Doctoral thesis submitted to
the Faculty of Behavioural and Cultural Studies
Heidelberg University
in partial fulfillment of the requirements of the degree of
Doctor of Philosophy (Dr. phil.)
in Psychology

Title of the publication-based thesis

Why do infants imitate selectively?
Neural correlates of infants' action understanding in the head-touch paradigm

presented by
Miriam Langeloh

year of submission
2019

Dean: Prof. Dr. Dirk Hagemann
Advisors: Prof. Dr. Stefanie Hoehl
Prof. Dr. Sabina Pauen

ACKNOWLEDGEMENTS

I am deeply grateful to everyone who guided and accompanied me throughout my PhD journey.

First of all, I would like to thank Prof. Stefanie Hoehl. Dear Steffi, thank you so much for your support and your trust. Thank you for giving me the freedom to conduct the research that I was interested in. Working and discussing research with you has always been a great pleasure, from the first day of my master's studies onwards. In addition, thank you for inviting me to come to Leipzig to the MPI CBS with you. I cannot put in words how much I have learned during this time and how much I have grown as a researcher. Thank you!

Furthermore, I would like to thank Prof. Sabina Pauen. Dear Sabina, thank you so much for believing in me and, above all, for telling me. Thank you for fruitful discussions on the most exciting topics – infants & brains, of course. Beyond that, I would like to thank you for your advice – be it professional or personal. Thank you so much!

I would also like to thank Prof. Daniel Haun for being such a helpful TAC advisor at IMPRS. Thank you for your interest in my research and especially for taking so much time to discuss it with me.

Many thanks go to my co-authors Stefanie Hoehl, Sabina Pauen, David Buttelmann, Daniel Matthes, and Susanne Grassmann. Working with you was fun and very productive.

A special thanks goes to the IMPRS on Neuroscience of Communication. Thank you for offering me the opportunity to participate in your excellent seminars and workshops and for the financial support.

In addition, I would like to thank the secretaries, MTAs, PsTAs, and student assistants for their help in recruiting and testing babies. A special thanks goes to

Christiane Fauth-Scheurich at Heidelberg University. Thank you for always being there for me. Moreover, I am grateful to the video models of my stimuli Janina, Linda, Alex, Jana, Philipp, and Maxi. Of course, I would also like to thank all parents and infants for participating in my studies.

Furthermore, I would like to thank my colleagues and friends, I have worked with during the journey of my PhD. Thank you so much Heidelberg colleagues for making work feel like home. Christine, thank you from the bottom of my heart for sharing your knowledge on EEG with me and helping me to set up my first study. Thank you for always listening and growing together. Steffi P., you are such a lovely friend and an impressive researcher. Thank you so much for your help and advice and for sharing your excitement about research with me. Hanna, it was a pleasure going through the ups and downs of PhD life in an office together with you! Thanks for always being honest with me and bringing lots of Schabernack into my life. Thank you, Ezgi, for believing in me – that was highly encouraging! Thank you, Daniel, for your positive attitude, the fun lunches and, of course, the programming.

I would like to extend my thanks to all of my friends. Thank you for your endless support. A special thanks goes to my best friend, Aliner. Thank you for listening to me no matter what time and day. Thanks for cheering me up and sending me extraordinarily motivating postcards and gift boxes. You are the best! Furthermore, I would like to thank Susan. Thank you so much for always being there for me – be it for discussing research or any other topic. You are my person (for anyone who hasn't watched Grey's anatomy – that means a lot)! Nadene, Lena, & Charlotte, meeting you here in Leipzig was the greatest gift! Thank you for your emotional and research support. Thank you for fun lunches and girls (or mixed) nights. Charlotte & Robert, you have been like a family to me in Leipzig. Thanks for always making me feel welcome and for all the unforgettable moments we have had together. I would also like to thank the most glorious tennis team: Thank you 3. Damen LTC for distracting me with the most fun thing on this planet – TENNIS! Thank you for listening and caring so much, also off-court. #MORETHANATEAM

Finally, I would like to thank my family. Mami, it is difficult to put in words how grateful I am to you. Seeing how proud you are of me and how much you love me has always given me the strength to continue this journey. Thank you for your calls and postcards and for never giving up on me. Papi, I am deeply thankful to you for being there for me. You have always been a great example for me and I am so grateful and happy to have you in my life. Of course, I would also like to thank my kind (and also sometimes a bit crazy :D) brothers, Jonas and David, and my lovely sister, Diane, for making my life joyful and for accepting that I always had to ‘get back to work’ (that is over – for now ;)).

Last but not least, I would like to thank Philipp. Thank you for sticking with me – no matter what. Thank you for moving to Leipzig with me so that I can pursue my dreams. Meeting you at the beginning of this journey was the best thing that has ever happened to me. You are the most amazing person and having you in my life is better than anything I could have ever hoped for. Ich danke dir von tiefem Herzen!

TABLE OF CONTENTS

LIST OF SCIENTIFIC PUBLICATIONS FOR THE PUBLICATION-BASED THESIS

I. Manuscript

Langeloh, M., Buttelmann, D., Matthes, D., Grassmann, S., Pauen, S., & Hoehl, S. (2018). Reduced mu power in response to unusual actions is context-dependent in 1-year-olds. *Front Psychol, 9*, 36. doi:10.3389/fpsyg.2018.00036

II. Manuscript

Langeloh, M., Buttelmann, D., Pauen, S., & Hoehl, S. (2019). 12- to 14-month-olds expect unconstrained agents to act efficiently: ERP evidence from the head-touch paradigm. *Manuscript under review in Developmental Psychology.*

III. Manuscript

Langeloh, M., Pauen, S., Buttelmann, D., Hoehl, S. (2019). One-year-olds' event-related potentials differentiate expected from unexpected action outcomes without context information. *Manuscript under review in Infancy.*

1. INTRODUCTION

Suppose you come home with your hands full of groceries, pushing the front door open with your shoulder. Your 1-year-old daughter stands before you and watches you closely. What would she do after you entered? Perhaps she would close the door with her hands, as usual. Would you expect a different behavior if you were being silly, pushing the front door open with your shoulder, even though your hands had been free? Indeed, research suggests that in this case, your daughter might take up the game and imitate your unusual action, opening or closing the door with her shoulder (Gergely, Bekkering, & Király, 2002). Infants watch their parents performing actions that are more or less familiar every day. What factors determine whether the infant copies your exact action, or instead performs a more efficient action that leads to the same goal as your original action?

The first years of life are a period of intense learning in which infants rapidly acquire social and physical skills to navigate through our complex world successfully. Infants can learn tremendously from observing their environment and the people acting in it, as well as from interacting with the environment themselves. Within these interactions, infants' early socio-cognitive skills are trained. A vital skill is to understand others' actions as being goal-directed. Action understanding enables infants to predict and interpret others' behavior and to react accordingly (Csibra & Gergely, 2007; Gredebäck & Daum, 2015). It is at the core of social cognition and a precursor to the development of theory of mind, the ability to attribute mental states to oneself and others (e.g., Aschersleben, Hofer, & Jovanovic, 2008; Filippi, Choi, Fox, & Woodward, 2019).

Infants can increase their knowledge of others' and their own goal-directed actions by observing and imitating others. Imitation, that is copying a behavior that another person has previously demonstrated, is one of the first forms of cultural learning and an important social learning mechanism (Jones, 2009; Paulus, 2011; Tomasello, 1999). However, infants do not blindly imitate every action they observe. The central question for the infant still remains of which actions she should attend to and imitate and which ones she can ignore.

Let us return to the example of opening a door and say your infant imitates the unusual action. She opens the door with her shoulder after watching you doing this with your hands being free. The following question immediately arises: why does your infant selectively imitate this unusual action, that is, why does she alter her actions depending on whether or not your hands were free?

Examining situations in which infants selectively imitate actions provides a useful research approach to gain insights in their understanding of others' goal-directed actions. Based on these research findings, we can evoke and adequately foster the ideal observational learning processes. So far, scientists conducting behavioral research have proposed contrasting theoretical accounts, which aim to tackle the underlying mechanisms of selective imitation. One account suggests that infants selectively imitate unusual actions because they are surprised by the inefficiency of the action and want to figure out the reason why an actor would possibly behave that way (Gergely et al., 2002; Gergely & Csibra, 2003). In contrast, it has been proposed that when the infant's body posture is highly similar to the observed position of the adult, an automatic motor program is activated. This leads to imitation because action execution and observation are linked (Paulus, Hunnius, Vissers, & Bekkering, 2011a, 2011b).

Despite the large body of behavioral research on selective imitation, the question of what are the neural mechanisms underlying these processes remains unanswered. What happens in infants' brains when they observe actions that elicit selective imitation? In my dissertation, I will present three studies investigating the cognitive processes involved in infants' action understanding in an adaptation of a widely applied behavioral paradigm. In the first part, I will give a short introduction to selective imitation and how it has been measured so far. I will then introduce two contradicting theoretical explanatory accounts, and a more recent integrative approach combining both accounts (Zmyj & Buttelmann, 2014). I aim to add the underlying cognitive processes to this recent integrative model. To this end, I conducted three empirical studies to test the neural indices of infants' action understanding. I will summarize these studies and finally, I will discuss the findings in the light of current theories on infants' action understanding and propose directions for future research.

2. WHAT IS SELECTIVE IMITATION?

As mentioned in the Introduction, imitation is a social learning mechanism to transfer information between individuals, evident already in infancy (Jones, 2009). To date, various definitions of imitation have been brought forward. In line with Paulus (2011), I distinguish between behavior-based definitions and intention-based definitions. Behavior-based definitions of imitation refer to "copying by an observer of a feature of the body movement of a model" (Heyes, 2001; p. 254). This does not apply if an action co-occurs by chance or if the action effect is not specific to the executed action (Heyes, 2001; Jones, 2007; Paulus, 2011). Intention-based definitions, on the other hand, claim that imitative learning only comprises situations in which someone recognizes and intentionally reproduces an intended human action. Accordingly, imitation needs to be differentiated from stimulus enhancement, i.e. attention being drawn to the relevant object, and emulation, i.e. copying the end-state only independent of the action means (Tomasello, 1999; Tomasello & Carpenter, 2005; Want & Harris, 2002; Whiten, Horner, & Litchfield, 2004; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). Thus, behavior-based definitions, in contrast to intention-based definitions, do not judge or specify the underlying mechanisms and leave the investigation of the exact mechanisms open for research (Paulus, 2011). In my thesis I apply a behavior-based definition, defining imitation as copying an action that has previously been demonstrated by another person, not requiring intentional processes.

Coming back to infants – what kind of actions do they imitate and what can we conclude from that as developmental scientists? Meltzoff (1995) has demonstrated that 18-month-old infants imitated an intended action goal after observing a failed attempt of an adult model to perform such an action. For instance, infants successfully pulled apart two pieces of a dumbbell, even though the adult demonstrator failed to separate the two pieces (not, however, when they observed the action attempts of a non-human mechanical device). Similarly, 14- to 18-month-olds were more likely to imitate transitive actions, if an adult model commented them with "there" compared to "whoops" (Carpenter, Akhtar, & Tomasello, 1998). One interpretation of these findings is that infants imitate selectively depending on the intention of the model (for alternative interpretations, see Heyes, 2001; Jones, 2009).

Irrespective of the interpretation, these two examples show that from the age of 14 months onwards infants do not just blindly imitate every action they see – they imitate selectively. Beyond intentions (Buttelmann, Carpenter, Call, & Tomasello, 2008; Carpenter et al., 1998), infants' selective imitation depends on characteristics of the model such as age (Zmyj, Aschersleben, Prinz, & Daum, 2012), reliability (Zmyj, Buttelmann, Carpenter, & Daum, 2010), group membership (Buttelmann, Zmyj, Daum, & Carpenter, 2013), and ostensive communication (Király, Csibra, & Gergely, 2013). In addition, external factors such as the necessity of a performed action (Nielsen, 2006) and the context or the constraints of a given situation (Gergely et al., 2002) influence infants' selective imitation. In particular, the effects of situational constraints on infants' selective imitation have led to a lively debate in cognitive developmental psychology (Paulus, 2012b; Zmyj & Buttelmann, 2014). Selective imitation which is dependent on the action context has mainly been tested with the well-known behavioral head-touch paradigm (Gergely et al., 2002). In the following section, I will elaborate on the head-touch paradigm, which I have adapted in my thesis to study neural indices of infants' action understanding (see Chapter 4).

In the seminal study by Gergely et al. (2002), 14-month-old infants observed an adult model turning on a lamp with her head (head touch) within two different action contexts. One group of infants watched the unusual action while the model's hands were free (hands-free condition), similar to the original setting by Meltzoff (1988). The second group of infants watched the same unusual action while the model's hands were occupied with a blanket (hands-occupied condition). One week later, infants were given the opportunity to play with the lamp themselves. Results revealed that infants imitated the unusual head-touch action more often in the hands-free (69 %) than in the hands-occupied condition (21 %). Thus, 14-month-olds selectively[1] imitated an unusual and inefficient action whenever the model had no discernible reason to perform the action in such a manner. Copying an inefficient action seems to be paradoxical at first sight and, therefore, caught the attention of many researchers.

---

[1] Please note that in the literature this phenomenon is often termed rational imitation. However, I will refer to it as selective imitation to avoid any judgment about the underlying mechanisms.

Since the original demonstration, this finding has been replicated multiple times with similar paradigms (Gellén & Buttelmann, 2017; Schwier, von Maanen, Carpenter, & Tomasello, 2006), younger age groups (Zmyj, Daum, & Aschersleben, 2009), humans' closest relatives, chimpanzees (Buttelmann, Carpenter, Call, & Tomasello, 2007), and even dogs (Range, Viranyi, & Huber, 2007) (but for an alternative explanation in dogs, see Kaminski et al., 2011). For instance, Zmyj et al. (2009) added a novel condition to the head-touch paradigm, in which the model's hands were involuntarily restrained by being tied to table (hands-restrained condition). Twelve-month-old infants imitated the unusual head touch significantly more often in the hands-free (75 %) compared to the hands-restrained (25 %) but not to the hands-occupied condition (50 %). Thus, past research suggests that selective imitation of unusual actions with varying situational constraints develops around the age of 12 months for explicit, involuntary constraints (e.g., hands are restrained by duct tape; Zmyj et al., 2009) and at the age of 14 months for voluntary, implicit constraints (e.g., holding a blanket; Gergely et al., 2002).

3. WHY DO INFANTS IMITATE SELECTIVELY? RECENT EXPLANATORY ACCOUNTS

In the literature there is consensus concerning the existence of selective imitation. However, explanations differ with regard to the level of cognitive abilities considered requisite for selective imitation and underlying mechanisms. In the following section, I will review the two current explanations of selective imitation in the head-touch paradigm: rational- and non-rational imitation accounts.

3.1 RATIONAL-IMITATION ACCOUNTS

Proponents of the rational-imitation accounts claim that selective imitation occurs as a result of an infant's efficiency evaluation of an action within a specific action context (Buttelmann et al., 2008; Gergely et al., 2002). By applying the principle of rational action, infants can relate and evaluate three aspects of reality in terms of another person's goal-directed action: situational constraints (here: hands free or occupied), goal states (here: turn on the light), and action means (here: head touch). When given information about any two of these three elements, infants can predict the third aspect based on the assumption that agents execute actions with the most efficient means available (Gergely & Csibra, 2003). Consequently, whether infants imitate a demonstrated action or not depends on infants' rational evaluation of the model's behavior. When the model's hands were occupied, infants interpreted the head touch as being the most efficient means to turn on the lamp. This implies that the model would have used her hands if that had been possible. As infants did not share this situational constraint, they predominantly used their hands to illuminate the lamp. However, when the model's hands were free while she turned on the lamp with her head, infants were surprised and might have surmised that the unusual head touch offers some advantage or a learning opportunity (Gergely et al., 2002; Király & Oláh, 2018). Thus, infants may have inferred that the head touch is the most efficient means in this situation, which led to selective imitation of the respective action.

This theory does not necessarily require infants to ascribe intentions to the model during action evaluation (Gergely & Csibra, 2003). The teleological stance posits that infants interpret actions as goal-directed and evaluate their efficiency based on the principle of rational action. However, the principle of rational action can also be applied to a mentalistic stance, that is, selective imitation is guided by the contents of a model's mental state. In this view, infants were more likely to imitate the unusual head touch in order to figure out the reason why the model acted in this peculiar way (Buttelmann et al., 2008).

Note that researchers have recently combined the theory of rational action with the theory of natural pedagogy (Csibra & Gergely, 2009; Gergely & Jacob, 2012). In this tenet, infants are prepared to acquire novel or arbitrary actions by relying on others' communicative signals (e.g., eye contact). They expect a communicative agent to demonstrate relevant and novel information which should be reproduced (Gergely & Jacob, 2012). When infants observe a goal-directed action that cannot be explained by the principle of rational action and is accompanied by communicative cues, infants may assume that this arbitrary action is a subgoal of a higher-order goal. Rationality is adjusted to the subgoal such that infants may conclude that the goal is to touch the lamp with the forehead (Király et al., 2013).

To sum up, according to rational-imitation accounts, infants hold expectations of future actions and these expectations are violated when observing inefficient action outcomes. The violation of expectation (VOE) could result in increased imitation of the observed unusual action either because infants assume this action to have an advantage and be the most efficient means (teleological) or because they want to learn the reason why the model performed this action (mentalistic).

3.2 NON-RATIONAL IMITATION ACCOUNTS

In contrast, two non-rational imitation accounts have been brought forward, which relate infants' selective imitation to more basic, low-level processes, such as motor resonance or attention (Beisert et al., 2012; Paulus, Hunnius, et al., 2011a, 2011b). Supporters of the motor resonance account, also called the two-stage model, claim that two factors guide infants' imitation: first, action observation and action execution are automatically linked via simulation processes (i.e., motor resonance). Infants are more likely to imitate actions that are already represented in their own motor repertoire and elicit high motor resonance (Paulus, Hunnius, & Bekkering, 2013b; Paulus, Hunnius, et al., 2011a, 2011b). Second, salient action effects influence infants' imitative behavior (Elsner & Aschersleben, 2003; Hommel, Muesseler, Aschersleben, & Prinz, 2001). The two-stage model can also explain why infants would imitate the head touch more frequently in the hands-free condition. At 12- to 14-months of age, infants need to physically support themselves by putting their hands on the table next to the lamp in order to touch the lamp with their head. This is similar to the adult model in the hands-free but not in the hands-occupied condition, which therefore elicits more motor resonance in the hands-free condition.

The alternative low-level perceptual-distraction account (Beisert et al., 2012) states that selective imitation occurs because of differences in attention. Infants may have been distracted by the unfamiliar look of the blanket being wrapped around the model's torso and, thus, imitated the head touch less frequently in the hands-occupied condition (Beisert et al., 2012). However, recent eye-tracking findings challenge this view, for instance, because 14-month-olds and adults did not differ in their amount of time spent looking at the model's head or torso between the hands-free and hands-occupied condition (Buttelmann, Schieler, Wetzel, & Widmann, 2017; Elsner, Pfeifer, Parker, & Hauf, 2013; Kolling, Óturai, & Knopf, 2014).

To summarize, the two-stage model and the perceptual-distraction account assume that differences in imitation frequency can be explained by differences in motor resonance or attention. Thus, non-rational imitation accounts[2] depart from rational-imitation accounts in that they do not make any claims about infants' action expectations. However, in this thesis, I aim to investigate the neural underpinnings of infants' action evaluations based on the principle of rational action. Hence, non-rational imitation accounts are not tested directly in this dissertation, but need to be considered for a broader interpretation of the results.

3.3 EMPIRICAL EVIDENCE FOR THE MECHANISMS OF INFANTS' ACTION PERCEPTION BEYOND SELECTIVE IMITATION

Interestingly, infants' selective imitation behavior informs us about infants' underlying action perception and action understanding. Action perception is an umbrella term which encompasses the mechanisms taking place during the

[2] From now on, when I use the term non-rational imitation accounts, I only refer to the two-stage model as the perceptual-distraction account has recently been challenged by several eye-tracking experiments (e.g., Buttelmann et al., 2017).

processing and perception of actions. These mechanisms range from a basic sensory perception to an in-depth action understanding. Note that distinct aspects, which occur in sequence, are subsumed under the generic term action understanding (Figure 1; Gredebäck & Daum, 2015). First of all, infants need to identify an agent. Second, infants have to allocate covert attention to the future state of the agent (priming; e.g., Wronski & Daum, 2014) and can then predict action outcomes (prediction; e.g., Falck-Ytter, Gredebäck, & von Hofsten, 2006). Finally, after an action goal is achieved, infants can evaluate action outcomes (evaluation; e.g., Reid et al., 2009). In the current thesis, I examine the cognitive mechanisms underlying action evaluation based on predictions of the principle of rational action (Gergely & Csibra, 2003). As mentioned above, action evaluation can be assessed by overt imitative responses. Yet, action evaluation can as well be measured by infants' implicit reactions to action outcomes, that is, by looking times, pupil diameters and neural activity in the electroencephalogram (EEG).

