development should be investigated through longitudinal investigations and by multidisciplinary teams. This would give us more detailed understanding of the relationship between early, basic skills and later, more complex actions. This longitudinal and multidisciplinary approach should take into consideration infants’ individual differences related to the body and the environment. Furthermore, we should think about our body as a proxy for developmental changes in all possible domains. Thus, synthesising detailed and precise knowledge of body development, brain processing and motor interventions would be a major step forward. As expressed by Louise Barrett (2011, p. 92), *It is a mistake to think of the brain as somehow being in charge of the body.... (...) we can see that an animal’s brain and body cannot be divorced from the environment in which it lives. It is a mistake to think we can study an animal’s behaviour and cognition in isolation from the environment.*

**Final conclusions**

Our hands are undoubtedly the key to our physical and social world, and they also play a role in shaping our mind. Specifically, the findings of this thesis indicate that action production facilitates processing of other people’s actions. The data promote a neural component, P400, that indexes functional manual actions at an early age when the action production–perception link emerges. The P400, which most likely originates from the STS/TPJ area, is involved in the initial processing of actions and provides the input to MNS for more advanced processing. Additionally, the findings in this thesis emphasise the importance of the attentional process in action perception and its flexibility in
terms of active experience, as well as its powerful impact for encoding observed actions. The P400 has been also found to be sensitive to the non-verbal communicative gesture – the give-me gesture. This indicates its strong involvement in processing socially rich actions.

In sum, this thesis highlights the importance of our body and actions in shaping our mind, social development and in particular, action understanding. Our mind is embodied and cannot be understood in isolation from our body.
Summary in Swedish

Att kunna utföra handlingar och förstå andras handlingar är förmågor som är vitala för att kunna interagera med andra i en social värld. Redan från födseln använder vi vår kropp för att agera och för att lära oss mer om oss själva, om vår omvärld samt om andra människor, deras handlingar och intentioner. Våra tankar är förkroppsligade; på så sätt spelar våra handlingar en stor roll i vår kognitiva och sociala utveckling.

Denna avhandling fokuserar på den starka kopplingen mellan handling och perception, med särskilt focus på kroppens roll, och mer specifikt händernas roll i denna länk.

Tre empiriska studier om handlingsförståelse kommer att presenteras med utgångspunkt i teorin om förkroppsligande (embodiment) som betonar rollen av egen motorisk erfarenhet för vår sociala utveckling. I alla studier mättes ERP (event-related potentials) hos 4 till 9 månader gamla barn, när de fick se manuella handlingar så som grip-rörelser och ge-mig gesten.

Studie I visar att den neurala korrelaten - P400 pekar på handling-perception länken i den ålder då förmågan att funktionellt gripa efter objekt uppkommer. Den neurala bearbetningen har visat sig påverkas av erfarenhet med att själv utföra samma griprörelse.

Studie II visade att kort träning i att utföra målinriktade handlingar, redan innan barn normalt sett skulle ha lärt sig gripa, gör att barn ser och tolkar andras handlingar som målinriktade.

Studie III visade att samma neurala korrelat som indikerar processande av griprörelser är involverade i processandet av icke verbal kommunikation så som ge-mig gesten.

Zdolność równoczesnego wykonywania i rozumienia działań jest niezbędną umiejętnością umożliwiającą poprawne funkcjonowanie w świecie społecznym. Od narodzin nasze ciało umożliwia nam nabywanie nowych umiejętności, i to dzięki niemu uczymy się i poznajemy nasze otoczenie oraz działania i intencje innych osób. Nasz umysł jest ucieleśniony, dlatego też, nasze działania odgrywają kluczową rolę w poznawczym i społecznym rozwój. Głównym tematem niniejszej rozprawy doktorskiej jest określenie ścisłej relacji pomiędzy działaniem i postrzeganiem i określenie, jaką rolę pełni w tej relacji nasze ręce. Przedstawione zostaną trzy badania empiryczne, które skupiają się na roli, jaka odgrywają doświadczenia ucieleśnione w rozwój społecznym u niemowląt w wieku od 4 do 9 miesięcy. We wszystkich trzech badaniach zastosowano rejestrację potencjałów czynnościowych zebranych w odpowiedzi na obserwację różnych czynności manualnych, takich jak czynność chwytania czy gest “podaj-mi”.