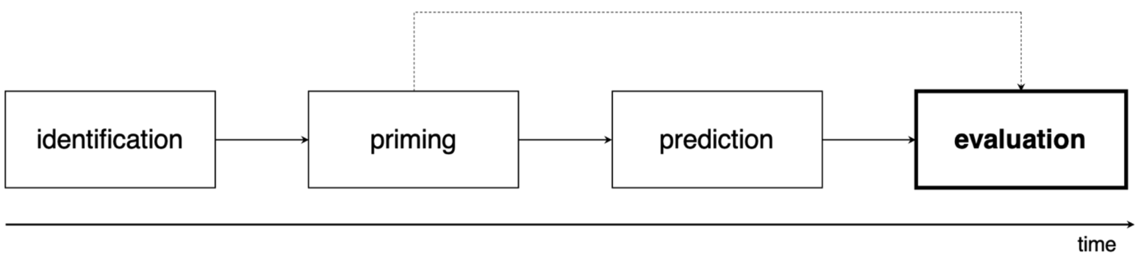

Figure 1. Timeline of action perception adapted from Gredebäck & Daum (2015). The underlying processes of action evaluation are assessed in the studies of this thesis.

Csibra and Gergely (2007) have posited three cognitive mechanisms of action evaluation or goal attribution (i.e., why an action is performed) in infancy, which are highly comparable to the mechanisms suggested by rational- and non-rational imitation accounts: action-effect associations, simulation procedures, and teleological reasoning. Rational-imitation accounts mainly refer to teleological reasoning, whereas non-rational imitation accounts rather consider action-effect associations and simulation procedures. Consequently, I propose that experimental evidence for the underlying mechanisms of action evaluation can also be interpreted in favor of the rational- or non-rational imitation accounts respectively. In the following section, I will review developmental research on infants' action perception, focusing on action evaluation in particular. With this overview I would like to emphasize that the debate in developmental psychology about the level of infants' cognitive abilities goes beyond the topic of selective imitation in the head-touch paradigm. The framework on the cognitive mechanisms of goal attribution (Csibra & Gergely, 2007) allows for a more general examination and discussion of the current results with regard to action perception (see Chapter 5).

On the one hand, there is evidence that teleological reasoning underlies infants' action perception, in line with the rational-imitation accounts. The basic component of teleological reasoning, interpreting others' actions as goal-directed, has been shown in infants as young as 6 months. In her seminal paradigm, Woodward (1998) habituated infants to a hand grasping one of two toys. The location was switched in the test phase and infants looked longer (dishabituated), indicating expectancy violation, at the scenario where the hand grasped the new toy at the old location (for an alternative interpretation, see Ganglmayer, Attig, Daum, & Paulus, 2019).

Furthermore, there is evidence for the second component of teleological reasoning, that is, infants applying the principle of rational action to human (Sodian, Schoeppner, & Metz, 2004) and non-human agents (Csibra, Bìró, Koós, & Gergely, 2003; Gergely, Nádasdy, Csibra, & Bíró, 1995). For instance, 9-months-old infants expected a circular object to take a direct, efficient path, rather than an indirect, inefficient path, when moving to a goal location (Csibra, Gergely, Bíró, Koós, & Brockbank, 1999). Further support for infants predicting and evaluating action outcomes based on the principle of rational action comes from studies with familiar everyday life actions. While observing inefficient feeding actions (i.e., food is placed on someone's back of the hand rather than into the mouth), 6- and 12-month-olds' pupils dilated, suggesting increased arousal and possibly VOE (Gredebäck & Melinder, 2010). When using more explicit, external constraints, even 4-month-olds' pupils dilated towards inefficient eating actions (Gredebäck & Melinder, 2011). Importantly, these reactions to inefficient outcomes are not just responses to novelty but indicate teleological evaluations as only the action context (i.e., an obstacle being present or not) was manipulated. In addition, infants anticipate and, thus, expect that adults use familiar objects efficiently (e.g., putting a phone to the ear but not to the head). Infants fixated the efficient action goal even before the action outcome was achieved, measured by infants’ anticipatory gaze shifts, by the age of 6 months (for objects) and 12 months (for feeding actions; Gredebäck & Melinder, 2010; Hunnius & Bekkering, 2010).

Similarly, studies employing neuroscientific methods, such as the EEG, have shown that infants anticipate and evaluate eating and drinking actions. When 9-month-olds observed unexpected action outcomes (e.g., a pretzel put to the head instead of to the mouth), their brains responded with an N400 component, reflecting the detection of violations of semantic action contexts (Kaduk et al., 2016; Reid et al., 2009). Furthermore, Stapel, Hunnius, van Elk, and Bekkering (2010) found stronger mu desynchronization, associated with motor activation, during the observation of unexpected object-directed actions in 12-month-olds (for more details on these findings, see Study 1 & Study 2 in Chapter 4).

To summarize, the presented studies are based on the idea that infants hold expectations about how other people should perform specific actions, i.e., in the most efficient manner. If this expectation is violated, infants respond with longer looking times, dilated pupils, increased negativity in their event-related potentials (ERPs) or with stronger mu desynchronization.

On the other hand, there is evidence suggesting that action-effect associations and simulation procedures underlie infants’ action perception, as proposed by the non-rational imitation accounts (Paulus, Hunnius, et al., 2011a, 2011b). Motor resonance and, thus, motor abilities, experiences and action effects seem to influence how infants perceive others’ actions (for a review on how experience shapes infants' action understanding, see Hunnius & Bekkering, 2014). Behavioral research has shown that infants are more likely to imitate actions producing action effects (for a review on action-effect learning, see Elsner, 2007; Hauf, 2007). In addition, Paulus et al. (2013b) found in an observational training study that 9-month-olds represent the effects of others’ actions in their own motor repertoire. That is, infants’ brains responded with stronger mu desynchronization, indicating motor activation, to the sound of a rattle they had been trained with before compared to an unfamiliar rattle sound. Consequently, infants acquired action-effect associations through observational learning but also through own experience. After being trained to shake the rattle themselves, 8-month-olds' brains also responded with stronger mu desynchronization when listening to the learned rattle sound compared to a novel sound (Paulus, Hunnius, van Elk, & Bekkering, 2012).

Further EEG studies have demonstrated that the observation of actions that are already in the infants' motor repertoire leads to a stronger activation of the motor system (Reid, Striano, & Iacoboni, 2011; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). For instance, 14- to 16-month-olds showed stronger mu desynchronization towards videos of a crawling compared to a walking infant. EEG findings were closely related to infants' own crawling experience (van Elk et al., 2008). Similarly, in eye-tracking studies, 12-month-olds only predicted human agents' goal states when they were already able to perform the action themselves. No proactive eye movements were found for mechanical motions (Falck-Ytter et al., 2006; Sommerville & Woodward, 2005; Sommerville, Woodward, & Needham, 2005).

To sum up, according to this line of research, infants' understanding of others' actions is shaped by motor abilities and action effects rather than by expectations based on rationality. Taken together, the empirical findings outlined in this chapter suggest that both mechanisms, proposed by the rational- and non-rational imitation accounts, can be supported by current developmental research on infants' action perception and understanding.

3.4 INTEGRATIVE MODEL & AIM OF THE CURRENT THESIS

This short excursus on infants' action perception and understanding has demonstrated evidence for the underlying mechanisms suggested by both rational- and non-rational imitation accounts (i.e., rational evaluation and motor resonance combined with action effects). In my view, each account in itself cannot comprehensively explain why infants may have imitated selectively in the head-touch paradigm.

In particular, rational-imitation accounts fail to explain how an observed behavior is transformed into a motor command in the first place (Zmyj & Buttelmann, 2014). Furthermore, the rational-imitation accounts are very hard to falsify at the current stage of research. Both outcomes, that is when infants do not reproduce the observed head touch in the hands-occupied condition and when infants do reproduce the unusual head touch in the hands-free condition are interpreted in favor of the rational-imitation accounts. Thus, by only focusing on the evaluation of rationality, some important puzzle pieces involved in selective imitation may be ignored (Király & Oláh, 2018).

Likewise, even though motor resonance and action effects may influence infants' imitation in general, no empirical evidence has clearly demonstrated that solely these two aspects affect selective imitation in the head-touch paradigm. Paulus, Hunnius, et al. (2011b) introduced novel conditions to the head-touch paradigm to verify the validity of the non-rational imitation accounts (two-stage model; Paulus, Hunnius, & Bekkering, 2013a; Paulus, Hunnius, et al., 2011a, 2011b). However, the interpretation of these conditions is somewhat ambiguous. For instance, in the so-called button condition, the model's hands were free but the blanket around the torso was fixated by a button. In the button condition infants imitated the head touch with a lower frequency than in the hands-free condition – in contrast to the predictions of the rational-imitation accounts. Yet, it is not clear at this point whether infants have a conceptual understanding of the function of a button (for a more elaborated discussion, see Buttelmann & Zmyj, 2012). Furthermore, non-rational imitation accounts cannot explain selective imitation in studies in which the context differed but the body posture of the model was the same in both conditions (Buttelmann et al., 2008; Schwier et al., 2006; Zmyj et al., 2009) or when the body position differed, but no selective imitation occurred (Király et al., 2013).

Therefore, it may be more adequate to step away from a dichotomous view of rich and lean interpretations of infants' cognitive abilities (Racine, 2012) and consider an integrative model of selective imitation of the head touch. Zmyj and Buttelmann (2014) have suggested that both motor resonance and rational evaluation operate on different processing levels and are not mutually exclusive. Motor resonance may explain why infants imitate at all, whereas the rational evaluation of action outcomes may account for selective imitation. Within this integrative framework, motor resonance is described as an automatic bottom-up process. It leads to imitation whenever the situational constraints are the same for the infant and the adult model, for a familiar action or at least for familiar action elements (e.g., bending the upper body forward or touching an object with the head; for a hierarchical organization of actions, see Byrne & Russon, 1998). A lack of motor resonance can lead to inhibition of imitation. However, if the situational constraints differ between infant and adult model, the rational evaluation (including ostensive cues, goals, means, and situational constraints) inhibits automatic imitation in a top-down process. The infant will then perform the most efficient action within his or her own action context. Importantly, the rational evaluation can inhibit automatic imitation even if the infant and the model have the same situational constraints, for instance, when an infant observes an unusual, inefficient action (e.g., a person turns on a lamp with her head despite her hands being free). Infants expect agents to act efficiently and, thus, they assume that this unusual action has an advantage or they would like to figure out the reason why a person performed this inefficient action.

As outlined in the last paragraph, the integrative model (Zmyj & Buttelmann, 2014) is a first attempt to combine two contradicting accounts and it provides a promising framework to explain the phenomenon of selective imitation in the head-touch paradigm. Still, the model postulates only theoretical assumptions and does not adequately address the underlying mechanisms. To answer the question why infants selectively imitate unusual actions, we need to measure the underlying cognitive mechanisms on a neural level beyond overt imitative behavior. In the following three studies, I aim to elucidate the underlying cognitive mechanisms of infants' action understanding in an adaptation of the head-touch paradigm, which has previously been used in behavioral research. Specifically, in this thesis, I test one puzzle piece of the integrative model, based on the rational-imitation accounts. Do infants hold expectations about others' actions (presumably based on the principle of rational action) in the head-touch paradigm? If so, I propose that these expectations should be violated while observing an unusual, inefficient head touch when the model's hands are free (Figure 2). In contrast, expectations should not be violated when the model's hands are restrained while performing a head touch (for details on the rationale, see Chapter 4).

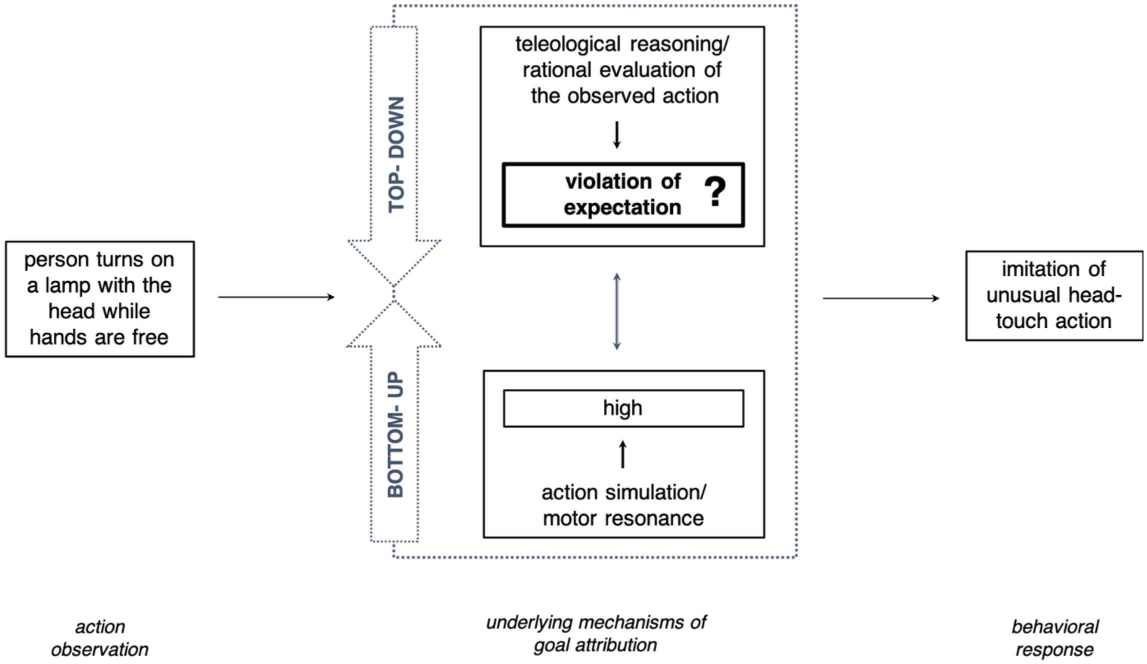

Figure 2. Adaptation of the integrative model by Zmyj & Buttelmann (2014). Note that this graph only illustrates a flowchart for the observation of a head touch in the hands-free condition. Neural correlates of the top-down processes based on the assumptions of the rational-imitation accounts (Gergely et al., 2002; Gergely & Csibra, 2003) are tested in this thesis.

4. EXPLORING INFANTS' NEURAL CORRELATES OF ACTION UNDERSTANDING IN THE HEAD-TOUCH PARADIGM

As outlined in the previous chapter, the debate on the cognitive mechanisms driving infants' selective imitation is still controversial. So far, behavioral research has examined in which situations infants imitate selectively to investigate infants' action understanding (e.g., Gergely et al., 2002; Zmyj et al., 2009). That is, infants' overt behavioral responses have been studied. In contrast, in the current thesis, I employ a novel research approach by measuring infants' neural processes underlying action understanding in an adaptation of the head-touch paradigm. Analyzing infants' neural indices of action understanding will help to infer why infants may have imitated selectively. In particular, I test infants' neural underpinnings of action evaluation based on predictions of the principle of rational action. Note that, previous selective imitation studies measured the behavioral response as a consequence of action evaluation, whereas in my thesis I directly assess the neural processes during action evaluation (illustrated by the rectangle with the dotted lines in Figure 2).

To this end, we adapted the behavioral head-touch paradigm to a neurophysiological paradigm using EEG recordings. Electrophysiological measures are perfectly suited to study infants' responses to observed actions (for a developmental cognitive neuroscience perspective on action understanding, see Ni Choisdealbha & Reid, 2014), because different stages of action processing can be reflected in the EEG response with a high temporal resolution. Furthermore, the EEG is suitable for young age groups and can be acquired during passive-viewing paradigms, in which no behavioral response is needed (for an overview on EEG in infants, see DeBoer, Scott, & Nelson, 2007; Hoehl & Wahl, 2012). Distinct analysis methods reveal different characteristics in the EEG data that are associated with specific cognitive processes. Here, I employ two analysis methods: EEG frequency based on fast Fourier transformations (FFTs; Study 1) and EEG amplitude based on ERPs (Studies 2 & 3).

Rational-imitation accounts imply that selective imitation can be explained by differences in VOE in response to the head touch between the hands-free and hands-occupied condition. Thus, the rationale of our approach was to design a paradigm that tests infants' action expectations in the head-touch paradigm (Figure

3). Note that non-rational imitation accounts do not make any claims about expectations and can, thus, neither be supported nor be completely ruled out by our research.

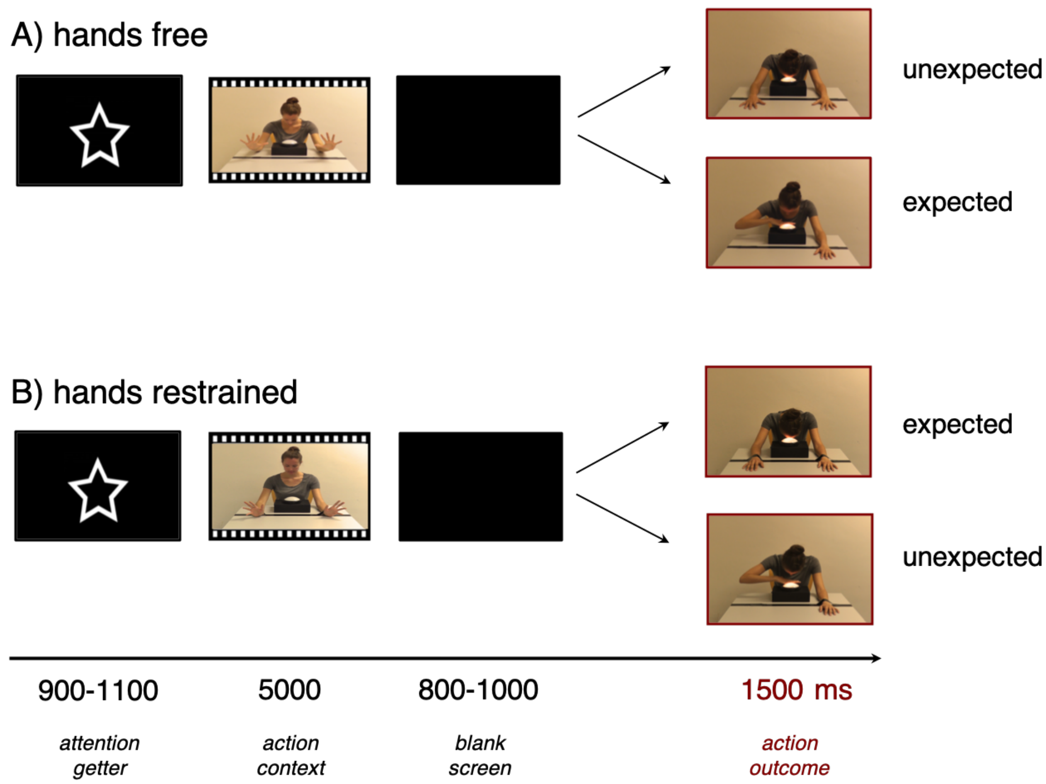

Figure 3. Illustration of the modified head-touch paradigm. Stimulus examples for the A) hands-free and B) hands-restrained condition. In Study 1 and Study 2, infants were presented with information on the action context in short video sequences. Subsequent static images illustrated expected and unexpected action outcomes. Note that in Study 3, we presented only action outcomes in the A) hands-free condition. Models did not establish eye contact with infants. EEG activity was analyzed in response to the action outcomes only.

In Study 1 and Study 2, each trial consisted of a video sequence and a static action outcome. We first presented infants with short videos (5000 ms) of adult models demonstrating that their hands were free (hands-free condition) or restrained (hands-restrained condition) in a between-subjects design (adapted from Gergely et al., 2002; Zmyj et al., 2009). Subsequent static images (1500 ms) showed action outcomes. The images depicted the same models turning on a lamp or a soundbox (i.e., a toy that makes a sound when being touched) using either their head or their hand (see Figure 3 for stimulus examples). Within each between-subjects condition, infants received the same information on the action context and only the action means to achieve the action outcome differed (hand touch or head touch). Consequently, whether hand- or head-touch action outcomes were evaluated as expected or unexpected depended on the action context only (hands free or hands restrained). Besides, this paradigm allowed us to analyze both FFTs and ERPs of the same EEG data as we did not present video sequences only (cf Stapel et al., 2010) but a combination of videos and static images. In Study 3, we slightly adapted our paradigm of the hands-free condition. Here, only static images, illustrating action outcomes without prior information on the action context, were presented.

After having introduced the EEG paradigm used in this thesis, I will summarize the main results of the three studies.

4.1 STUDY 1 – MOTOR SYSTEM ACTIVATION DURING ACTION EVALUATION

Past research has predominantly investigated infants' action prediction and evaluation in behavioral imitation or eye-tracking paradigms. Typically, infants responded with longer looking times (Woodward, 1998), dilated pupils (Gredebäck & Melinder, 2010, 2011) and increased imitation rates (Gergely et al., 2002) to inefficient or unexpected events.

The literature suggests that the motor system plays a pivotal role in predicting and evaluating others' action outcomes (Kilner, Friston, & Frith, 2007; Prinz, 2006; Wolpert & Flanagan, 2001). One neural marker associated with motor activation during action observation and execution in the EEG is the mu rhythm in the alpha frequency band across frontocentral electrode positions (Pfurtscheller & Da Silva, 1999). Mu rhythm activity has been studied in adults (8 - 13 Hz; Muthukumaraswamy, Johnson, & McNair, 2004) and in infants (6 - 9 Hz; Debnath, Salo, Buzzell, Yoo, & Fox, 2019; Fox et al., 2016; Marshall & Meltzoff, 2011). In particular, a reduction or desynchronization in the mu rhythm indicates stronger motor activation (Muthukumaraswamy et al., 2004). First evidence linking infants' motor activation to action prediction and evaluation was published by Stapel et al. (2010). Twelve-month-old infants responded with stronger motor activation on frontocentral channels, indicated by a stronger reduction in mu power, during the observation of unexpected actions (e.g., lifting a cup to the ear) compared to expected actions (e.g., lifting a cup to the mouth). Thus, differences in motor activation may reflect infants' action expectations and subsequent evaluations.

To my knowledge, no study has yet elucidated the role of motor activation in the head-touch paradigm (i.e., a novel and unfamiliar action context). In Study 1, we investigated whether there are differences in mu power between the processing of head- and hand-touch action outcomes in the hands-free and in the hands-restrained condition (paradigm, see Figure 3). Based on previous research (Koelewijn, van Schie, Bekkering, Oostenveld, & Jensen, 2008; Stapel et al., 2010), we expected a reduction in mu power in response to unexpected head-touch actions compared to hand-touch actions in the hands-free condition. In the hands-restrained condition, we expected the opposite result pattern, that is reduced mu power in response to physically impossible and thus unexpected hand- compared to head-touch actions. This would indicate that infants incorporated the situational constraints during action evaluation.

To test our hypotheses, we continuously recorded infants' neurophysiological signal during stimulus presentation and calculated infants' power via FFTs for each artifact-free action outcome. Infants' individual power responses were averaged across hand- and head-touch actions. Subsequently, grand average FFTs were computed across subjects for hand- and head-touch action outcomes for each between-subjects condition (hands free versus hands restrained). In line with infants' individual mu peaks on frontocentral electrodes (F3, F4, C3, C4) and previous literature (Marshall & Meltzoff, 2011), we conducted statistical analyses for the average power of the 6 – 8 Hz frequency range.

Langeloh, M., Buttelmann, D., Matthes, D., Grassmann, S., Pauen, S., & Hoehl, S. (2018). Reduced mu power in response to unusual actions is context-dependent in 1-year-olds. *Front Psychol, 9*, 36. doi:10.3389/fpsyg.2018.00036

Conforming our hypotheses, results in the hands-free condition revealed that 12- to 14-month-olds' brains responded with reduced mu power on frontal electrodes to unexpected actions (head touch) compared to expected actions (hand touch). We interpret this result in line with the predictive coding account (Kilner et al., 2007). Stronger motor activation is required for updating prior action predictions after observing an unexpected action outcome. In contrast to our hypotheses, in the hands-restrained condition, mu power did not differ between action outcomes. This might be attributed to insufficient visual processing of the duct tape, the inability to form action predictions in this context, the high salience of the head touch or an interaction between motor experience and conceptual knowledge (for details, see Langeloh et al., 2018).

To summarize, Study 1 gives a first indication on the underlying neural mechanisms of action processing in the head-touch paradigm. Reduced mu power in response to unexpected and inefficient head-touch outcomes may be one mechanism of infants' action understanding underlying selective imitation. So far, results of the hands-free condition are in line with the assumptions of top-down processes (Zmyj & Buttelmann, 2014) based on the rational-imitation accounts (Gergely et al., 2002; Gergely & Csibra, 2003). Infants form expectations about other agents' action outcomes. The VOE while observing unexpected action outcomes is associated with stronger motor activation (Kilner et al., 2007).

4.2 STUDY 2 – ERP EVIDENCE FROM THE HEAD-TOUCH PARADIGM

Study 1 indicates that infants' action expectations are violated when observing an adult model turning on a lamp with her head while her hands are free. Still, open questions regarding the neural processes underlying infants' observation of head-touch actions remain: First of all, the cognitive processes during VOE need to be examined further to strengthen the interpretation based on predictive coding (Kilner et al., 2007) in Study 1. Do 12- to 14-month-olds display a semantic VOE, which could be related to a violation of the assumptions of the principle of rational action (Gergely & Csibra, 2003)? Second, behavioral research suggests that the developmental onset of selective imitation occurs between 9 and 12 months of age

(Zmyj et al., 2009). What is the developmental onset of the underlying neural mechanisms associated with action understanding?

To address these questions and specify the processes measured in Study 1, I analyzed ERPs in three experiments[3] in Study 2 (paradigm, see Figure 3). In contrast to FFTs used in Study 1, ERPs have a very precise time resolution and consist of well-defined components, reflecting distinct cognitive processes that occur in a sequence (Hoehl & Wahl, 2012; Luck, 2005). Recent research using ERPs to study infants' action understanding or action evaluation predominantly focused on two ERP components: the N400 and the Negative central (Nc) component. The N400 component is sensitive to the violation of a semantic context in the language (Kutas & Federmeier, 2011) and action domain (Amoruso et al., 2013). Specifically, the N400 component has been linked to the detection of unexpected action outcomes in infants. For instance, 9-month-olds' brains responded with an N400 component towards unexpected (e.g., a pretzel at the person's ear) compared to expected eating outcomes (e.g., a pretzel at the person's mouth; Kaduk et al., 2016; Reid et al., 2009). Furthermore, infants discriminated between expected and unexpected eating actions on the Nc component (Kaduk et al., 2016; Reid et al., 2009), associated with the amount of attentional engagement (Reynolds, 2015; Reynolds & Richards, 2005).

By analyzing ERPs during the observation of unexpected action outcomes we aimed at discriminating low-level attentional mismatches (i.e., responses to novel or infrequent stimuli; Vaughan Jr & Kurtzberg, 1992) from more sophisticated detections of semantic violations (Amoruso et al., 2013). The latter process may point towards violations based on the principle of rational action.

In particular, in Experiment 1 (hands-free condition) we intended to explore whether, in accordance with the rational-imitation accounts, 1-year-olds' brains respond to head-touch actions with VOE. Furthermore, in Experiment 2 (hands-restrained condition), we assessed whether this effect is context-dependent. Finally, in Experiment 3 (hands-free condition), we tested 9-month-old infants to find out whether the developmental onset of the underlying neural mechanisms of action understanding and the behavioral onset of selective imitation are alike. If infants

---

[3] Please note that the data of Experiment 1 & 2 are similar but re-analyzed data of Study 1 in this thesis.

display VOE, we expected an increased Nc amplitude and an N400 component in response to unexpected action outcomes.

Similar to Study 1, the continuous EEG signal was segmented and averaged for the presentation of the action outcomes. ERPs in response to hand- versus head-touch actions were statistically compared within each experiment.

Langeloh, M., Buttelmann, D., Pauen, S., & Hoehl, S. (2019). 12- to 14-month-olds expect unconstrained agents to act efficiently: ERP evidence from the head-touch paradigm. *Manuscript under review in Developmental Psychology.*

Our results revealed that 12- to 14-month-olds, but not 9-month-olds, were surprised when observing head-touch actions when the model's hands were free as indicated by an increased Nc amplitude and an N400-like component (Experiments 1 & 3). I interpret the increased Nc amplitude in response to unexpected head-touch actions as an orienting response – a fast mismatch detection. Increased attentional engagement may put infants in a receptive state for learning (Sokolov, 1963, 1990; Vaughan Jr & Kurtzberg, 1992). The N400-like response to unexpected head-touch actions implies that infants had difficulties in constructing the meaning of this action outcome through the contextual information (Amoruso et al., 2013). This detection of semantic violations may reflect VOE based on the principle of rational action (for alternative interpretations, see Chapter 5). Thus, results of Experiments 1 and 3 are in line with the rational-imitation accounts (Gergely et al., 2002; Gergely & Csibra, 2003). In accordance with behavioral studies, the developmental onset of selective imitation and the underlying cognitive processes occurs between 9 and 12 months of age (Zmyj et al., 2009).

Contrary to our predictions, infants again did not show differences on our measures of VOE between hand- and head-touch outcomes when the model's hands were restrained (Experiment 2). Hence, infants' VOE to unusual head-touch outcomes is sensitive to contextual features. For now, my interim conclusion is that a VOE response to unusual actions used in previous behavioral studies (i.e., a person turning on a lamp with her head while her hands are free) may have influenced infants' selective imitation.

4.3 STUDY 3 – THE ROLE OF CONTEXT INFORMATION DURING ACTION EVALUATION

In Study 2, we showed that two processes occurred in a sequence during the observation of an unusual head touch when the model's hands were free. First, an increased Nc amplitude was elicited, associated with more attentional engagement (Reynolds, 2015), and then an N400-like component occurred, reflecting the detection of violations of semantic action contexts (Amoruso et al., 2013). In Study 3, we examined whether infants require the action context to semantically process action outcomes in this adaptation of the head-touch paradigm. In other words, we were interested in whether we tested infants' action expectations independent of the knowledge (context information) they were provided with during the experiment in Study 2.

To this end, we slightly changed our EEG paradigm such that we only presented 12-month-olds with action outcomes in the hands-free condition. Differing from Studies 1 and 2, context information was not provided prior to each trial. In previous research, adults but not 5-month-olds processed semantic violations without receiving prompts on the action context or initiation (Michel, Kaduk, Ni Choisdealbha, & Reid, 2017; Mudrik, Lamy, & Deouell, 2010). Information on the action context may have facilitated infants' detection of semantic violations in Study 2 and previous research (Kaduk et al., 2016; Reid et al., 2009).

If 12-month-olds experience VOE without prior context information, we expected an increased Nc amplitude and an N400 component in response to the unusual head touch. To test this hypothesis, we continuously recorded infants' EEG and performed the same ERP analyses on the data as in Study 2 (Experiment 1), for a high comparability.

Langeloh, M., Pauen, S., Buttelmann, D., Hoehl, S. (2019). One-year-olds' event-related potentials differentiate expected from unexpected action outcomes without context information. *Manuscript under review in Infancy.*

In the absence of context information, infants responded with increased negativity on the Nc amplitude but not with an N400 component to head-touch actions. Thus, we replicated the Nc effects of Study 2 (Experiment 1). For a fast detection of an unusual action outcome on an attentional level, infants do not need to be familiarized with the action context beforehand. However, a deeper semantic processing of unexpected actions seems to require prior context information in infants as compared to adults. Consequently, at least two distinct mechanisms underlie the processing of unusual and unexpected actions: a fast discrimination of action outcomes on an attentional level and a more specific mismatch processing on a semantic level (for a similar distinction in adults, see Szucs, Soltesz, Czigler, & Csepe, 2007).

Importantly, these results strengthen our interpretation of the results in Study 2. When infants received information on the action context, they built up action expectations based on the action context. These expectations were violated while observing an unexpected head-touch action. The context information may be necessary for infants to detect a semantic violation. Consequently, the N400-like component in Study 2 does not merely reflect a neural response towards an unusual action but rather indicates sophisticated semantic action processing. Likewise, an unpublished frequency analysis of the data of Study 3 revealed that infants did not distinguish between head- and hand-touch action outcomes via mu frequency power, associated with motor system activity. Thus, also the motor system needs context information to function as potential underlying mechanism of action evaluation in this paradigm (Langeloh et al., 2019, September).

In the following chapter, I would like to discuss what we can learn about the cognitive processes underlying infants' selective imitation in the head-touch paradigm across Studies 1, 2 and 3.

5. GENERAL DISCUSSION

Past research has shown that infants selectively imitate unusual head-touch actions depending on the action context in behavioral paradigms. Contradicting theoretical accounts have proposed explanations for this fascinating and highly discussed phenomenon. The integrative model by Zmyj and Buttelmann (2014) represents the first attempt to put together these opposing theories. Both rational-imitation accounts (Gergely et al., 2002; Gergely & Csibra, 2003) and non-rational imitation accounts (Paulus, Hunnius, et al., 2011a, 2011b) may operate on different processing levels. Bottom-up processes are related to non-rational imitation accounts, whereas top-down processing in the integrative model is based on the assumptions of the rational-imitation accounts. Accordingly, when infants observe a person who turns on a lamp with her head while her hands are free, these two processes may be involved and they may interact. First, infants automatically resonate with familiar elements of the observed action (e.g., body posture), leading to high motor resonance (bottom-up process). Second, infants evaluate the efficiency of the observed action via the principle of rational action (top-down process). As infants expect another person to achieve a goal in an efficient way, their action expectations are violated when they observe a person turning on a lamp with their head while their hands are free. Both underlying processes, that is high motor resonance and VOE when observing someone performing an unusual, inefficient action, may lead to infants' selective imitation of the head touch (Zmyj & Buttelmann, 2014).

In my thesis, I aimed to uncover the underlying cognitive processes during the observation of head-touch actions by recording infants' neurophysiological responses. To test the assumptions of the top-down processes linked to the rational-imitation accounts, I examined neural markers associated with VOE in an adaptation of the head-touch paradigm.

Overall, results of Studies 1 to 3 suggest that 12- to 14-month-old infants, but not 9-month-old infants, display VOE when observing a person performing a head touch. This VOE response is context-dependent and is elicited when the model's hands are free but not when the hands are restrained. In Study 1, VOE has been linked to a reduction in mu power in response to the unexpected head touch. In Study 2, we extended this finding such that when 12- to 14-month-old infants observed an unexpected head touch, their brains responded with increased attentional engagement (enhanced Nc amplitude) and a detection of a semantic violation (N400 component). Finally, in Study 3, in the absence of contextual information, 1-year-olds discriminated between hand- and head-touch outcomes on the Nc component only. Thus, infants require information of the action context to detect semantic violations within the head-touch paradigm. Based on Study 3, I propose that infants' action expectations in Study 1 and 2 were built up and then subsequently violated within the experiments and do not reflect a low-level response to unfamiliar actions. Furthermore, I suggest that VOE may have increased infants' curiosity to imitate the unusual head-touch action and thus may have induced learning behaviors in previous behavioral studies on selective imitation.

VOE has recently been linked to learning (Stahl & Feigenson, 2015, 2017, 2019). For instance, 11-month-olds engaged in increased object-exploration and hypothesis-testing behavior after having observed objects behaving in a physically unexpected way (e.g., a car driving through a wall; Stahl & Feigenson, 2015). Similar results have been found in the domain of word learning in 3- to 6-year-old children (Stahl & Feigenson, 2017). Children learned new verbs better after observing events that violated the spatiotemporal principle of continuity (i.e., a toy was hidden under one of two cups and was magically revealed under the other cup) compared to events that did not violate infants' expectations (i.e., a toy was hidden under one of two cups and was revealed under the original cup). Interestingly, VOE does not only shape early learning processes but can also affect memory processes in adults such that surprising outcomes are recalled better than less-surprising outcomes (Foster & Keane, 2019). Leslie (2004) endorses the notion that VOE indicates and supports learning in his commentary on Baillargeon (2004): "A violation of expectation happens when you detect that the world does not conform to your representation of it. Bringing representation and world back into kilter requires representation change and computing the right change is a fair definition of learning" (p. 418).

Taken together, observing surprising events can support learning across different ages and knowledge domains. It may put infants in a receptive state for knowledge acquisition. Accordingly, observing adults who are behaving oddly or surprisingly may support infants' learning of novel actions and lead to higher imitation rates of the respective actions (e.g., turning on a lamp with the head; Gergely et al., 2002). Importantly, VOE responses do not always reflect the same underlying mechanism. VOE can occur at different levels of complexity, from basic motor responses and proprioception to a more sophisticated understanding of the physical and social environment (for a unifying perspective on infants' learning based on VOE, see Köster, Kayhan, Langeloh, & Hoehl, in press).

Which mechanisms, associated with infants' action understanding, underlie VOE in my thesis? I suggest that the VOE responses measured in this thesis can be linked to the observation of inefficient action means and, thus, the violation of the principle of rational action (Gergely et al., 2002; Gergely & Csibra, 2003). In the following chapter, I will critically discuss this teleological interpretation. Furthermore, I will outline additional cognitive principles involved in infants' action understanding that need to be considered to compile a detailed picture of what is going on in infants' brains when they observe a head-touch action.

5.1 CRITICAL REFLECTION ON THE RESULTS IN THE LIGHT OF CURRENT THEORIES ON INFANTS' ACTION UNDERSTANDING

Past research has shown that infants predict and evaluate others' actions (Gredebäck & Daum, 2015). In Chapter 3.3, I outlined three processes guiding infants' understanding of others' goal-directed actions (Csibra & Gergely, 2007). Accordingly, the VOE responses towards unexpected action outcomes in my thesis can be interpreted with regard to different levels of infants' cognitive abilities.

Teleological reasoning.

According to rational-imitation accounts, the mechanism underlying selective imitation is based on teleological reasoning via the principle of rational action (Gergely et al., 2002; Gergely & Csibra, 2003). Infants' expectations about other agents behaving rationally and reaching goals efficiently have been examined by comparing infants' responses towards inefficient versus efficient action outcomes (Csibra et al., 1999; Gergely et al., 1995; Gredebäck & Melinder, 2010, 2011; Reid et al., 2009; Stapel et al., 2010).

We extended these findings with the inclusion of the hands-free condition in Study 1 and Study 2. More specifically, we identified two neurophysiological measures which suggest VOE in response to inefficient head-touch action outcomes when the action context is considered. First, the combination of an Nc and N400-like component in response to an unexpected head touch may imply that infants used the action context to predict and evaluate action goals based on the principle of rational action. One could argue that the increased Nc component only indicates a fast orienting response (Sokolov, 1963, 1990; Vaughan Jr & Kurtzberg, 1992), a mechanism that does not rely on inferential principles. Thus, the increased attentional engagement may not reflect a VOE response based on teleological reasoning. Still, it could have put infants into a receptive state, facilitating the subsequent detection of semantic violation (see also Study 3). The presence of the N400 component, however, may suggest that infants tried to construct semantic meaning of the action outcome while considering the action context[4]. If the action outcome does not fit with the meaning built up by the action context, more processing capacities are needed, indicated by the N400 response (Amoruso et al., 2013; Balconi & Caldiroli, 2011; Reid et al., 2009; Reid & Striano, 2008).

Second, infants' brains responded with a reduction in mu power, that is stronger motor activation, towards unexpected head-touch actions. Thus, this frequency analysis also suggests that infants require more processing capacities, when observing unexpected action outcomes. This is in line with other adult (Koelewijn et al., 2008; Manthey, Schubotz, & von Cramon, 2003) and infant studies (Stapel et al., 2010) which demonstrate stronger motor activation in response to incorrect or unexpected action outcomes. When observing actions that unfold differently than expected (prediction error), new predictions have to be generated (prediction updating), resulting in stronger motor activation (predictive coding theory of the motor system; Kilner et al., 2007).

Whereas the results of the hands-free condition indicate that infants may have applied rational inferential principles, the results of the hands-restrained condition are not as clear-cut. In the hands-restrained condition (Study 1 & Study 2), infants did not

[4] Note that the interpretation of EEG data or any observable data is limited by the reverse inference problem. That is, reasoning backward from patterns of activation to infer a specific underlying cognitive process (Poldrack, 2006, 2011). Here, I only provide one possible interpretation of the EEG activity associated with the observation of unusual, inefficient head-touch actions.

respond with neural indices of VOE towards physically impossible actions. In general, by the age of one year and even earlier, infants understand basic physical principles (Baillargeon, 2004; Spelke & Kinzler, 2007). Nevertheless, infants need specific background knowledge of relevant physical properties to form action predictions and evaluate action outcomes. Csibra (2007) stated that “insufficient knowledge about the constraints of the actor or the situation may produce wrong predictions or goal attribution by teleological reasoning” (p. 70). Thus, infants may simply not have been familiar enough with the physical properties of the restraining duct tape to know what action outcome to predict next. It is more likely, however, that infants processed the duct tape and its physical characteristics extensively (e.g., Zmyj et al., 2009) and that the neural mechanisms underlying the detection of a physically impossible action outcome differed from the detection of a semantic violation in a social action context (for neural processing of physically unexpected outcomes, see Berger, Tzur, & Posner, 2006; Köster, Langeloh, & Hoehl, 2019).

To sum up, I propose that one interprets the neural indices of VOE revealed in the hands-free condition in line with the rational-imitation accounts (Gergely et al., 2002; Gergely & Csibra, 2003) and, thus, within the top-down process of the integrative model by Zmyj and Buttelmann (2014). Teleological reasoning may kick in when infants infer the goals of novel actions, functioning as social learning mechanism of novel means in longer terms (Csibra & Gergely, 2007).

Simulation procedures.

However, this is only one interpretation of the present data. We need to consider alternative mechanisms for an extensive understanding of the results. Infants can also predict and evaluate goal states by simulation procedures or action-effect associations (Csibra & Gergely, 2007), as posited by the non-rational imitation accounts (Paulus et al., 2013a; Paulus, Hunnius, et al., 2011a, 2011b) or the bottom-up process of the integrative model (Zmyj & Buttelmann, 2014). Past research has suggested that infants can only interpret others’ actions as goal-directed when they have already had sensorimotor experience with the respective action (Gerson, Bekkering, & Hunnius, 2015; Sommerville & Woodward, 2005; van Elk et al., 2008). Accordingly, the direct-matching hypothesis (Rizzolatti, Fogassi, & Gallese, 2001) postulates that actions are understood through an automatic bottom-up process, in which the motor system of the observer resonates in response to the observed action. The observer's motor knowledge is used to understand the action by activating the same motor representation of the observed action in her or his own brain (Rizzolatti et al., 2001). This bottom-up mechanism provides humans with a fast and effective simulation of action goals. However, this mechanism is limited as it does not apply to novel actions or actions beyond the current own motor repertoire (be it due to immaturity or individual motor deficits). Furthermore, it does not work when observing non-human agents and whenever the observed actor does not have the same motor constraints as the observer (Csibra & Gergely, 2007). Results from the hands-free condition in Study 1, that is reduction in mu power in response to the head-touch outcomes, could also be interpreted in line with bottom-up processes. As Paulus, Hunnius, et al. (2011b) suggested, infants' body posture during data acquisition may have been more similar to the presented action in response to the head touch compared to the hand touch. Yet, low-level, bottom-up processes should have applied to both the hands-free and hands-restrained condition and would have led to similar processing in both conditions. Thus, pure bottom-up processes cannot account for the observed pattern of results.