Wyniki pierwszego badania wykazały, że neuronalne korelaty wzajemnego powiązania pomiędzy wykonywaniem a postrzeganiem pojawiają się w wieku, w którym pojawia się zdolność do funkcjonalnego chwytnia przedmiotów. Wykazano również, że doświadczenia manualne niemowląt mają wpływ na przetwarzanie neuronalne tych samych czynności.

W badaniu drugim wykazano, że krótki trening czynności motorycznych skupionych na celu może ułatwić rozumienie tych samych czynności wykonywanych przez inne osoby.

Trzecie badanie wskazało, że te same korelaty neuronalne, które powiązane są z czynnościami chwytania są również związane z odczytywaniem nieverbalnych komunikatów, takich jak gest “podaj-mi” skierowany do innej osoby. Wykazano również, że zdolność do odczytywania i rozumienia tego komunikatu nie zależy bezpośrednio od umiejętności niemowląt do reagowania na gest innej osoby.

Podsumowując, prezentowane wyniki badań wskazują na kluczową rolę komponentu P400 będącego neuronalnym korelatem z przetwarzaniem gestów i czynności zorientowanych osiągnięciu celu. Uzyskane wyniki wskazują również na ważną rolę doświadczeń motorycznych i aktywności naszej uwagi w rozumieniu czynności wykonywanych przez inne osoby.
Ponadto, dane zebrane w trakcie z trzeciego badania wskazują na prawdopodobne powiązanie umiejętności chwytania z przetwarzania komunikacji nieverbalnej.
Acknowledgements

As my PhD time comes to end, there is a great opportunity to say some final words to those who made it all possible and supported this work in many different ways.

First of all, I would like to thank my supervisors Gustaf Gredebäck and Claes von Hofsten. You both are so knowledgeable and enthusiastic about child development and science in general that anyone would wish to get a chance to work with you, and you gave it to me! Thank you for that, it was an amazing journey! Gustaf, I was very lucky to have you as my scientific father. You gave me so much support, personal understanding, endless positive feedback and a lot of freedom to develop during all those years that it is hard to find the right words to express how grateful I am. During all those years, you were always ready to clear up all my doubts, provide answers to all my questions and serve them all with great sense of humor. I will never be able to use the word “brilliant” without having a direct link to you. Thank you! Claes and Kerstin, thank you for opening the door to your lab to me! You are so inspirational that my first visit in the Babylab, when you gave me the lab tour and told me with passion about ongoing projects, made me want to stay in the lab for much longer. Thank you for sharing your expertise and knowledge on many occasions and making it possible for all of us to build upon your great achievements.

My research would not have been possible without wonderful babies and their amazing parents, who gave their time, efforts and trust to come to the lab and be part of my work. Scientific advancement of developmental psychology is very much based on your involvement and goodwill! Thank you!

I would like to thank all my co-authors, especially those who contributed their work to the articles included in this thesis (Moritz Daum, Claudia Elsner Andrea Handl, Joshua Juvrud, Katharina Kaduk, Jessica Sommerville, and of course Gustaf Gredebäck) Thank you, for your contribution to my success.

I want to thank Christine Fawcett and Ronald van den Berg for their useful and thoughtful feedback during my final seminar and earlier version of my thesis. It was a pleasure to have you as my examiners.

During my PhD time, I had the opportunity to meet extraordinary people in Uppsala Child and Babylab and the BabyBRAIN group in the Netherlands. You all inspired me with your knowledge, ideas, hard work and made the time at work very enjoyable. Thank you, Sabine Hunnius for opening the door to
your great lab when I moved to the Netherlands and for your very warm wel-
come, support and all the nice conversations we had. I appreciate it very 
much!