To sum up, I cannot rule out that bottom-up simulation processes contributed to our results, alongside top-down teleological reasoning. Future research should scrutinize the distinction between bottom-up and top-down motor processes. For instance, by presenting infants with non-human versus human actors, a more comprehensive picture of how these two processes interact could be developed.

Action-effect associations.

Furthermore, infants' prediction of action outcomes may be facilitated by action-effect-associations (Adam & Elsner, 2018). According to ideomotor theory (Hommel et al., 2001), actions and effects can be coupled by repeated observations through bidirectional associations. The observation of an action elicits the anticipation of the associated effect and, in turn, the desired effect automatically activates the associated action (e.g., Elsner, 2007; Elsner & Aschersleben, 2003). Likewise, the activated motor program is tied to the representation of the action effect (Paulus, 2012a, 2014). This mechanism works efficiently when observing familiar actions, however, it is limited when observing novel actions or encountering situational constraints that require an adjustment of the action to the current action context (Csibra & Gergely, 2007). Thus, in the studies of my thesis it is rather unlikely that action-effect associations built-up within the experiment accounted for the VOE response towards the head touch in the hands-free condition (Study 1 & Study 2). The design we used did not foster action-effect associations as the action outcome (head/hand), modality (sound/lamp), and gender of the model (male/female) were not presented in a blocked design but in randomized order (for a blocked design, see Stapel et al., 2010). Still, I cannot exclude the possibility that infants had already built up action-effect associations for the hand touch before attending the experiment. They may have been surprised when observing a person turning on a lamp with her head, just because the effect did not fit the associated action. In addition, we only presented infants with action outcomes illustrating action effects (i.e., lamp lightens up or sound is played). This may have facilitated infants' action processing in general in our task (Hauf, 2007). However, differences between the hands-free and hands-restrained condition cannot solely be explained by this mechanism.

Statistical learning.

After having discussed the findings with regard to the three mechanisms of infants' goal attribution, as suggested by Csibra and Gergely (2007), I would like to add a mechanism that may have contributed to the results and may have been neglected in past reviews on action prediction and evaluation (however, see Gergely & Jacob, 2012): statistical or frequency learning. Young infants are sensitive to statistical information. They can detect regularities or structure in continuous sensory input and, thus, distinguish random from selective sampling (Saffran & Kirkham, 2018). Initial evidence for statistical learning in infants came from the language domain (Saffran, Aslin, & Newport, 1996). Recently, this line of research has been extended to visual (Kirkham, Slemmer, & Scott, 2002; Slone & Johnson, 2015) and action domains (Baldwin, Andersson, Saffran, & Meyer, 2008; Monroy, Gerson, & Hunnius, 2017). For instance, 19-month-old infants learned the structure of deterministic versus random action pairs while observing a continuous action stream and correctly predicted the next action, measured by predictive gaze shifts (Monroy et al., 2017). Still, research with regard to action prediction is sparse. Paulus, Hunnius, van Wijngaarden, et al. (2011) posited that infants specifically track the frequency of an agent's previous actions to predict the next action. Put simply, infants may expect that people behave in the same way as they have most frequently done before. Accordingly, 9-month-olds were habituated to an agent taking a longer path to reach a goal, while the shorter efficient path was blocked. In the test-phase, both paths were accessible. Infants, but not adults, continued to expect the agent to take the longer, inefficient path and did not switch their expectations based on teleological reasoning (Paulus, Hunnius, van Wijngaarden, et al., 2011).

How could frequency learning explain the results of this thesis? During daily life infants gather plenty of new information about agents and the actions they produce. I assume that infants mostly observe other agents manipulating objects with their hands. In that sense, touching an object with the head is a highly infrequent and odd action. Observing such an infrequent action could elicit a novelty response. Consequently, the VOE responses towards the head touch when the model's hands were free could be interpreted with regard to low-level attention processes. Results of Study 3 fit into this interpretation. Infants came to the experimental session with some general expectations about other people's actions based on previous experiences. It might be that they had never seen a person touch a lamp with their head and, thus, responded with an increased Nc component, implying increased attentional engagement. In addition, when the model's hands were tied to the table in the hands-restrained condition (Study 1 & Study 2), infants may have not known what to predict next, as they had probably never observed a person whose hands were tied by duct tape before. To rule out frequency learning across time during the experiment in the hands-restrained condition in Study 2, I compared neural responses to head- and hand-touch outcomes in the first versus the second half of the trials. Even in the first half of trials, infants did not distinguish between hand- and head-touch outcomes, suggesting that no initial action expectation had been overwritten by repeated observations (Langeloh et al., 2018).

Hence, I cannot completely rule out the influence of frequency learning prior to the experimental session in our design. Future research should integrate this mechanism for infants' action-goal attribution more thoroughly and disentangle it from teleological reasoning (see Scott & Baillargeon, 2013).

Taken together, in our studies, neural processes generated in response to observing an unusual head touch point towards inferential rather than to low-level mechanisms solely, such as automatic motor programs or novelty responses. To interpret the neural indices of VOE in response to the head-touch actions comprehensively, alternative mechanisms need to be considered in addition to teleological reasoning. Simulation procedures, action effects and statistical learning may have contributed to infants' neural processing of unusual actions.

5.2 FUTURE PERSPECTIVES

So far, I have discussed the results of the present thesis in the light of current theories on infants' action understanding. In this chapter, I would like to summarize what our findings add to the integrative model of Zmyj and Buttelmann (2014). Furthermore, I will suggest directions for future studies in this field of research.

In this thesis, I zoomed in closely into the top-down part of the integrative model based on the assumptions of the principle of rational action (Gergely et al., 2002; Gergely & Csibra, 2003). Specifically, I asked if infants have expectations of the model's action outcomes in the head-touch paradigm. The answer is: yes, they do. These expectations seem to be violated when observing an unusual or inefficient head-touch action. Thus, I can add neural indices of VOE, potentially underlying infants' selective imitation, to the top-down part of the integrative model. These neural indices are reduced mu power (Study 1), an Nc (Study 2 & Study 3) and N400-like component (Study 2) in response to the unusual head touch, when the model's hands are free. Consequently, the findings of my thesis are in line with assumptions of the rational-imitation accounts (Gergely et al., 2002).

At this point, I cannot further disentangle whether the VOE displayed by infants was based on the non-mentalistic teleological stance or the mentalistic stance (Gergely & Csibra, 2003). Moreover, we did not measure the influence of ostensive cues on action understanding in the present paradigm, as the adult models did not establish eye contact with infants. There is evidence to suggest that ostensive cues, such as direct eye contact or infant-directed speech, create learning environments supporting a fast transmission of generic knowledge (Csibra & Gergely, 2009). Thus, in line with rational-imitation accounts (see Chapter 3.1), ostensive cues could have facilitated action processing in our paradigm (Király et al., 2013). These issues need to be addressed in future research. In addition, I surmise that the mechanisms underlying selective imitation are too complex to be fully understood by the paradigm used in my thesis. For a full-fledged understanding of why infants imitate selectively, future research should study the interaction of both top-down and bottom-up processes of the integrative model (Zmyj & Buttelmann, 2014). In more detail, future research should consider that motor resonance and rationality evaluation may co-occur and that they may function at different points in time during action processing (e.g., high motor resonance may be followed by VOE based on the principle of rational action). Finally, other mechanisms of infants' action understanding, such as statistical or frequency learning, should be added to the integrative model in future research.

Similarly, the integrative model should be applied to study action understanding in a more general sense. A first step in this direction has been taken by Quadrelli and Turati (2016). The authors have proposed that the motor system (as an underlying mechanism of infants' action understanding) can benefit from an interplay between top-down and bottom-up processes in a dynamic and multilayer fashion. In this tenet, to construe the meaning of an action, infants need to process multiple dimensions and reconstruct actions based on familiarity, motivation, efficiency, visual, auditory, emotional, and social cues. The authors suggest that infants' action understanding is driven by top-down processes at first. With increasing action experience, bottom-up mechanisms work for familiar actions (a narrowing process based on experience). In line with what I have suggested earlier, inferential processes and direct matching of familiar actions should not be considered as mutually exclusive, but rather as complementing each other (Quadrelli & Turati, 2016).

These integrative models inspire future research to investigate the neural mechanisms underlying infants' action understanding within a broader framework. First of all, future research should extend our knowledge of the phenomenon of selective imitation in infancy. For instance, the paradigm used in this thesis could be adapted to test the assumptions of non-rational imitation accounts (two-stage model; Paulus, Hunnius, et al., 2011a; Paulus, Hunnius, et al., 2011b). That is, infants could be presented with head-touch action outcomes only in two within-subjects conditions: hands-free and hands-occupied. According to non-rational imitation accounts, mu power should be reduced in response to the hands-free compared to the hands-occupied head touch. In addition, the developmental trajectories of neural and behavioral correlates of infants' action understanding should be examined. Interestingly, infants' selective imitation of the unusual head touch occurs with 12 to 14 months of age but disappears or transforms into faithful imitation at around 18 months of age (Gellen & Buttelmann, 2019). Does the function of imitative learning change from instrumental to social with increasing age (Over & Carpenter, 2012; Uzgiris, 1981)? And what happens to the associated neural mechanisms – are toddlers still surprised when observing unusual and inefficient actions, or do they become accustomed to viewing them as a function of cultural learning (Tennie, Call, & Tomasello, 2009)? To answer these questions, the developmental path from selective imitation to over-imitation (i.e., imitating causally unnecessary actions in relation to the action goal; for a review, see Hoehl et al., 2019) should be explored.

Furthermore, future research should scrutinize the link between the neural correlates of action observation and imitative behavior. Even though we suggest a relation between motor activation and infants' imitation in Study 1, this still awaits further clarification beyond the head-touch paradigm. Accordingly, we conducted a study combining the assessment of infants' neural processes during action observation and their subsequent imitation behavior (Köster, Langeloh, Kliesch, Kanngiesser, & Hoehl, 2019). While measuring EEG, we presented 10- and 20-month-olds with novel, transitive actions, preceded by a communicative or non-communicative cue. Subsequently, 20-month-olds' imitation behavior was tested. In both age groups, we found an increase in 7 – 10 Hz neural activity during the observation of novel actions. This 7 – 10 Hz activity predicted 20-month-olds' imitation rates. Communicative signals neither affected infants' neural processing of observed actions nor their imitation behavior. We surmise that infants acquire novel actions via a common neural code for own and others' actions in the motor system (Köster, Langeloh, Kliesch, et al., 2019). These results are very promising. Still, future research should address why several studies have reported a decrease in infants' 6 – 9 Hz activity during action observation (e.g., Study 1; Filippi et al., 2016;

Saby, Meltzoff, & Marshall, 2013) compared to the 7 – 10 Hz increase observed in the aforementioned study.

Finally, a promising and related direction for future research is to extend and quantify the currently existing measures of VOE in infants. In doing so, the idea that situations evoking VOE provide infants with unique learning opportunities could be strengthened. We took a first step in this direction by applying an innovative rhythmic visual brain stimulation method to 9-month-olds (Köster, Langeloh, & Hoehl, 2019). We visually entrained infants' theta (4 Hz) and alpha (6 Hz) rhythms while presenting expected (e.g., a person puts a pretzel to the mouth) versus unexpected events (e.g., a person puts a pretzel to the ear). Our results revealed that visually entrained theta oscillations sharply increased for unexpected compared to expected events. In contrast, visually entrained alpha oscillations did not differ between conditions. We suggest that this increase in entrained theta oscillations reflects the integration of novel information into existing representations and, thus, learning (Köster, Langeloh, & Hoehl, 2019). In a next step, VOE on a neural level should be directly related to learning measures, such as imitation behavior (for additional learning measures in infants and children, see Stahl & Feigenson, 2015, 2017).

All in all, in this thesis I added neural indices of VOE, implying surprise during the observation of inefficient action means in the head-touch paradigm, to the top-down processes of the integrative model (Zmyj & Buttelmann, 2014). When infants observed inefficient actions, which have recently been used in studies on selective imitation, their brains responded with enhanced processing or VOE. This neural process can only be understood within the context of granting infants the ability to form rational inferences.

6. CONCLUSION

Let us return to the example of opening a door, used in the Introduction. Imagine your infant imitates the unusual action (i.e., opening the door with the shoulder) but only when you did so with your hands free. Why does your infant selectively imitate this unusual action and what happens in your infant's brain during the observation of this action?

To answer these questions, I have investigated the neural cognitive processes underlying the observation of actions in an adaptation of the head-touch paradigm. By measuring infants' neurophysiological responses, I demonstrated neural indices of VOE towards unusual and inefficient head-touch actions. Thus, 12-month-olds, but not 9-month-olds, were surprised when they observed actors not behaving in an efficient way. This surprise reaction was dependent on the action context and did not occur when the model's hands were tied to the table.

Even though pre-verbal infants cannot explicitly express their surprise, we were able to measure this implicit response in the EEG. By doing so, we have moved a step closer to unravelling one question that has occupied developmental scientists for the last decade: why do infants imitate selectively? The findings of this dissertation strengthen the assumptions of the rational-imitation accounts (Gergely et al., 2002; Gergely & Csibra, 2003), reflected by the top-down processes in the integrative model of selective imitation (Zmyj & Buttelmann, 2014). Future work should consider the interaction of different cognitive processes underlying infants' action understanding from automatic low-level processes to teleological reasoning.

To conclude, our studies have paved the way to further our understanding of infants' action perception and observational learning. Understanding the neural processes and mechanisms of infants' action perception in more depth, will help us to adequately foster the ideal observational learning conditions of novel actions. The results of this dissertation suggest that presenting infants with surprising action means puts them in an optimal receptive state for knowledge acquisition.

7. REFERENCES

Adam, M., & Elsner, B. (2018). Action effects foster 11-month-olds' prediction of action goals for a non-human agent. *Infant Behav Dev, 53*, 49-55. doi:10.1016/j.infbeh.2018.09.002

Amoruso, L., Gelormini, C., Aboitiz, F., Alvarez Gonzalez, M., Manes, F., Cardona, J. F., & Ibanez, A. (2013). N400 ERPs for actions: Building meaning in context. *Front Hum Neurosci, 7*, 57. doi:10.3389/fnhum.2013.00057

Aschersleben, G., Hofer, T., & Jovanovic, B. (2008). The link between infant attention to goal-directed action and later theory of mind abilities. *Dev Sci, 11*(6), 862-868. doi:10.1111/j.1467-7687.2008.00736.x

Baillargeon, R. (2004). Infants' physical world. *Current Directions in Psychological Science, 13*(13), 89-94. doi:10.1111/j.0963-7214.2004.00281.x

Balconi, M., & Caldiroli, C. (2011). Semantic violation effect on object-related action comprehension: N400-like event-related potentials for unusual and incorrect use. *Neuroscience, 197*, 191-199. doi:10.1016/j.neuroscience.2011.09.026

Baldwin, D., Andersson, A., Saffran, J., & Meyer, M. (2008). Segmenting dynamic human action via statistical structure. *Cognition, 106*(3), 1382-1407. doi:10.1016/j.cognition.2007.07.005

Beisert, M., Zmyj, N., Liepelt, R., Jung, F., Prinz, W., & Daum, M. (2012). Rethinking 'Rational Imitation' in 14-month-old infants: A perceptual distraction approach. *PLoS ONE, 7*(3), e32563. doi:10.1371/journal.pone.0032563.g001

Berger, A., Tzur, G., & Posner, M. I. (2006). Infant brains detect arithmetic errors. *PNAS, 103*(33), 12649-12653. doi:10.1073/pnas.0605350103

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Dev Sci, 10*(4), F31-38. doi:10.1111/j.1467-7687.2007.00630.x

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2008). Rational tool use and tool choice in human infants and great apes. *Child Dev, 79*(3), 609-626. doi:10.1111/j.1467-8624.2008.01146.x

Buttelmann, D., Schieler, A., Wetzel, N., & Widmann, A. (2017). Infants' and adults' looking behavior does not indicate perceptual distraction for constrained modelled actions - An eye-tracking study. *Infant Behav Dev, 47*, 103-111. doi:10.1016/j.infbeh.2017.04.001

Buttelmann, D., & Zmyj, N. (2012). Evaluating the empirical evidence for the two-stage-model of infant imitation: A commentary on Paulus, Hunnius, Vissers, and Bekkering (2011). *Front Psychol, 3*, 512. doi:10.3389/fpsyg.2012.00512

Buttelmann, D., Zmyj, N., Daum, M., & Carpenter, M. (2013). Selective imitation of in-group over out-group members in 14-month-old infants. *Child Dev, 84*(2), 422-428. doi:10.1111/j.1467-8624.2012.01860.x

Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences, 21*(5), 667-684. doi:10.1017/s0140525x98001745

Carpenter, M., Akhtar, N., & Tomasello, M. (1998). Fourteen- through 18-month-old infants differentially imitate intentional and accidental actions. *Infant Behav Dev, 21*(2), 315-330. doi:10.1016/S0163-6383(98)90009-1

Csibra, G. (2007). Action mirroring and action understanding: An alternative account. In P. Haggard, Y. Rosetti, & M. Kawato (Eds.), *Sensorimotor foundations of higher cognition: Attention and performance*. Oxford, UK: Oxford University Press.

Csibra, G., Bìró, S., Koós, O., & Gergely, G. (2003). One-year-old infants use teleological representations of actions productively. *Cognitive Science, 27*(1), 111-133. doi:10.1207/s15516709cog2701_4

Csibra, G., & Gergely, G. (2007). 'Obsessed with goals': Functions and mechanisms of teleological interpretation of actions in humans. *Acta Psychol (Amst), 124*(1), 60-78. doi:10.1016/j.actpsy.2006.09.007

Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends Cogn Sci, 13*(4), 148-153. doi:10.1016/j.tics.2009.01.005

Csibra, G., Gergely, G., Bíró, S., Koós, O., & Brockbank, M. (1999). Goal attribution without agency cues: The perception of 'pure reason' in infancy. *Cognition, 72*(3), 237-267. doi:10.1016/S0010-0277(99)00039-6

Debnath, R., Salo, V. C., Buzzell, G. A., Yoo, K. H., & Fox, N. A. (2019). Mu rhythm desynchronization is specific to action execution and observation: Evidence from time-frequency and connectivity analysis. *NeuroImage, 184*, 496-507. doi:10.1016/j.neuroimage.2018.09.053

DeBoer, T., Scott, L. S., & Nelson, C. A. (2007). Methods for acquiring and analyzing infant event-related potentials. In M. de Haan (Ed.), *Infant EEG and event-related potentials* (pp. 5-38). New York: Psychology Press.

Elsner, B. (2007). Infants' imitation of goal-directed actions: The role of movements and action effects. *Acta Psychol, 124*(1), 44-59. doi:10.1016/j.actpsy.2006.09.006

Elsner, B., & Aschersleben, G. (2003). Do I get what you get? Learning about the effects of self-performed and observed actions in infancy. *Consciousness and Cognition, 12*(4), 732-751. doi:10.1016/s1053-8100(03)00073-4

Elsner, B., Pfeifer, C., Parker, C., & Hauf, P. (2013). Infants' perception of actions and situational constraints: An eye-tracking study. *J Exp Child Psychol, 116*(2), 428-442. doi:10.1016/j.jecp.2012.11.014

Falck-Ytter, T., Gredebäck, G., & von Hofsten, C. (2006). Infants predict other people's action goals. *Nat Neurosci, 9*(7), 878-879. doi:10.1038/nn1729

Filippi, C., Choi, Y. B., Fox, N. A., & Woodward, A. L. (2019). Neural correlates of infant action processing relate to theory of mind in early childhood. *Dev Sci*, e12876. doi:10.1111/desc.12876

Filippi, C. A., Cannon, E. N., Fox, N. A., Thorpe, S. G., Ferrari, P. F., & Woodward, A. L. (2016). Motor system activation predicts goal imitation in 7-month-old infants. *Psychol Sci, 27*(5), 675-684. doi:10.1177/0956797616632231

Foster, M. I., & Keane, M. T. (2019). The role of surprise in learning: Different surprising outcomes affect memorability differentially. *Top Cogn Sci, 11*(1), 75-87. doi:10.1111/tops.12392

Fox, N. A., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N., Vanderwert, R. E., . . . van IJzendoorn, M. H. (2016). Assessing human mirror activity with EEG mu rhythm: A meta-analysis. *Psychol Bull, 142*(3), 291-313. doi:10.1037/bul0000031

Ganglmayer, K., Attig, M., Daum, M. M., & Paulus, M. (2019). Infants' perception of goal-directed actions: A multi-lab replication reveals that infants anticipate paths and not goals. *Infant Behav Dev, 57*, 101340. doi:10.1016/j.infbeh.2019.101340

Gellen, K., & Buttelmann, D. (2019). Rational imitation declines within the second year of life: Changes in the function of imitation. *J Exp Child Psychol, 185*, 148-163. doi:10.1016/j.jecp.2019.04.019

Gellén, K., & Buttelmann, D. (2017). Fourteen-month-olds adapt their imitative behavior in light of a model's constraints. *Child Development Research, 2017*, 1-11. doi:10.1155/2017/8080649

Gergely, G., Bekkering, H., & Király, I. (2002). Rational imitation in preverbal infants. *Nature, 415*(6873), 755. doi:10.1038/415755a

Gergely, G., & Csibra, G. (2003). Teleological reasoning in infancy: The naïve theory of rational action. *Trends Cogn Sci, 7*(7), 287-292. doi:10.1016/s1364-6613(03)00128-1

Gergely, G., & Jacob, P. (2012). Reasoning about instrumental and communicative agency in human infancy. *Advances in Child Development and Behavior, 43*, 59-94. doi:10.1016/B978-0-12-397919-3.00003-4

Gergely, G., Nádasdy, Z., Csibra, G., & Bíró, S. (1995). Taking the intentional stance at 12 months of age. *Cognition, 56*(2), 165-193. doi:10.1016/s0010-0277(98)00058-4

Gerson, S. A., Bekkering, H., & Hunnius, S. (2015). Short-term motor training, but not observational training, alters neurocognitive mechanisms of action processing in infancy. *J Cogn Neurosci, 27*(6), 1207-1214. doi:10.1162/jocn_a_00774

Gredebäck, G., & Daum, M. (2015). The microstructure of action perception in infancy: Decomposing the temporal structure of social information processing. *Child Development Perspectives, 9*(2), 79-83. doi:10.1111/cdep.12109

Gredebäck, G., & Melinder, A. (2010). Infants' understanding of everyday social interactions: A dual process account. *Cognition, 114*(2), 197-206. doi:10.1016/j.cognition.2009.09.004

Gredebäck, G., & Melinder, A. (2011). Teleological reasoning in 4-month-old infants: Pupil dilations and contextual constraints. *PLoS ONE, 6*(10), e26487. doi:10.1371/journal.pone.0026487

Hauf, P. (2007). Infants’ perception and production of intentional actions. *Progress in Brain Research, 164*, 285-301. doi:10.1016/s0079-6123(07)64016-3

Heyes, C. (2001). Causes and consequences of imitation. *Trends in Cognitive Sciences, 5*(6), 253-261. doi:10.1016/S1364-6613(00)01661-2

Hoehl, S., Keupp, S., Schleihauf, H., McGuigan, N., Buttelmann, D., & Whiten, A. (2019). ‘Over-imitation’: A review and appraisal of a decade of research. *Developmental Review, 51*, 90-108. doi:10.1016/j.dr.2018.12.002

Hoehl, S., & Wahl, S. (2012). Recording infant ERP data for cognitive research. *Dev Neuropsychol, 37*(3), 187-209. doi:10.1080/87565641.2011.627958

Hommel, B., Muesseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding: A framework for perception and action planning. *Behav Brain Sci, 24*(5), 849-937. doi:10.1017/S0140525X01000103

Hunnius, S., & Bekkering, H. (2010). The early development of object knowledge: A study of infants' visual anticipations during action observation. *Dev Psychol, 46*(2), 446-454. doi:10.1037/a0016543

Hunnius, S., & Bekkering, H. (2014). What are you doing? How active and observational experience shape infants' action understanding. *Philos Trans R Soc Lond B Biol Sci, 369*(1644), 20130490. doi:10.1098/rstb.2013.0490

Jones, S. S. (2007). Imitation in infancy: The development of mimicry. *Psy Sci, 18*(7), 593-599. doi:10.1111/j.1467-9280.2007.01945.x

Jones, S. S. (2009). The development of imitation in infancy. *Philos Trans R Soc Lond B Biol Sci, 364*(1528), 2325-2335. doi:10.1098/rstb.2009.0045

Kaduk, K., Bakker, M., Juvrud, J., Gredebäck, G., Westermann, G., Lunn, J., & Reid, V. M. (2016). Semantic processing of actions at 9 months is linked to language proficiency at 9 and 18 months. *J Exp Child Psychol, 151*, 96-108. doi:10.1016/j.jecp.2016.02.003

Kaminski, J., Nitzschner, M., Wobber, V., Tennie, C., Bräuer, J., Call, J., & Tomasello, M. (2011). Do dogs distinguish rational from irrational acts? *Animal Behaviour, 81*(1), 195-203. doi:10.1016/j.anbehav.2010.10.001

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. *Cogn Process, 8*(3), 159-166. doi:10.1007/s10339-007-0170-2

Király, I., Csibra, G., & Gergely, G. (2013). Beyond rational imitation: Learning arbitrary means actions from communicative demonstrations. *J Exp Child Psychol, 116*(2), 471-486. doi:10.1016/j.jecp.2012.12.003

Király, I., & Oláh, K. (2018). Rational Imitation. In J. Vonk & T. Shackelford (Eds.), *Encyclopedia of Animal Cognition and Behavior* (pp. 1-8): Springer, Cham.

Kirkham, N. Z., Slemmer, J. A., & Scott, P. (2002). Visual statistical learning in infancy: Evidence for a domain general learning mechanism. *Cognition, 83*(2), B35-B42. doi:10.1016/S0010-0277(02)00004-5

Koelewijn, T., van Schie, H. T., Bekkering, H., Oostenveld, R., & Jensen, O. (2008). Motor-cortical beta oscillations are modulated by correctness of observed action. *NeuroImage, 40*(2), 767-775. doi:10.1016/j.neuroimage.2007.12.018

Kolling, T., Óturai, G., & Knopf, M. (2014). Is selective attention the basis for selective imitation in infants? An eye-tracking study of deferred imitation with 12-month-olds. *J Exp Child Psychol, 124*, 18-35. doi:10.1016/j.jecp.2014.01.016

Köster, M., Kayhan, E., Langeloh, M., & Hoehl, S. (in press). Making sense of the world – Infant learning from a predictive processing perspective. *Perspectives on Psychological Science*.

Köster, M., Langeloh, M., & Hoehl, S. (2019). Visually entrained theta oscillations increase for unexpected events in the infant brain. *Psychol Sci, 30*(11), 1656-1663. doi:10.1177/0956797619876260

Köster, M., Langeloh, M., Kliesch, C., Kanngiesser, P., & Hoehl, S. (2019). Motor cortex activity during action observation predicts infants' subsequent imitation behavior. *Manuscript submitted for publication*.

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annu Rev Psychol, 62*(1), 621-647. doi:10.1146/annurev.psych.093008.131123

Langeloh, M., Buttelmann, D., Matthes, D., Grassmann, S., Pauen, S., & Hoehl, S. (2018). Reduced mu power in response to unusual actions is context-dependent in 1-year-olds. *Front Psychol, 9*, 36. doi:10.3389/fpsyg.2018.00036

Langeloh, M., Buttelmann, D., Matthes, D., Grassmann, S., Pauen, S., & Hoehl, S. (2019, September). *One-year-olds' mu power reduction in response to* *unexpected actions is context-dependent and requires context information*. Talk presented at PAEPSY, Leipzig.

Leslie, A. M. (2004). Who's for learning? *Dev Sci, 7*(4), 417-419. doi:10.1111/j.1467-7687.2004.00359.x

Luck, S. J. (2005). An introduction to event-related potentials and their neural origins. In S. J. Luck (Ed.), *An introduction to the event-related potential technique* (pp. 1-50). Cambridge, Mass.: MIT Press.

Manthey, S., Schubotz, R. I., & von Cramon, D. Y. (2003). Premotor cortex in observing erroneous action: An fMRI study. *Cognitive Brain Research, 15*(3), 296-307. doi:10.1016/S0926-6410(02)00201-X

Marshall, P. J., & Meltzoff, A. N. (2011). Neural mirroring systems: Exploring the EEG mu rhythm in human infancy. *Dev Cogn Neurosci, 1*(2), 110-123. doi:10.1016/j.dcn.2010.09.001

Meltzoff, A. N. (1988). Infant imitation after a 1-week delay: Long-term memory for novel acts and multiple stimuli. *Dev Psychol, 24*(4), 470-476. doi:10.1037/0012-1649.24.4.470

Meltzoff, A. N. (1995). Understanding the intentions of others: Re-enactment of intended acts by 18-month-old children. *Dev Psychol, 31*(5), 838-850. doi:10.1037/0012-1649.31.5.838

Michel, C., Kaduk, K., Ni Choisdealbha, A., & Reid, V. M. (2017). Event-related potentials discriminate familiar and unusual goal outcomes in 5-month-olds and adults. *Dev Psychol, 53*(10), 1833-1843. doi:10.1037/dev0000376

Monroy, C. D., Gerson, S. A., & Hunnius, S. (2017). Toddlers' action prediction: Statistical learning of continuous action sequences. *J Exp Child Psychol, 157*, 14-28. doi:10.1016/j.jecp.2016.12.004

Mudrik, L., Lamy, D., & Deouell, L. Y. (2010). ERP evidence for context congruity effects during simultaneous object-scene processing. *Neuropsychologia, 48*(2), 507-517. doi:10.1016/j.neuropsychologia.2009.10.011

Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Cogn Brain Res, 19*(2), 195-201. doi:10.1016/j.cogbrainres.2003.12.001

Ni Choisdealbha, A., & Reid, V. M. (2014). The developmental cognitive neuroscience of action: Semantics, motor resonance and social processing. *Exp Brain Res, 232*(6), 1585-1597. doi:10.1007/s00221-014-3924-y

Nielsen, M. (2006). Copying actions and copying outcomes: Social learning through the second year. *Dev Psychol, 42*(3), 555-565. doi:10.1037/0012-1649.42.3.555

Over, H., & Carpenter, M. (2012). Putting the social into social learning: Explaining both selectivity and fidelity in children's copying behavior. *J Comp Psychol, 126*(2), 182-192. doi:10.1037/a0024555

Paulus, M. (2011). Imitation in infancy: Conceptual considerations. *Theory & Psychol, 21*(6), 849-856. doi:10.1177/0959354310395990

Paulus, M. (2012a). Action mirroring and action understanding: An ideomotor and attentional account. *Psychol Res, 76*(6), 760-767. doi:10.1007/s00426-011-0385-9

Paulus, M. (2012b). Is it rational to assume that infants imitate rationally? A theoretical analysis and critique. *Hum Dev, 55*(3), 107-121. doi:10.1159/000339442

Paulus, M. (2014). How and why do infants imitate? An ideomotor approach to social and imitative learning in infancy (and beyond). *Psychon Bull Rev, 21*(5), 1139-1156. doi:10.3758/s13423-014-0598-1

Paulus, M., Hunnius, S., & Bekkering, H. (2013a). Examining functional mechanisms of imitative learning in infancy: Does teleological reasoning affect infants' imitation beyond motor resonance? *J Exp Child Psychol, 116*(2), 487-498. doi:10.1016/j.jecp.2012.10.009

Paulus, M., Hunnius, S., & Bekkering, H. (2013b). Neurocognitive mechanisms underlying social learning in infancy: Infants' neural processing of the effects of others' actions. *Soc Cogn Affect Neurosci, 8*(7), 774-779. doi:10.1093/scan/nss065

Paulus, M., Hunnius, S., van Elk, M., & Bekkering, H. (2012). How learning to shake a rattle affects 8-month-old infants' perception of the rattle's sound: Electrophysiological evidence for action-effect binding in infancy. *Dev Cogn Neurosci, 2*(1), 90-96. doi:10.1016/j.dcn.2011.05.006

Paulus, M., Hunnius, S., van Wijngaarden, C., Vrins, S., van Rooij, I., & Bekkering, H. (2011). The role of frequency information and teleological reasoning in infants' and adults' action prediction. *Dev Psychol, 47*(4), 976-983. doi:10.1037/a0023785

Paulus, M., Hunnius, S., Vissers, M., & Bekkering, H. (2011a). Bridging the gap between the other and me: The functional role of motor resonance and action effects in infants' imitation. *Dev Sci, 14*(4), 901-910. doi:10.1111/j.1467-7687.2011.01040.x

Paulus, M., Hunnius, S., Vissers, M., & Bekkering, H. (2011b). Imitation in infancy: Rational or motor resonance? *Child Dev, 82*(4), 1047-1057. doi:10.1111/j.1467-8624.2011.01610.x

Pfurtscheller, G., & Da Silva, F. L. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology, 110*(11), 1842-1857. doi:10.1016/S1388-2457(99)00141-8

Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends Cogn Sci, 10*(2), 59-63. doi:10.1016/j.tics.2005.12.004

Poldrack, R. A. (2011). Inferring mental states from neuroimaging data: From reverse inference to large-scale decoding. *Neuron, 72*(5), 692-697. doi:10.1016/j.neuron.2011.11.001

Prinz, W. (2006). What re-enactment earns us. *Cortex, 42*(4), 515-517. doi:10.1016/s0010-9452(08)70389-7

Quadrelli, E., & Turati, C. (2016). Origins and development of mirroring mechanisms: A neuroconstructivist framework. *Br J Dev Psychol, 34*(1), 6-23. doi:10.1111/bjdp.12110

Racine, T. P. (2012). Conceptual Analysis and Rational Imitation. *Hum Dev, 55*(3), 129-135. doi:10.1159/000339592

Range, F., Viranyi, Z., & Huber, L. (2007). Selective imitation in domestic dogs. *Curr Biol, 17*(10), 868-872. doi:10.1016/j.cub.2007.04.026

Reid, V. M., Hoehl, S., Grigutsch, M., Groendahl, A., Parise, E., & Striano, T. (2009). The neural correlates of infant and adult goal prediction: Evidence for semantic processing systems. *Dev Psychol, 45*(3), 620-629. doi:10.1037/a0015209

Reid, V. M., & Striano, T. (2008). N400 involvement in the processing of action sequences. *Neurosci Lett, 433*(2), 93-97. doi:10.1016/j.neulet.2007.12.066

Reid, V. M., Striano, T., & Iacoboni, M. (2011). Neural correlates of dyadic interaction during infancy. *Dev Cogn Neurosci, 1*(2), 124-130. doi:10.1016/j.dcn.2011.01.001

Reynolds, G. D. (2015). Infant visual attention and object recognition. *Behav Brain Res, 285*, 34-43. doi:10.1016/j.bbr.2015.01.015

Reynolds, G. D., & Richards, J. E. (2005). Familiarization, attention, and recognition memory in infancy: An event-related potential and cortical source localization study. *Dev Psychol, 41*(4), 598-615. doi:10.1037/0012-1649.41.4.598

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci, 2*(9), 661-670. doi:10.1038/35090060

Saby, J. N., Meltzoff, A. N., & Marshall, P. J. (2013). Infants' somatotopic neural responses to seeing human actions: I've got you under my skin. *PLoS ONE, 8*(10), e77905. doi:10.1371/journal.pone.0077905

Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science, 274*(5294), 1926-1928. doi:10.1126/science.274.5294.1926

Saffran, J. R., & Kirkham, N. Z. (2018). Infant statistical learning. *Annu Rev Psychol, 69*, 181-203. doi:10.1146/annurev-psych-122216-011805

Schwier, C., von Maanen, C., Carpenter, M., & Tomasello, M. (2006). Rational Imitation in 12-month-old infants. *Infancy, 10*(3), 303-311. doi:10.1207/s15327078in1003_6

Scott, R. M., & Baillargeon, R. (2013). Do infants really expect agents to act efficiently? A critical test of the rationality principle. *Psychol Sci, 24*(4), 466-474. doi:10.1177/0956797612457395

Slone, L. K., & Johnson, S. P. (2015). Infants' statistical learning: 2- and 5-month-olds' segmentation of continuous visual sequences. *J Exp Child Psychol, 133*, 47-56. doi:10.1016/j.jecp.2015.01.007

Sodian, B., Schoeppner, B., & Metz, U. (2004). Do infants apply the principle of rational action to human agents? *Infant Behav Dev, 27*(1), 31-41. doi:10.1016/j.infbeh.2003.05.006

Sokolov, E. N. (1963). *Perception and the conditioned reflex*. Oxford: Pergamon Press.

Sokolov, E. N. (1990). The orienting response, and future directions of its development. *Pavlov J Biol Sci, 25*(3), 142-150. doi:10.1007/BF02974268

Sommerville, J. A., & Woodward, A. L. (2005). Pulling out the intentional structure of action: the relation between action processing and action production in infancy. *Cognition, 95*(1), 1-30. doi:10.1016/j.cognition.2003.12.004

Sommerville, J. A., Woodward, A. L., & Needham, A. (2005). Action experience alters 3-month-old infants' perception of others' actions. *Cognition, 96*(1), B1-11. doi:10.1016/j.cognition.2004.07.004

Spelke, E. S., & Kinzler, K. D. (2007). Core knowledge. *Dev Sci, 10*(1), 89-96. doi:10.1111/j.1467-7687.2007.00569.x

Stahl, A. E., & Feigenson, L. (2015). Observing the unexpected enhances infants' learning and exploration. *Science, 348*(6230), 91-94. doi:10.1126/science.aaa3799

Stahl, A. E., & Feigenson, L. (2017). Expectancy violations promote learning in young children. *Cognition, 163*, 1-14. doi:10.1016/j.cognition.2017.02.008

Stahl, A. E., & Feigenson, L. (2019). Violations of core knowledge shape early learning. *Top Cogn Sci, 11*(1), 136-153. doi:10.1111/tops.12389

Stapel, J. C., Hunnius, S., van Elk, M., & Bekkering, H. (2010). Motor activation during observation of unusual versus ordinary actions in infancy. *Soc Neurosci, 5*(5-6), 451-460. doi:10.1080/17470919.2010.490667

Szucs, D., Soltesz, F., Czigler, I., & Csepe, V. (2007). Electroencephalography effects to semantic and non-semantic mismatch in properties of visually presented single-characters: The N2b and the N400. *Neurosci Lett, 412*(1), 18-23. doi:10.1016/j.neulet.2006.08.090

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philos Trans R Soc Lond B Biol Sci, 364*(1528), 2405-2415. doi:10.1098/rstb.2009.0052

Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, Mass.: Harvard Univ. Press.

Tomasello, M., & Carpenter, M. (2005). Intention reading and imitative learning. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From Neuroscience to social science* (Vol. 2, pp. 133-148). Cambridge, Mass.: London: MIT Press.

Uzgiris, I. C. (1981). Two functions of imitation during infancy. *International Journal of Behavioral Development, 4*(1). doi:10.1177/016502548100400101

van Elk, M., van Schie, H. T., Hunnius, S., Vesper, C., & Bekkering, H. (2008). You'll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy. *NeuroImage, 43*(4), 808-814. doi:10.1016/j.neuroimage.2008.07.057

Vaughan Jr, H. G., & Kurtzberg, D. (1992). Electrophysiologic indices of human brain maturation and cognitive development. In M. R. Gunnar & C. A. Nelson (Eds.), *Minnesota Symposia on Child Psychology* (pp. 1-36). Hillsdale, NJ: Erlbaum.

Want, S. C., & Harris, P. L. (2002). How do children ape? Applying concepts from the study of non-human primates to the developmental study of 'imitation'in children. *Dev Sci, 5*(1), 1-14. doi:10.1111/1467-7687.00194

Whiten, A., Horner, V., & Litchfield, C. A. (2004). How do apes ape? *Animal Learning & Behavior, 32*(1), 36-52. doi:10.3758/BF03196005

Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philos Trans R Soc Lond B Biol Sci, 364*(1528), 2417-2428. doi:10.1098/rstb.2009.0069

Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology, 11*(18), R729-R732. doi:10.1016/S0960-9822(01)00432-8

Woodward, A. L. (1998). Infants selectively encode the object of an actor's reach. *Cognition, 69*(1), 1-34. doi:10.1016/S0010-0277(98)00058-4

Wronski, C., & Daum, M. M. (2014). Spatial orienting following dynamic cues in infancy: grasping hands versus inanimate objects. *Dev Psychol, 50*(8), 2020-2029. doi:10.1037/a0037155

Zmyj, N., Aschersleben, G., Prinz, W., & Daum, M. M. (2012). The peer model advantage in infants' imitation of familiar gestures performed by differently aged models. *Front Psychol, 3*, 252. doi:10.3389/fpsyg.2012.00252

Zmyj, N., & Buttelmann, D. (2014). An integrative model of rational imitation in infancy. *Infant Behav Dev, 37*(1), 21-28. doi:10.1016/j.infbeh.2013.10.001

Zmyj, N., Buttelmann, D., Carpenter, M., & Daum, M. M. (2010). The reliability of a model influences 14-month-olds' imitation. *J Exp Child Psychol, 106*(4), 208-220. doi:10.1016/j.jecp.2010.03.002

Zmyj, N., Daum, M. M., & Aschersleben, G. (2009). The development of rational imitation in 9- and 12-month-old infants. *Infancy, 14*(1), 131-141. doi:10.1080/15250000802569884

LIST OF FIGURES

DECLARATION IN ACCORDANCE TO § 8 (1) C) AND D) OF THE DOCTORAL DEGREE REGULATION OF THE FACULTY

UNIVERSITÄT HEIDELBERG
ZUKUNFT
SEIT 1386

FAKULTÄT FÜR VERHALTENS- UND EMPIRISCHE KULTURWISSENSCHAFTEN

Promotionsausschuss der Fakultät für Verhaltens- und Empirische Kulturwissenschaften der Ruprecht-Karls-Universität Heidelberg
Doctoral Committee of the Faculty of Behavioural and Cultural Studies of Heidelberg University

Erklärung gemäß § 8 (1) c) der Promotionsordnung der Universität Heidelberg für die Fakultät für Verhaltens- und Empirische Kulturwissenschaften
Declaration in accordance to § 8 (1) c) of the doctoral degree regulation of Heidelberg University, Faculty of Behavioural and Cultural Studies

Ich erkläre, dass ich die vorgelegte Dissertation selbstständig angefertigt, nur die angegebenen Hilfsmittel benutzt und die Zitate gekennzeichnet habe.
I declare that I have made the submitted dissertation independently, using only the specified tools and have correctly marked all quotations.