I was lucky enough to share my PhD journey not only with great co-work-
ers but also wonderful friends. There are no words to express how grateful I 
am to two amazing girls: Laura and Martyna! Martyna Galazka-Carney, thank 
you for being just you, wonderful friend! I am so happy that we shared this 
time together not only at work but also outside the Blåsenhus. Thank you for 
all your help in improving my work on many different levels through all those 
years. Thank you for offering your time to work on the language check of this 
thesis, endless intellectual discussions and many hours of “chatty-chatty” in 
polish. Laura Sakka, so many time you showed me what good friendship 
means! Thank you for your endless support on so many occasions! Thank you 
for the proofreading and helping me with all administrative work related to 
my thesis production. I am really grateful that I could experience so often your 
good heart and your amazing perspective on life! I appreciate it a lot! Claudia 
Elsner, it was really great to start the PhD journey with you. Your presence 
added so much good laugh to our work. I truly enjoyed your company not 
only every day at work, but also while travelling around the world to learn 
more about our field. Our Montreal “run” and hilarious art work ball will al-
ways stay in my mind. Thank you for all fun memories and intellectual sup-
port. Dorota Green, thank you for answering this email in 2009 from a com-
plete stranger! and later for your friendship and support. Thank you for all 
inspiring scientific discussions, feedback to my work and your help with 
translating my abstract into Swedish. Olga Kochukhova, thank you for all 
your support at the time when a PhD position was only a dream. You believed 
in me more than I did myself, which I am very grateful for. Janny Stapel, the 
way you can handle family, incredible top quality of work, and constant read-
iness to support your friends and co-workers – namely me, is worth a medal. 
You are totally getting one from me! Clara Schmitow, thank you for being 
always so open and relaxed about everything, you impress by your creative 
and positive approach to life! I was great to have you around. Janna Gottwald, 
thank you for inspiring discussions on embodied cognition and all the nice 
moments at work! Hanna Skagerström, it was great to share moments in 
Blåsenhus with you and also to have you always on board for all the social 
events with your extraordinary creativity and humor. You rock! Maria Johans-
son, thank you for all the nice lunch breaks together and great conversations!

Thank you to all my wonderful colleagues, in particular: Gonçalo Barrades, 
Matilda Frick, Kahl Hellmer, Johan Lundin Kelberg, Ben Kenward, Benjamin 
Koch, Marcus Lindskog, Therese Ljunghammar, Pär Nyström, Emilia Tho-
rup, Terje Falck-Ytter, and all the other great members of the Uppsala Child 
and Babylab! You all made my work very enjoyable.
I would also like to express my gratitude to Karin Brocki, Lars-Gunnar Karlsson, Annika Landgren, Håkan Nilsson, Cecilia Sundberg, Cecilia Wåhlstedt for taking care of me with all the administrative work and teaching responsibilities during all those years!

I would also like to thank the “Nijmegen girls”: Beata Grzyb, Anna-Sophie Immel, Hinke Endedijk, Stefania Vacaru, thank you for supporting me during difficult moments and turning the new land into a home for me.

Special words of appreciation go to my friends: wonderful Zuzanna Zelazny, Kasia Paszke, Margot van Wermeskerken-Drijfhout, Marta Trębicka-Ryś, thank you for all those years of friendship! You are all amazing!

Costis Chatzidakis, thank you for keeping an eye on the artistic side of my thesis and supporting it with your extraordinary talent!

Most importantly, I want to express my deepest gratitude to my beloved family and relatives for keeping me grounded in constant support, care, and encouragement. My parents, Irena and Władysław: Z całego serca dziękuję za Waszą bezwarunkową miłość i ogromne wsparcie! Here, special words of appreciation go to three super women: my amazing mum, my awesome sister Agnieszka and my wonderful mother-in law Froukje. I would not make it without you! Thank you for your endless help. Kocham Was i dziękuję!

Gabriel and Esther, you gave me the most incredible lessons and insights into developmental psychology! I could not dream of better teachers then both of you! You amaze me every day!

Last, but certainly not least, Jimmy, thank you for being my other half and ALWAYS being there for me. Without you I would never accomplish this journey, I would actually not even start. You found the Babylab in the far, far away Sweden especially for me and later gave me support in all possible meanings of this word. You even created the whole Matlab course when I needed to learn it, everything especially for me. Your love, open mind, exceptional intelligence and ability to keep calm are precious. You are simply THE BEST!
References


80


A doctoral dissertation from the Faculty of Social Sciences, Uppsala University, is usually a summary of a number of papers. A few copies of the complete dissertation are kept at major Swedish research libraries, while the summary alone is distributed internationally through the series Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Social Sciences. (Prior to January, 2005, the series was published under the title “Comprehensive Summaries of Uppsala Dissertations from the Faculty of Social Sciences”.)