Erklärung gemäß § 8 (1) d) der Promotionsordnung der Universität Heidelberg für die Fakultät für Verhaltens- und Empirische Kulturwissenschaften
Declaration in accordance to § 8 (1) d) of the doctoral degree regulation of Heidelberg University, Faculty of Behavioural and Cultural Studies

Ich erkläre, dass ich die vorgelegte Dissertation in dieser oder einer anderen Form nicht anderweitig als Prüfungsarbeit verwendet oder einer anderen Fakultät als Dissertation vorgelegt habe.
I declare that I did not use the submitted dissertation in this or any other form as an examination paper until now and that I did not submit it in another faculty.

Vorname Nachname
First name Family name Miriam Langeloh

Datum, Unterschrift
Date, Signature 18.11.2019, ____

SCIENTIFIC PUBLICATIONS FOR THE PUBLICATION-BASED THESIS

I. Manuscript

Langeloh, M., Buttelmann, D., Matthes, D., Grassmann, S., Pauen, S., & Hoehl, S. (2018). Reduced mu power in response to unusual actions is context-dependent in 1-year-olds. *Front Psychol, 9*, 36. doi:10.3389/fpsyg.2018.00036

II. Manuscript

Langeloh, M., Buttelmann, D., Pauen, S., & Hoehl, S. (2019). 12- to 14-month-olds expect unconstrained agents to act efficiently: ERP evidence from the head-touch paradigm. *Manuscript under review in Developmental Psychology.*

III. Manuscript

Langeloh, M., Pauen, S., Buttelmann, D., Hoehl, S. (2019). One-year-olds' event-related potentials differentiate expected from unexpected action outcomes without context information. *Manuscript under review in Infancy.*

MANUSCRIPT I

Langeloh, M., Buttelmann, D., Matthes, D., Grassmann, S., Pauen, S., & Hoehl, S. (2018). Reduced mu power in response to unusual actions is context-dependent in 1-year-olds. *Front Psychol, 9*, 36. doi:10.3389/fpsyg.2018.00036

ORIGINAL RESEARCH
published: 30 January 2018
doi: 10.3389/fpsyg.2018.00036

Reduced Mu Power in Response to Unusual Actions Is Context-Dependent in 1-Year-Olds

Miriam Langeloh[1,2], David Buttelmann[3], Daniel Matthes[1], Susanne Grassmann[4], Sabina Pauen[2] and Stefanie Hoehl[1,5]*

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany, [2] Department of Psychology, Heidelberg University, Heidelberg, Germany, [3] Department of Psychology, University of Bern, Bern, Switzerland, [4] Institute of Educational Research and Development, University of Applied Sciences and Arts Northwestern Switzerland, Windisch, Switzerland, [5] Faculty of Psychology, University of Vienna, Vienna, Austria

During social interactions infants predict and evaluate other people's actions. Previous behavioral research found that infants' imitation of others' actions depends on these evaluations and is context-dependent: 1-year-olds predominantly imitated an unusual action (turning on a lamp with one's forehead) when the model's hands were free compared to when the model's hands were occupied or restrained. In the present study, we adapted this behavioral paradigm to a neurophysiological study measuring infants' brain activity while observing usual and unusual actions via electroencephalography. In particular, we measured differences in mu power (6 – 8 Hz) associated with motor activation. In a between-subjects design, 12- to 14-month-old infants watched videos of adult models demonstrating that their hands were either free or restrained. Subsequent test frames showed the models turning on a lamp or a soundbox by using their head or their hand. Results in the hands-free condition revealed that 12- to 14-month-olds displayed a reduction of mu power in frontal regions in response to unusual and thus unexpected actions (head touch) compared to usual and expected actions (hand touch). This may be explained by increased motor activation required for updating prior action predictions in response to unusual actions though alternative explanations in terms of general attention or cognitive control processes may also be considered. In the hands-restrained condition, responses in mu frequency band did not differ between action outcomes. This implies that unusual head-touch actions compared to hand-touch actions do not necessarily evoke a reduction of mu power. Thus, we conclude that reduction of mu frequency power is context-dependent during infants' action perception. Our results are interpreted in terms of motor system activity measured via changes in mu frequency band as being one important neural mechanism involved in action prediction and evaluation from early on.

Keywords: EEG, infants, action perception, action understanding, mu frequency, mirror neuron system

OPEN ACCESS

Edited by:
Markus Paulus, Ludwig-Maximilians-Universität München, Germany

Reviewed by:
Janny Christina Stapel, Uppsala University, Sweden
Joni Saby, Children's Hospital of Philadelphia, United States

***Correspondence:**
Miriam Langeloh
langeloh@cbs.mpg.de

Specialty section:
This article was submitted to Developmental Psychology, a section of the journal Frontiers in Psychology

Received: *28 July 2017*
Accepted: *10 January 2018*
Published: *30 January 2018*

Citation:
Langeloh M, Buttelmann D, Matthes D, Grassmann S, Pauen S and Hoehl S (2018) Reduced Mu Power in Response to Unusual Actions Is Context-Dependent in 1-Year-Olds. Front. Psychol. 9:36. doi: 10.3389/fpsyg.2018.00036

INTRODUCTION

From birth on, infants take part in social interactions. These interactions with others are essential for the development of social-cognitive skills (Striano and Reid, 2006). An important ability trained in such interactions is to predict another person's behavior and to react accordingly. This ability comprises that if the prediction turns out to be wrong (prediction error), the corresponding representation is updated appropriately (Kilner et al., 2007). Even though it is well established that the underlying action understanding starts developing early in life (Gredebäck and Daum, 2015), many open questions regarding its mechanisms remain. In the current study, we present evidence that motor activation in the mu frequency band is involved in infants' action processing in the context of unknown objects and that infants take into account visible action constraints when evaluating actions on unknown objects.

Action understanding consists of both the ability to predict and to evaluate others' actions (Gredebäck and Daum, 2015). The ability to *predict* what others will do next has been observed from 6 months on. By this age, infants show predictive eye movements to a target location of a goal-directed action involving everyday objects (e.g., phone or cup). In the second half of their 1st year, they predict more general action goals such as putting a ball into a bucket or bringing food or a cup to another person's mouth (Falck-Ytter et al., 2006; Gredebäck and Melinder, 2010; Hunnius and Bekkering, 2010). The ability to *evaluate* actions has also been observed from 6 months on. Action evaluation is usually measured following the execution of an either expected or unexpected action (Gredebäck and Daum, 2015). Looking time studies demonstrate that infants look longer at actions with unexpected changes in the goal of a directional action (e.g., Woodward, 1998; Reid et al., 2007). Measuring pupil dilation in response to usual vs. unusual actions offers another method to gain insight into infants' action evaluation. Pupil dilation usually follows after attention grabbing or unusual events (Libby et al., 1973). Gredebäck and Melinder (2010) found that 6- and 12-month-old infants' pupils dilated in response to unusual feeding actions (e.g., spoon with food put to the hand). Hence, we already know that infants predict and evaluate another person's behavior indicating a quite elaborate action understanding that emerges during the 1st year of life. Behavioral imitation studies provide yet another approach to examine infants' action understanding, but are often used with slightly older children (e.g., Gampe et al., 2016). Interestingly, behavioral studies show that infants do not imitate every action they observe. They do so selectively depending on characteristics of the model, such as his or her reliability (Zmyj et al., 2010), group membership (Buttelmann et al., 2013) or external factors such as situational constraints (Gergely et al., 2002).

Gergely et al. (2002) investigated how infants imitate another person's action according to efficiency and situational constraints. The authors found that 14-month-old infants were more likely to imitate an unusual head-touch action (i.e., turning on a lamp using the head) when the model's hands were free compared to when her hands were occupied by holding a blanket. Gergely et al. (2002) concluded that this is because infants evaluated actions according to their efficiency or rationality in the given situation (Gergely and Csibra, 2003). This finding was replicated using similar paradigms and designs, and by testing even younger age groups (Schwier et al., 2006; Buttelmann et al., 2008; Zmyj et al., 2009; Gellén and Buttelmann, 2017). In particular, Zmyj et al. (2009) showed that 12- but not 9-month-old infants considered non-voluntary physical restraints (i.e., model's hands tied to the table) when imitating unusual head-touch actions. However, divergent interpretations relating infants' selective imitation behavior to more basic attention processes or motor resonance (i.e., to map others' actions onto one's own motor repertoire) have been brought forward (Paulus et al., 2011a,b; Beisert et al., 2012; but see also Buttelmann and Zmyj, 2012; Buttelmann et al., 2017).

Thus, in the present study, we measured infants' neural responses when observing head-touch actions similar to the original paradigm by Gergely et al. (2002) in order to investigate possible neural mechanisms, particularly the role of motor activation during the observation of unusual actions. In contrast to previous imitation studies, we did not focus on behavioral responses (i.e., imitation rates) as dependent variable, but rather explored the role of motor activation in infants' brains. The rationale of this approach is that selective motor activation during action observation is likely to be involved in action understanding, as action understanding is shaped by action skills. In particular, Hunnius and Bekkering (2014) found that any progress in motor development is typically associated with improved action understanding, resulting mainly from actively experiencing motor actions (see also Sommerville et al., 2005). This is in accordance with results that suggest that 10-month-olds' motor actions develop ahead of their ability to predict action outcomes (Rosander and von Hofsten, 2011). In addition, Stapel et al. (2016) showed that infants who were experienced crawlers but not yet walkers were more accurate in predicting crawling actions than walking actions in an eye-tracking experiment (see also the eye-tracking study by Bache et al., 2017).

These studies suggest that one of the functional mechanisms underlying action understanding is the mirror neuron system (MNS). Mirror neurons discharge during both action observation and action execution (Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004). Thus, observed actions seem to activate motor processes or schemas in the observer's brain that would also be activated if the person executed the action themself (Prinz, 1997). Consequently, this motor system might be highly relevant for action prediction and evaluation (Wolpert and Flanagan, 2001; Prinz, 2006; Kilner et al., 2007).

One neural marker indicating motor activation and activation of the MNS during action observation and execution is the mu rhythm in the electroencephalogram (EEG) across central electrode sites. Mu rhythm activity has been examined in adults (e.g., Muthukumaraswamy et al., 2004; Lepage and Theoret, 2006) and in infants (e.g., van Elk et al., 2008; Southgate et al., 2009; Stapel et al., 2010; Marshall and Meltzoff, 2011; Cuevas et al., 2014). It is measured in the standard alpha frequency band (for adults at about 8–13 Hz and for infants at about 6–9 Hz) and is thought to reflect sensorimotor cortical activation (for a meta-analysis on EEG mu rhythm, see Pfurtscheller and Da Silva, 1999; Pineda, 2005; Fox et al., 2016). In particular, a suppression or desynchronization in the mu frequency band is associated with motor activation during action observation and execution. The decreasing mu power with movement onset indicates a decrease in neuronal synchrony reflecting the processing of movement-related information. Thus, mu rhythm is often interpreted as a neural correlate representing a link between action perception and production (Muthukumaraswamy et al., 2004).

Several infant studies suggest that the infant central mu rhythm is analogous to the adult mu rhythm (Marshall and Meltzoff, 2011). Southgate et al. (2009) demonstrated stronger mu desynchronization for observation and execution of reaching actions relative to baseline in 9-month-old infants. A second study showed similar results and reported stronger mu desynchronization in response to a reaching hand in a grasping posture even when the action outcome was not visible (Southgate et al., 2010). Thus, mu desynchronization additionally reflects infants' prediction of the motor program of an anticipated action. Furthermore, significantly stronger mu desynchronization compared to baseline was found in 14-month-olds for the observation and execution of button presses in a live EEG paradigm (Marshall et al., 2011).

Mu desynchronization in infants seems to depend on active experience and, thus, on whether or not an action is already in the infants' motor repertoire (van Elk et al., 2008; Gerson et al., 2015). In this line, spectral power in the 7–9 Hz frequency band was more suppressed in 14- to 16-month-olds for the observation of crawling compared to walking (van Elk et al., 2008). This effect was highly related to infants' own crawling experience in that more experienced crawlers showed stronger mu desynchronization. In addition, mu desynchronization was sensitive to bidirectional action-effect associations (of sounds and rattles) in 8-month-olds (Paulus et al., 2012). In sum, this branch of research indicates that motor activation measured by mu desynchronization depends on experience with stronger reduction of mu frequency power occurring for more familiar or trained actions.

In addition, mu desynchronization can be related to generating action predictions (Stapel et al., 2010; Saby et al., 2012). Stapel et al. (2010) found stronger mu desynchronization on fronto-central and mid-frontal channels in 12-month-olds in response to extraordinary actions (e.g., lifting a cup to the ear) compared to ordinary actions (e.g., lifting a cup to the mouth). The authors interpreted this result by applying the theory of predictive coding (Kilner et al., 2007): According to this theory, the MNS forms predictions about another person's action given an assumed goal. The MNS constantly checks whether the predicted action goal still matches what is being observed. For unusual action outcomes, like putting a cup to the ear, there is a mismatch between prediction and observation. Consequently, a new prediction has to be generated and this results in stronger motor activation (Gardner et al., 2015).

To summarize, analyzing mu frequency band power allows us to investigate infants' action processing. While studies on infants' own action experiences reported increased motor activation when observing more familiar actions, studies manipulating action outcomes found that unexpected outcomes elicit a stronger mu desynchronization than expected outcomes. Thus, the mu frequency seems to be involved in both motor resonance depending on action experiences and on action prediction. However, previous research predominantly investigated mu frequency power in response to actions with familiar objects (e.g., a cup or food). This offers us a unique opportunity to study the cognitive processes during infants' observation of head-touch actions with novel objects as used in previous behavioral studies on selective imitation. In particular, reduced mu power during unusual head-touch actions (compared to hand-touch actions) would speak for the induction of a prediction error while watching these actions in the absence of situational constraints. On the other hand, stronger mu suppression in response to hand actions would argue for the role of previous motor experience in processing these actions, since infants much more frequently manipulate objects with their hands.

Thus, this is the first study investigating the neural mechanisms underlying the observation of an unusual head touch in adaptation to paradigms previously used in imitation studies (Gergely et al., 2002; Zmyj et al., 2009). Here, we explored possible neuronal mechanisms that might have influenced selective imitation demonstrated in previous studies. In addition, we aimed to elucidate whether these neural mechanisms are sensitive to the action context or not (cf. Zmyj et al., 2009). To examine infants' neural processing, we designed an EEG study measuring context-dependent motor system activity via mu frequency power during infants' perception of different action outcomes. In a between-subjects design, 12- to 14-month-olds watched short video sequences of models demonstrating that their hands were free (hands-free condition) or restrained (hands-restrained condition). Subsequent test frames showed the same model turning on a lamp or soundbox using either their head or their hand. We intended to explore whether there were differences in mu power between processing of head- and hand-action outcomes in the hands-free condition and whether mu power varied depending on situational constraints in the hands-restrained condition.

We hypothesized that if prediction error and updating (cf Kilner et al., 2007; Stapel et al., 2010) take place when infants observe others using their head rather than their hand to manipulate an object, then reduced mu power on central channels in response to head actions compared to hand actions should occur in the hands-free condition. In the hands-restrained condition, we expected the opposite result pattern if infants incorporate situational factors while predicting and evaluating action outcomes (i.e., reduced mu power in response to hand compared to head actions). If motor experience influences mu frequency power (van Elk et al., 2008; Gerson et al., 2015), then lower mu power indicating motor resonance in response to familiar hand actions compared to less familiar head actions should be demonstrated in the hands-free condition and possibly also in the hands-restrained condition. If infants do not take into account context information, then results should be similar in both the hands-free and the hands-restrained condition.

MATERIALS AND METHODS

Participants

The final sample consisted of 22 12- to 14-month-old infants (11 girls, M = 13 months 2 days, SD = 23 days, age range = 12 months 5 days – 14 months 24 days) in the hands-free condition and 20 infants (9 girls, M = 12 months 25 days, SD = 22 days, age range = 12 months 1 day – 14 months 29 days) in the hands-restrained condition. Infants were recruited from a midsized

German city and surrounding areas. They were from middle-class background, born full-term (37–41 weeks of gestation), Caucasian and without any known neurological problems. In addition, 32 infants were tested but excluded from the final sample due to fussiness (i.e., infants showed too many movement artifacts or started crying before being presented with the required number of trials), another 39 infants failed to provide 10 artifact-free trials per within-subjects condition, in 4 additional infants contact of the reference electrode was not satisfactory (i.e., very spiky signal of all electrode channels) and in two sessions technical and experimental errors occurred. This attrition rate is within the typical range for infant EEG studies of 50–75% (e.g., DeBoer et al., 2007; Stets et al., 2012). The loss of participants mainly resulted from 12- to 14-month-olds' difficulty to sit motionless during the presentation of multiple trials, as it is required for acquiring valid EEG data. There is no indication for a systematic distortion of our sample. Informed verbal and written consent were obtained from each participant's parent before conducting the experiment. Infants received a certificate with their photo for participation. Experimental procedures were approved by the ethics committee of Friedrich Schiller University in Jena (reference 3752-04/13).

Stimuli

Infants were presented with video clips and photographs showing adult models performing head or hand actions (adapted from Gergely et al., 2002; Zmyj et al., 2009). Two different types of videos were used: To establish context and motivation at the beginning of the experiment, infants watched two pre-demonstration videos showing a female or male adult sitting at an empty table demonstrating that the hands were free or restrained by turning them. Each participant watched both videos in randomized order regarding sex of the model and situational constraints.

Following the pre-demonstration videos, each trial of the demonstration-phase videos illustrated the action context depicting one of four models (two males, two females) sitting at a table with a touch light in front of them. Subsequent test frames depicted action outcomes. In the hands-restrained condition (adapted from Zmyj et al., 2009), the model's hands were tied to the table with duct tape and could not be moved freely. In the hands-free condition, a line of duct tape was visible on the table but the model's hands were free. In both conditions, subsequent test frames showed a model turning on a lamp using either their hand or their head (see **Figure 1**). The model did not establish eye contact with the observer during the whole experiment. In half of the trials, a round lamp (12 cm diameter) mounted on a black box (27 cm × 20 cm × 6 cm) was illuminated while the model was touching it (cf Meltzoff, 1988). To increase infants' attention toward the presentation, in the other half of trials a toy-squeezing sound was generated while the model was touching a blue and green soundbox (13 cm × 13 cm × 11.5 cm) (in accordance with Buttelmann et al., 2007). The sound was presented with a maximum intensity of 75 dB.

In the test frames, the model was presented on screen with a width of approximately 9.13 cm (visual angle of 9.49°) and a height of 10.34 cm (visual angle of 10.74°) measured from head to table. The touch light was presented with a size of 4.6 cm × 8.4 cm (visual angle of 4.79° × 8.73°) and the soundbox with a size of 4 cm × 4.5 cm (visual angle of 4.17° × 4.69°). Test frames were adjusted to each other with Adobe Photoshop CS4 extended in terms of brightness and contrast (all $ps > 0.05$). **Figure 1** depicts example trials in which the model turns on the light or produces a sound by using either his or her hand or head in both conditions.

Procedure

Infants were tested individually in a quiet, dimly lit room. The testing area was separated from the rest of the laboratory by dark blue colored room dividers. Infants sat on their parent's lap in front of a 75 Hz 19-inch stimulus monitor with a viewing distance of 55 cm. Parents were instructed not to interact with the infant during data collection. In both the hands-free and hands-restrained condition, the experiment consisted of one block of a maximum of 120 trials. This block comprised 60 trials illustrating a hand touch and 60 trials illustrating a head touch. The videos were displayed in semi-randomized order via the software Presentation (Neurobehavioral Systems, Albany, CA, United States) with the constraint that the same modality (light/sound), gender (male/female) or outcome (hand touch/head touch) were not presented three times consecutively and that all 16 possible test pictures (light/sound, head touch/hand touch, for each of the four models) were displayed within the first 48 trials. To avoid confounding effects of the first observed action, action outcomes (head and hand touch) were counterbalanced between participants in the first trial of each condition.

Figure 1 shows an exemplary stimulus trial sequence. At the beginning of the trial, a central attractor was presented for an average of 1000 ms to catch infants' attention. The subsequent video sequence depicted the model showing that the hands were free or restrained by wiggling for 5000 ms. After that, a blank screen was presented for a random period between 800 and 1000 ms. Lastly, the test frame representing hand- or head-action outcomes was presented for 1500 ms. Each trial lasted 8500 ms leading to a maximum total testing time of 17 min. Short breaks could be taken after the end of a trial, when the infant became tired or fussy. The session ended when the infant no longer attended to the screen. EEG activity was recorded continuously and infants were video-recorded throughout the experiment for offline coding of looking behavior and movements.

EEG Recording and Analyses

Electroencephalogram was measured by a 32-channels ActiCap system (Brain Products, Gilching, Germany) with 32 active silver/silver chloride (Ag/AgCl) electrodes arranged according to the 10–10 system. Horizontal and vertical electrooculograms were recorded bipolarly. Impedances were controlled at the beginning of the experiment and accepted when below 20 kΩ. Sampling rate was set at 250 Hz. Electrode signals were referenced to the right mastoid electrode and amplified via a BrainAmp amplifier.

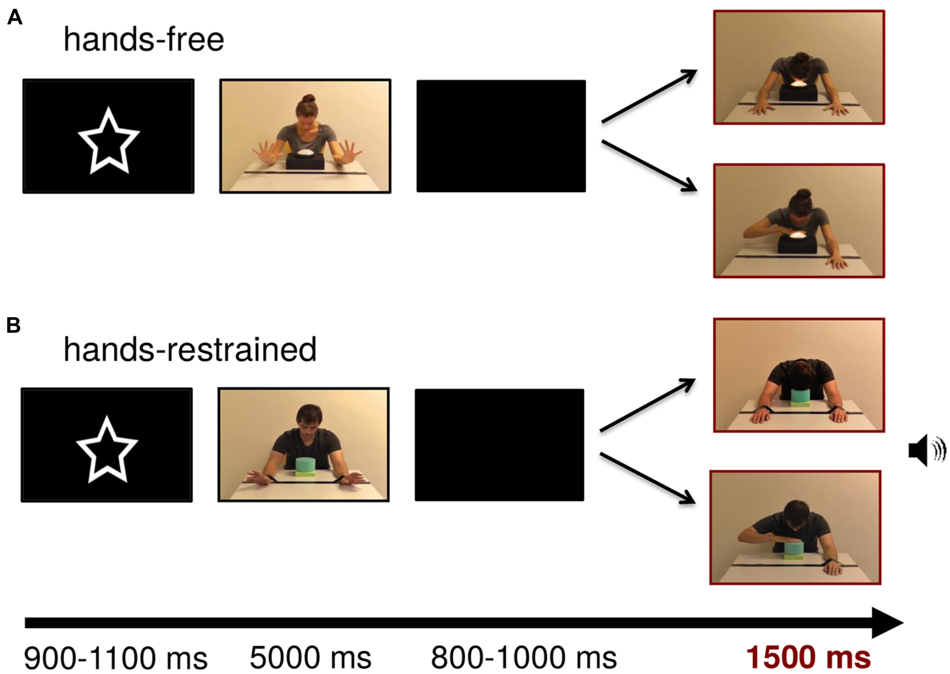

FIGURE 1 | Stimulus examples of lamp and sound modality for **(A)** hands-free and **(B)** hands-restrained condition. Persons appearing in this figure consented to the publication of these images.

EEG Preprocessing

Electroencephalogram data were first processed by using BrainVision Analyzer 2 (Brain Products, Gilching, Germany) and further analyzed in Fieldtrip (Oostenveld et al., 2011). Raw data were filtered off-line with a 0.3–30 Hz band-pass filter to remove frequencies not related to cortical processes of interest. Data were then re-referenced to the average mastoids (TP9, TP10). Data were automatically excluded if the amplitude of the analyzed channels exceeded a voltage threshold of 200 μV within a 200 ms interval. Thus, data including gross motor movements were rejected from final analysis by this automatic artifact rejection algorithm. Data were then segmented into epochs of waveforms that comprised 200 ms before stimulus onset of the test frame, demonstrating a head touch or a hand touch, through 1500 ms following stimulus onset. Infants' looking behavior was video-coded offline. Only trials in which infants did not blink and paid attention to the whole presentation of the test frame, showing head- and hand-action outcomes, were included in further analyses. In addition, videos were coded for more subtle movements of infants, such as hand or head movements that resembled actions performed by the video models in our stimuli (i.e., pressing a button by hand or by head or similar actions, like reaching or pointing) (cf Marshall et al., 2011). An independent rater, blind to hypotheses, coded infants' movements during all observed action outcomes. An additional coder rated 25% of the videos from each condition (hands-free and hands-restrained). A high degree of inter-rater reliability was found between 758 measurements with an average measure intraclass correlation (ICC) of 0.840. To ensure that motor activation related to the target actions (head touch and hand touch) was equivalent between conditions (hands-free and hands-restrained) and within conditions, we conducted a mixed analysis of variance (ANOVA) with the between-subjects factor *condition* (hands-free, hands-restrained) and the within-subjects factor *outcome* (target action movement during head-touch outcomes, target action movement during hand-touch outcomes). The ANOVA did not yield a significant main effect of *outcome*, $F(1,40) = 2.394$, $p = 0.130$, or *condition*, $F(1,40) = 0.985$, $p = 0.327$. Likewise, no significant interaction between *condition* and *outcome* was found, $F(1,40) = 2.394$, $p = 0.130$. Overall, infants very rarely performed actions similar to the hand and head touch demonstrated by the video models during the whole experiment ($M = 1.69$ movements, $SD = 1.62$ movements). Thus, significant differences between conditions and/or action outcomes cannot result from differences in infants' movements similar to the presented target actions (hand and head touch). Data were then baseline-corrected using 200 ms prior to the onset of the test frame and finally segmented for hand and head touch in both hands-free and hands-restrained conditions, respectively.

Frequency Domain Analysis

Artifact-free data segments were submitted to fast Fourier transformations (FFTs). For each segmented test frame (hand or head touch), the power was computed from 0 to 1,500 ms relative to the onset of the related stimulus using a Hanning-tapered window of the same length (by applying the 'ft freqanalysis' function with 'mtmfft' method as implemented in Fieldtrip). Power estimates were calculated for frequencies ($\frac{2}{3}$ Hz bins) between 0 and 124.667 Hz. Grand averages of the FFTs were

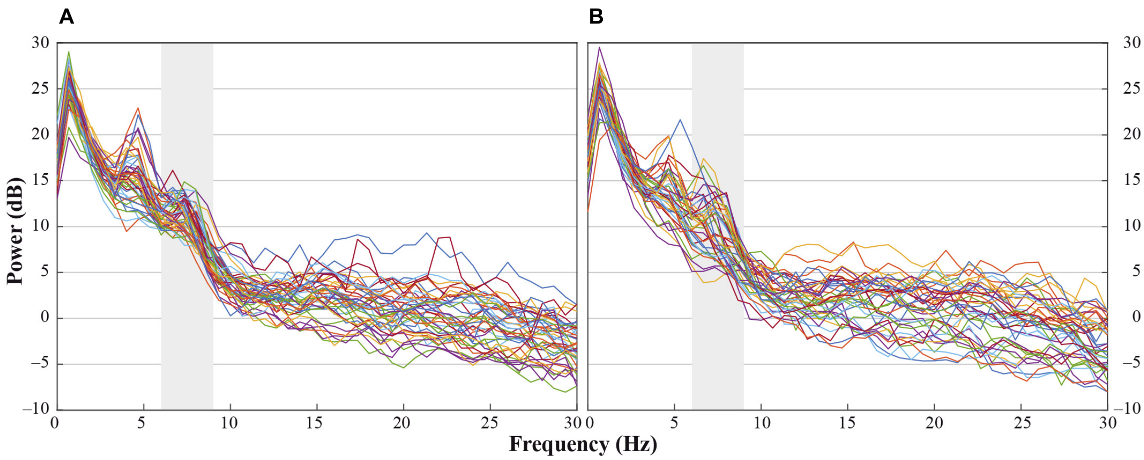

FIGURE 2 | Individual power spectra across an average for hand- and head-touch actions across an average of frontal and central electrodes (F3, F4, C3, C4) for **(A)** hands-free and **(B)** hands-restrained condition.

computed for both hand- and head-action outcomes in the hands-free and hand-restrained condition.

A minimum of 10 artifact-free trials per outcome was required for an infant to be included in the statistical analyses. In the hands-free condition, each infant contributed 13 to 56 trials (M = 21.23, SD = 9.88) to the head outcome and 11 to 56 trials (M = 19.18, SD = 9.81) to the hand outcome. In the hands-restrained condition, each infant contributed 10 to 34 trials (M = 17.25, SD = 5.87) to the head outcome and 10 to 29 trials (M = 16.05, SD = 5.45) to the hand outcome. Across conditions each infant contributed 10 to 56 (M = 19.33, SD = 8.36) valid trials to the head outcome and 10 to 56 valid trials to the hand (M = 17.69, SD = 8.10) outcome.

In accordance with previous research we analyzed central electrode positions on the left and right hemisphere (C3, C4) to investigate differences in motor activation indicated by mu frequency power (e.g., Paulus et al., 2012). As visual inspection indicated differences between unusual head-touch and familiar hand-touch actions especially on frontal channels and as previous studies also investigated the role of frontal activation in infants' action perception (e.g., van Elk et al., 2008; Stapel et al., 2010), we included lateral frontal channels (F3, F4) into the final analysis. In addition, parietal channels P3 and P4 were included in the analysis in order to exclude the possibility that potential alpha-band effects were widespread across the scalp (including posterior regions) suggesting general arousal rather than involvement of the motor system. Occipital channels (O1, O2) were not selected for comparison to fronto-central electrode positions because channels were too noisy and did not provide enough artifact-free data for valid analyses. For each participant, a dominant mu peak was identified for frontal and central electrodes (F3, F4, C3, C4) between 6 and 9 Hz. Analyses revealed that in the hands-free condition up to 20 infants peaked between 6.7 and 8 Hz in response to the hand touch and up to 19 infants in response to the head touch (see **Figure 2A**). Similarly, in the hands-restrained condition up to 15 infants peaked in response to the hand touch and 15 infants in response to the head touch between 6.7 and 8 Hz (see **Figure 2B**). This is in accordance with previous research on mu frequency in infants indicating that mu frequency band falls between 6 to 9 Hz in infants (Marshall and Meltzoff, 2011) and peaks at about 8 Hz in 1-year-olds (Marshall et al., 2002). Thus, the statistical analyses were conducted across the average power of the 6 to 8 Hz frequency range.

Statistical Analysis

To investigate overall differences between conditions, data were analyzed by a mixed ANOVA with the between-subjects factor *condition* (hands-free, hands-restrained) and the within-subjects factors *action outcome* (head, hand), *region of interest* (frontal: F3/F4, central: C3/C4, parietal: P3/P4) and *hemisphere* (left, right). Partial eta squared (η_p^2) or Cohen's d (d) are reported as estimates of the effect size. Greenhouse-Geisser correction for non-sphericity was employed if applicable for conservative corrections. Fractional degrees of freedom (df) were reported when Greenhouse-Geisser correction was necessary (i.e., when Mauchly's test for sphericity was significant) and applied. The significance level was set at $p < 0.05$ (two-tailed) for all statistical analyses.

RESULTS

Hands-Free vs. Hands-Restrained Condition

To compare results between the hands-free and hands-restrained condition, we first computed a mixed ANOVA with the between-subjects factor *condition* (hands-free, hands-restrained) and the within-subjects factors *action outcome* (head, hand), *region of interest* (frontal, central, and parietal) and *hemisphere* (left, right). Analysis yielded a significant interaction between *condition*, *action outcome*, *region of interest*

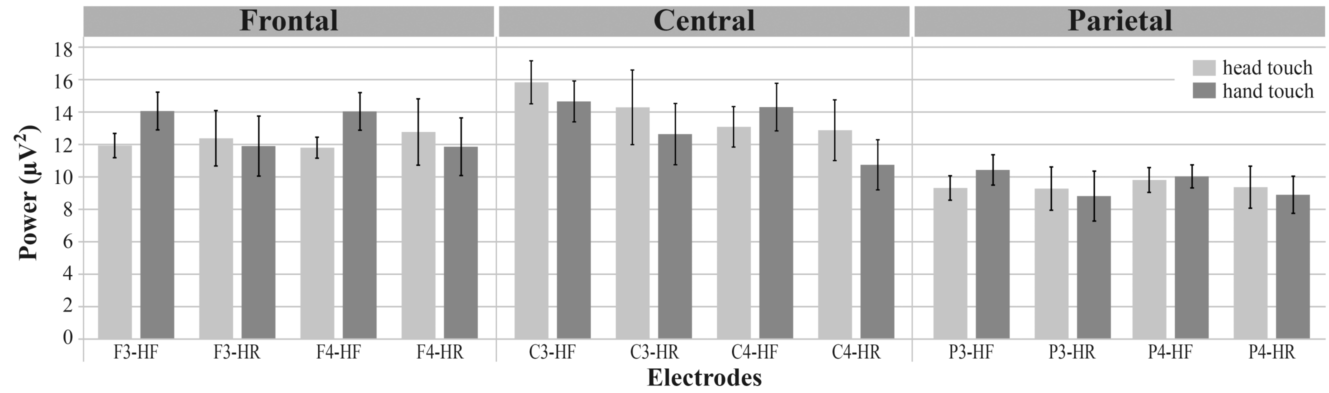

FIGURE 3 | Grand average EEG power across mu frequency band (6–8 Hz) for electrodes of interest (F3, F4, C3, C4, P3, P4) in response to hand touch (dark gray) and head touch (light gray) for both hands-free (HF) and hands-restrained (HF) condition. Error bars represent standard errors of the mean.

and *hemisphere*, $F(2,80) = 3.390$, $p = 0.039$, $\eta_p^2 = 0.08$ (for a detailed illustration of main effects and interactions, see Supplementary Table 1). Thus, conditions were further analyzed separately to explain this interaction effect. Mu power of all electrodes of interest (F3, F4, C3, C4, P3, P4) is plotted in **Figure 3**.

Hands-Free Condition

Infants demonstrated dominant peaks in response to observing head- and hand-action outcomes in the frequencies of interest (6–8 Hz) especially on frontal and central electrodes (see **Figure 2A**). Visual inspection of the grand average FFTs indicated reduced mu power in response to the head touch compared to the hand touch. This tendency was more pronounced on frontal electrodes (see **Figure 4**).

The repeated-measures ANOVA (rmANOVA) revealed a significant interaction of *action outcome*, *region of interest* and *hemisphere*, $F(2,42) = 6.918$, $p = 0.003$, $\eta_p^2 = 0.25$ (for a detailed illustration of main effects and interactions, see Supplementary Table 2). In order to resolve this significant interaction, we conducted three two-way rmANOVAs with the within-subjects factors *action outcome* (head, hand) and *hemisphere* (left, right) for each region of interest. For frontal channels (F3, F4), we found a significant main effect of *action outcome*, $F(1,21) = 8.675$, $p = 0.008$, $\eta_p^2 = 0.29$, indicating that mu power in both frontal electrodes was significantly lower in response to head-touch outcomes ($M = 11.87$, $SD = 2.96$) compared to hand-touch outcomes ($M = 14.05$, $SD = 5.35$) independent of *hemisphere*, $F(1,21) = 0.28$, $p = 0.868$. Analysis of frontal regions did not reveal a significant interaction between *action outcome* and *hemisphere*, $F(1,21) = 0.044$, $p = 0.836$. For central channels (C3, C4), the rmANOVA analysis yielded a significant interaction of *action outcome* and *hemisphere*, $F(1,21) = 7.990$, $p = 0.010$, $\eta_p^2 = 0.28$. *Post hoc* *t*-tests for left (C3) and right (C4) hemisphere compared mu frequency power of hand- and head-action outcomes. On the right hemisphere mu power was slightly lower in response to head-touch ($M = 13.09$, $SD = 5.86$) compared to hand-touch outcomes ($M = 14.31$, $SD = 6.89$). However, it did not reach significance, $t(21) = -1.932$, $p = 0.067$, $d = 0.41$. No significant differences in mu power were found on the left hemisphere, $t(21) = 1.175$, $p = 0.253$. For parietal channels (P3, P4), the rmANOVA did not reveal a significant main effect of *action outcome*, $F(1,21) = 1.076$, $p = 0.311$, *hemisphere*, $F(1,21) = 0.004$, $p = 0.952$, nor a significant interaction between *action outcome* and *hemisphere*, $F(1,21) = 1.869$, $p = 0.186$.

Thus, we found reduced mu power in response to head-touch actions compared to hand-touch actions especially on frontal electrode positions and a tendency for the same effect at the right central electrode site.

Hands-Restrained Condition

In the hands-restrained condition we investigated whether infants incorporate contextual information while evaluating action outcomes via the motor system measured by differences in mu frequency power. Comparable to the hands-free condition, the majority of infants peaked in response to observing head- and hand-action outcomes in the frequencies of interests (6 – 8 Hz) especially on frontal and central electrodes (see **Figure 2B**). Visual inspection indicated increased mu power in response to the head touch and reduced mu power in response to the hand touch (see **Figure 5**).

We again conducted a rmANOVA with the within-subjects factors *action outcome* (head, hand), *region of interest* (frontal, central, parietal) and *hemisphere* (left, right). There were, however, no significant interactions of *action outcome*, *region of interest*, and *hemisphere*, all *p*s > 0.29. Likewise the analyses did not reveal main effects of *action outcome*, $F(1,19) = 1.601$, $p = 0.221$ or *hemisphere*, $F(1,19) = 0.753$, $p = 0.396$. We only found a significant main effect of *region of interest*, $F(2,27.25) = 15.220$, $p < 0.001$, $\eta_p^2 = 0.45$, indicating that across action outcomes overall mu power was lower at parietal regions ($M = 9.09$, $SD = 5.49$) than at frontal ($M = 12.23$, $SD = 7.60$) and central regions ($M = 12.64$, $SD = 7.79$). In sum, results showed no differences in mu power between head and hand touch in the hands-restrained condition.

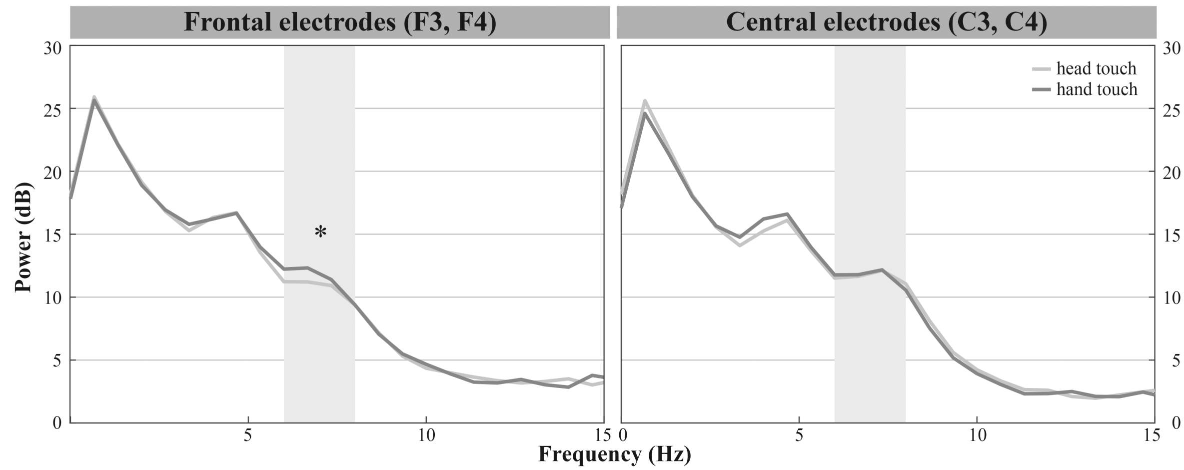

FIGURE 4 | Grand average EEG mu power for hand touch (dark gray) and head touch (light gray) for an average of frontal electrodes (F3, F4) and for an average of central electrodes (C3, C4) in the hands-free condition. Asterisks depict significant differences with $p < 0.05$.

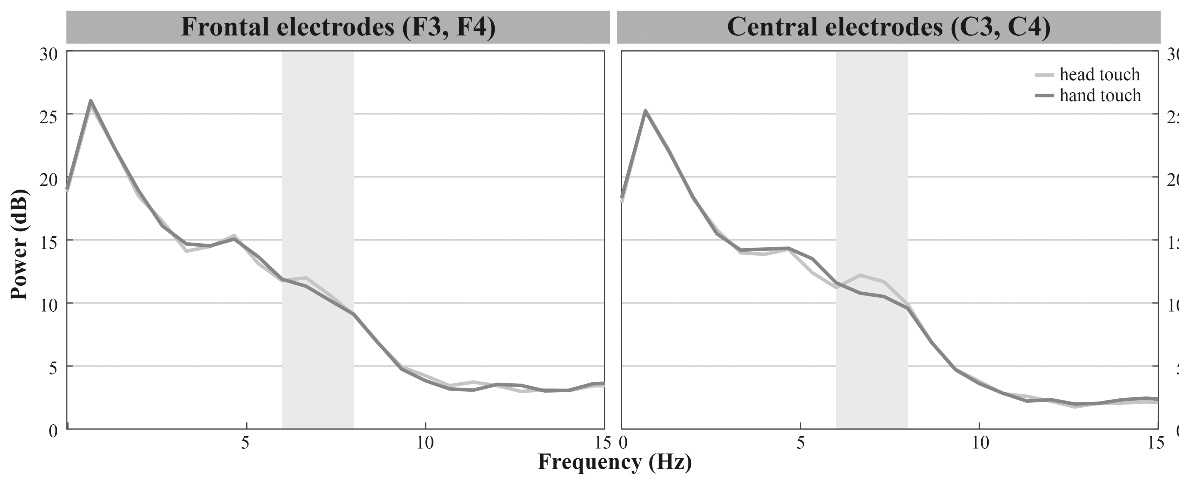

FIGURE 5 | Grand average EEG mu power for hand touch (dark gray) and head touch (light gray) for an average of frontal electrodes (F3, F4) and for an average of central electrodes (C3, C4) in the hands-restrained condition.

DISCUSSION

This study was designed to shed light on the neural mechanisms underlying infants' observation of unusual head-touch actions used previously in selective imitation studies (e.g., Gergely et al., 2002; Gellén and Buttelmann, 2017). For this, we investigated the role of motor activation through measuring differences in mu frequency power. In addition, we aimed to explore whether motor activation during action perception is sensitive to contextual factors. To this end, we adapted a well-known behavioral imitation paradigm (Gergely et al., 2002; Zmyj et al., 2009) to an EEG experiment for the first time: In a between-subjects design, infants were presented with short video sequences of adult models demonstrating that his or her hands were either free or restrained. Subsequent test frames showed the same person turning on a lamp or soundbox using their head or their hand. Results in the hands-free condition revealed that 12- to 14-month-old infants displayed reduced mu frequency power in response to unusual head-touch actions compared to familiar hand-touch actions. Interestingly, in the hands-restrained condition we did not find differences in mu frequency power in response to hand- vs. head-touch actions.

Previous research associated mu desynchronization with motor activation or cortical processing of movement-related activity (Fox et al., 2016). In the hands-free condition, significant changes in mu frequency band in response to the observation of head-touch vs. hand-touch actions were predominantly found in frontal regions (F3, F4). Despite other studies demonstrating changes in mu frequency band on frontal or fronto-central channels (van Elk et al., 2008; Stapel et al., 2010), effects of mu frequency band are often more pronounced on central electrode positions (Marshall and Meltzoff, 2011). Since in our study no significant differences in mu power were found on central channels, an interpretation of our results in terms of alpha power associated with general attention or cognitive control processes unrelated to motor activation may be considered (Marshall et al., 2009; Quandt et al., 2011; Klimesch, 2012).

In adults, tasks-related modulations in alpha power can be associated with two controlled functions of attention, namely selection and suppression. Here, alpha frequency activity is thought to function as an attention filter and a decrease in alpha amplitude reflects a release from inhibition. In addition, alpha-band activity has been suggested to indicate controlled access of a semantic knowledge system (Klimesch, 2012). Alpha desynchronization across the whole scalp was reported in 9-month-old infants in response to objects that were presented after engaging in mutual eye contact vs. no eye contact. Eye contact might have put infants in a receptive state of semantic knowledge acquisition (Hoehl et al., 2014). According to these accounts, infants may have been more attentive in response to the unusual head touch.

However, we found significant differences in alpha power between unusual and familiar actions only on frontal sites (parietal channels did not show the same result pattern). This is in line with previous neurophysiological studies relating changes in frontal alpha rhythm to early states of observational and imitative learning (Marshall et al., 2009; Quandt et al., 2011). Accordingly, brief imitative experience of unfamiliar actions is associated with larger alpha desynchronization on frontal channels (Marshall et al., 2009) independent of the type of training (visual and/or active experience; Quandt et al., 2011). Thus, neural processing of action observation, especially on frontal channels, is influenced by a moderate amount of initial experience with these actions. Neuroimaging literature suggests that this frontal activation for unfamiliar actions reflects dorsolateral prefrontal cortex (DLPFC) activation during an active process of consolidating or forming motor representations of previously unknown actions (Jeannerod, 2006; Vogt et al., 2007). With increasing active experience, activation shifts toward more posterior motor regions for high levels of expertise (Shadmehr and Holcomb, 1997; Calvo-Merino et al., 2005; Kelly and Garavan, 2005). In this view, the reduction in alpha power on frontal channels in response to unusual head-touch actions compared to hand-touch actions may reflect a process of mapping observed movements onto previously created motor memories (Jeannerod, 2006; Marshall et al., 2009).

Finally, we suggest a third explanation for the frontal effects in the hands-free condition based on our hypotheses. If prediction error and updating (Kilner et al., 2007) take place when infants observed an unusual action, we expected reduced mu power in response to unusual compared to familiar action outcomes (Stapel et al., 2010). If motor experience influenced mu frequency power in the present study, lower mu power in response to familiar hand actions compared to unfamiliar head actions was expected (van Elk et al., 2008; Gerson et al., 2015). We found reduced mu power in response to the unusual head touch compared to the familiar hand touch and, thus, propose that infants updated their action predictions via the motor system for action outcomes that violated their prior action expectations (Kilner et al., 2007).

Our neural findings are in line with previous behavioral research on action understanding suggesting that by the age of 6 months infants are able to predict another person's actions (for a similar explanation of the results, see principle of rationality, Gergely and Csibra, 2003). For example, 6-month-olds anticipated action outcomes more frequently for functional compared to non-functional goal-object combinations (e.g., cup to mouth or to ear) or their pupils dilated in response to unexpected feeding actions (Gredebäck and Melinder, 2010; Hunnius and Bekkering, 2010). In addition, our results are in accordance with previous EEG studies on action processing. In the hands-free condition, we replicated the finding by Stapel et al. (2010) that 12-month-olds showed stronger mu desynchronization in response to extraordinary compared to ordinary actions. Further EEG studies demonstrated that even 9-month-old infants discriminated familiar vs. unusual eating actions. Infants responded with an N400-like component only to unexpected action outcomes (e.g., pretzel put to ear) indicating a violation of semantic action context (Reid et al., 2009; Kaduk et al., 2016). Furthermore, infants have been shown to distinguish between disrupted and complete actions in terms of increased frontal gamma band activity or more negative slow wave components (Reid et al., 2007; Pace et al., 2013). However, low-level explanations (e.g., variability in stimulus materials) might have accounted for differences between conditions in previous studies. To sum up, in the hands-free condition reduced mu power in response to the unusual head touch indicates that 12- to 14-month-old infants were able to predict action outcomes after being presented with the action context.

In addition, we investigated whether context information influenced motor activation in the hands-restrained condition. We expected opposite result patterns to the hands-free condition. Accordingly, the head touch did not elicit lower mu power compared to hand touch in the hands-restrained condition. Thus, it seems that infants incorporate situational factors while evaluating action outcomes. This is in accordance with previous behavioral studies suggesting that by 6–12 months of age infants are able to interpret actions as goal-directed and take into account situational constraints (e.g., Gergely et al., 1995; Woodward and Sommerville, 2000; Schwier et al., 2006; Zmyj et al., 2009; Gredebäck and Melinder, 2010). Despite visual inspection indicating differences in mu power especially on central channels, we did not find significant different brain responses between hand- and head-action outcomes in the hands-restrained condition. In line with previous behavioral and imitation studies (Gergely and Csibra, 2003; Schwier et al., 2006; Zmyj et al., 2009), we would have expected infants to discriminate both action outcomes also in this scenario. The predictive coding theory proposes that the MNS functions to recognize and code for goals of observed actions (Kilner et al., 2004, 2007). Infants should have been able to encode both action goals and context-specific information to predict action outcomes and update their predictions in case of prediction error. When observing a model turning on a lamp by hand despite the fact that hands were previously tied to the table, prediction error and prediction updating were expected to take place in response to the physically impossible action.

There are several possible explanations for why we did not find differences between hand and head touches in the hands-restrained condition. First, infants might have not entirely processed the restraining duct tape visually. Second, it might be that infants did not know what to predict when they observed a person whose hands were tied to the table. In this case subsequent action outcomes would have not been evaluated in comparison to prior action predictions (for a similar explanation in word learning by exclusion, see Grassmann et al., 2015). These explanations are rather unlikely, as Zmyj et al. (2009) demonstrated that 1-year-olds imitated selectively depending on the same external physical constraint when presented on a computer screen. Besides, if infants did not recognize our situational constraint at all, results should have revealed similar effects to the hands-free condition. Another explanation might be that infants visually processed the situational constraint but the head touch was still highly salient. This hypothesis is supported by a recent eye-tracking study demonstrating that 14-month-old infants paid a similar high amount of attention to the head touch of a model irrespective of whether or not the model was able to use his or her hands (Buttelmann et al., 2017).

Finally, two different processes might have played a role in the hands-restrained condition: One-year-olds already have numerous experiences with hand-touch actions as they can observe other humans turning on switches resulting in visual (e.g., light) or auditory effects (e.g., sounds) repeatedly in everyday life. Increased experience might have enhanced motor activation at central sites during action observation (van Elk et al., 2008; Cannon et al., 2014; Gerson et al., 2015). In addition, infants might have formed action predictions based on semantic knowledge. Action outcomes that violated these prior predictions might have led to prediction updating and, thus, increased motor activation (Kilner et al., 2007). Both high experience and prediction updating in response to hand actions might have affected mu power at the same time in the hands-restrained condition. Hence, we conclude that motor activation measured via mu frequency band is context-sensitive in the present study. However, effects of experience might have interfered with brain activity based on predictive coding. This is in accordance with an adult study measuring influences of motor experience and conceptual knowledge on brain activity in action perception (Gerson et al., 2017). Here, motor experience and predictions based on conceptual familiarity were experimentally manipulated in a 1-week pre-/post-training design. Results revealed that motor system activity measured via beta power changed in response to both factors in a parallel but distinct way: Increased experience led to increased motor activity whereas increased conceptual information about a previously unfamiliar action led to a relative decrease of motor activity across time. To summarize, results of the hands-restrained condition differed from the hands-free condition in terms of mu power indicating that mu power reflecting motor activation during action observation is context-dependent.

The stimuli used in the present study were based on previous behavioral imitation studies indicating that 12- to 14-month-olds are more likely to imitate an unusual head touch depending on varying situational constraints (Gergely et al., 2002; Zmyj et al., 2009). Our neural findings extend recent behavioral results as we revealed differences in mu power in response to head vs. hand touch dependent on external situational constraints. In addition, our results suggest a neural mechanism underlying previous behavioral findings: Infants might form action predictions and update their predictions for deviating action outcomes via the motor system (Kilner et al., 2007). In accordance with the predictive coding framework, increased motor activation in response to the unusual head touch might reflect the process of updating predictions in case of prediction error. This is in line with research on adults demonstrating increased motor activation in response to deviating or unusual action outcomes (e.g., Manthey et al., 2003; Koelewijn et al., 2008). Motor system activity in adults was even sensitive to the degree of prediction with increased activation in response to highly predictable action outcomes (Braukmann et al., 2017).

The present results highlight the role of motor activation during action perception by utilizing stimuli adapted to previous behavioral studies. However, with the present neurophysiological findings we cannot draw any conclusions regarding the possible effect on infants' imitative behavior. Here, we offer one possible explanation for why infants show increased motor activation in response to unusual actions; this explanation is in accordance with the predictive coding theory. The relation between motor activation and infants' imitation still awaits further clarification.

In sum, the present study revealed a reduction in mu power, which might be related to the motor system, in response to an unusual head-touch action in 12- to 14-month-old infants. Reduced mu power in response to unusual compared to familiar actions may indicate prediction error and updating according to the predictive coding framework (Kilner et al., 2007). This effect was only pronounced in the hands-free condition, suggesting that the motor system activated during action prediction and evaluation is context-dependent. Our neuroscientific findings extend previous behavioral results suggesting that a reduction of mu frequency power is one possible functional mechanism underlying infants' early action understanding.

ETHICS STATEMENT

This study was conducted in the Baby Laboratory of the Department of Biological and Developmental Psychology at Heidelberg University, Heidelberg, Germany. The study and experimental procedures were approved by the ethics committee of Friedrich Schiller University, Jena, Germany (reference: 3752-04/13) and were in accordance with the Declaration of Helsinki. Participants were recruited from a database of parents interested in participating in infant studies at the Department of Biological and Developmental Psychology at Heidelberg University, Heidelberg, Germany. Parents of all subjects gave written and verbal consent before conducting the experiment.

AUTHOR CONTRIBUTIONS

ML, DB, SG, SP, and SH conceived and designed the study. ML collected the data. ML and DM analyzed the data. SH was consulted about data interpretation. ML drafted the manuscript. All authors revised the work and approved the final version for publication.

FUNDING

This research was funded by the German Research Foundation (Deutsche Forschungsgemeinschaft, DFG) [grant numbers: HO 4342/7-1, PA 691/10-1].

ACKNOWLEDGMENTS

The study was conducted in partial fulfillment of the doctoral dissertation of ML. We are grateful to the infants and their parents for participating in our study and our student assistants for their support in data collection. We further thank Christine Michel for help and advice with implementing the study.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2018.00036/full#supplementary-material

REFERENCES

Bache, C., Springer, A., Noack, H., Stadler, W., Kopp, F., Lindenberger, U., et al. (2017). 10-Month-Old infants are sensitive to the time course of perceived actions: Eye-tracking and EEG evidence. *Front. Psychol.* 8:1170. doi: 10.3389/fpsyg.2017.01170

Beisert, M., Zmyj, N., Liepelt, R., Jung, F., Prinz, W., and Daum, M. (2012). Rethinking 'Rational Imitation' in 14-month-old infants: a perceptual distraction approach. *PLOS ONE* 7:e32563. doi: 10.1371/journal.pone.0032563.g001

Braukmann, R., Bekkering, H., Hidding, M., Poljac, E., Buitelaar, J. K., and Hunnius, S. (2017). Predictability of action sub-steps modulates motor system activation during the observation of goal-directed actions. *Neuropsychologia* 103, 44–53. doi: 10.1016/j.neuropsychologia.2017.07.009

Buttelmann, D., Carpenter, M., Call, J., and Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Dev. Sci.* 10, F31–F38. doi: 10.1111/j.1467-7687.2007.00630.x

Buttelmann, D., Carpenter, M., Call, J., and Tomasello, M. (2008). Rational tool use and tool choice in human infants and great apes. *Child Dev.* 79, 609–626. doi: 10.1111/j.1467-8624.2008.01146.x

Buttelmann, D., Schieler, A., Wetzel, N., and Widmann, A. (2017). Infants' and adults' looking behavior does not indicate perceptual distraction for constrained modelled actions - An eye-tracking study. *Infant Behav. Dev.* 47, 103–111. doi: 10.1016/j.infbeh.2017.04.001

Buttelmann, D., and Zmyj, N. (2012). Evaluating the empirical evidence for the two-stage-model of infant imitation: a commentary on Paulus, Hunnius, Vissers, and Bekkering (2011). *Front. Psychol.* 3:512. doi: 10.3389/fpsyg.2012.00512

Buttelmann, D., Zmyj, N., Daum, M., and Carpenter, M. (2013). Selective imitation of in-group over out-group members in 14-month-old infants. *Child Dev.* 84, 422–428. doi: 10.1111/j.1467-8624.2012.01860.x

Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., and Haggard, P. (2005). Action observation and acquired motor skills: An FMRI study with expert dancers. *Cereb. Cortex* 15, 1243–1249. doi: 10.1093/cercor/bhi007

Cannon, E. N., Yoo, K. H., Vanderwert, R. E., Ferrari, P. F., Woodward, A. L., and Fox, N. A. (2014). Action experience, more than observation, influences mu rhythm desynchronization. *PLOS ONE* 9:e92002. doi: 10.1371/journal.pone.0092002

Cuevas, K., Cannon, E. N., Yoo, K., and Fox, N. A. (2014). The infant EEG mu rhythm: methodological considerations and best practices. *Dev. Rev.* 34, 26–43. doi: 10.1016/j.dr.2013.12.001

DeBoer, T., Scott, L. S., and Nelson, C. A. (2007). "Methods for acquiring and analyzing infant event-related potentials," in *Infant EEG and Event-Related Potentials*, ed. M. de Haan (New York, NY: Psychology Press), 5–38.

Falck-Ytter, T., Gredebäck, G., and von Hofsten, C. (2006). Infants predict other people's action goals. *Nat. Neurosci.* 9, 878–879. doi: 10.1038/nn1729

Fox, N. A., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N., Vanderwert, R. E., et al. (2016). Assessing human mirror activity with EEG mu rhythm: a meta-analysis. *Psychol. Bull.* 142, 291–313. doi: 10.1037/bul0000031

Gampe, A., Prinz, W., and Daum, M. M. (2016). Measuring action understanding: relations between goal prediction and imitation. *Br. J. Dev. Psychol.* 34, 53–65. doi: 10.1111/bjdp.12125

Gardner, T., Goulden, N., and Cross, E. S. (2015). Dynamic modulation of the action observation network by movement familiarity. *J. Neurosci.* 35, 1561–1572. doi: 10.1523/JNEUROSCI.2942-14.2015

Gellén, K., and Buttelmann, D. (2017). Fourteen-month-olds adapt their imitative behavior in light of a model's constraints. *Child Dev. Res.* 2017, 1–11. doi: 10.1155/2017/8080649

Gergely, G., Bekkering, H., and Király, I. (2002). Rational imitation in preverbal infants. *Nature* 415:755. doi: 10.1038/415755a

Gergely, G., and Csibra, G. (2003). Teleological reasoning in infancy: the naïve theory of rational action. *Trends Cogn. Sci.* 7, 287–292. doi: 10.1016/s1364-6613(03)00128-1

Gergely, G., Nádasdy, Z., Csibra, G., and Bíró, S. (1995). Taking the intentional stance at 12 months of age. *Cognition* 56, 165–193. doi: 10.1016/S0010-0277(98)00058-4

Gerson, S. A., Bekkering, H., and Hunnius, S. (2015). Short-term motor training, but not observational training, alters neurocognitive mechanisms of action processing in infancy. *J. Cogn. Neurosci.* 27, 1207–1214. doi: 10.1162/jocn_a_00774

Gerson, S. A., Meyer, M., Hunnius, S., and Bekkering, H. (2017). Unravelling the contributions of motor experience and conceptual knowledge in action perception: a training study. *Sci. Rep.* 7:46761. doi: 10.1038/srep46761

Grassmann, S., Schulze, C., and Tomasello, M. (2015). Children's level of word knowledge predicts their exclusion of familiar objects as referents of novel words. *Front. Psychol.* 6:1200. doi: 10.3389/fpsyg.2015.01200

Gredebäck, G., and Daum, M. M. (2015). The microstructure of action perception in infancy: decomposing the temporal structure of social information processing. *Child Dev. Perspect.* 9, 79–83. doi: 10.1111/cdep.12109

Gredebäck, G., and Melinder, A. (2010). Infants' understanding of everyday social interactions: a dual process account. *Cognition* 114, 197–206. doi: 10.1016/j.cognition.2009.09.004

Hoehl, S., Michel, C., Reid, V. M., Parise, E., and Striano, T. (2014). Eye contact during live social interaction modulates infants' oscillatory brain activity. *Soc. Neurosci.* 9, 300–308. doi: 10.1080/17470919.2014.884982

Hunnius, S., and Bekkering, H. (2010). The early development of object knowledge: a study of infants' visual anticipations during action observation. *Dev. Psychol.* 46, 446–454. doi: 10.1037/a0016543

Hunnius, S., and Bekkering, H. (2014). What are you doing? How active and observational experience shape infants' action understanding. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 369:20130490. doi: 10.1098/rstb.2013.0490

Jeannerod, M. (2006). *Motor Cognition: What Actions Tell the Self*. New York, NY: Oxford University Press. doi: 10.1093/acprof:oso/9780198569657.001.0001

Kaduk, K., Bakker, M., Juvrud, J., Gredebäck, G., Westermann, G., Lunn, J., et al. (2016). Semantic processing of actions at 9 months is linked to language proficiency at 9 and 18 months. *J. Exp. Child Psychol.* 151, 96–108. doi: 10.1016/j.jecp.2016.02.003

Kelly, A. M., and Garavan, H. (2005). Human functional neuroimaging of brain changes associated with practice. *Cereb. Cortex* 15, 1089–1102. doi: 10.1093/cercor/bhi005

Kilner, J. M., Friston, K. J., and Frith, C. D. (2007). Predictive coding: an account of the mirror neuron system. *Cogn. Process* 8, 159–166. doi: 10.1007/s10339-007-0170-2

Kilner, J. M., Vargas, C., Duval, S., Blakemore, S. J., and Sirigu, A. (2004). Motor activation prior to observation of a predicted movement. *Nat. Neurosci.* 7, 1299–1301. doi: 10.1038/nn1355

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.* 16, 606–617. doi: 10.1016/j.tics.2012.10.007

Koelewijn, T., van Schie, H. T., Bekkering, H., Oostenveld, R., and Jensen, O. (2008). Motor-cortical beta oscillations are modulated by correctness of observed action. *NeuroImage* 40, 767–775. doi: 10.1016/j.neuroimage.2007.12.018

Lepage, J. F., and Theoret, H. (2006). EEG evidence for the presence of an action observation-execution matching system in children. *Eur. J. Neurosci.* 23, 2505–2510. doi: 10.1111/j.1460-9568.2006.04769.x

Libby, W. L., Lacey, B. C., and Lacey, J. I. (1973). Pupillary and cardiac activity during visual attention. *Psychophysiology* 10, 270–294. doi: 10.1111/j.1469-8986.1973.tb00526.x

Manthey, S., Schubotz, R. I., and von Cramon, D. Y. (2003). Premotor cortex in observing erroneous action: An fMRI study. *Cogn. Brain Res.* 15, 296–307. doi: 10.1016/S0926-6410(02)00201-X

Marshall, P. J., Bar-Haim, Y., and Fox, N. A. (2002). Development of the EEG from 5 months to 4 years of age. *Clin. Neurophysiol.* 113, 1199–1208. doi: 10.1016/S1388-2457(02)00163-3

Marshall, P. J., Bouquet, C. A., Shipley, T. F., and Young, T. (2009). Effects of brief imitative experience on EEG desynchronization during action observation. *Neuropsychologia* 47, 2100–2106. doi: 10.1016/j.neuropsychologia.2009.03.022

Marshall, P. J., and Meltzoff, A. N. (2011). Neural mirroring systems: exploring the EEG mu rhythm in human infancy. *Dev. Cogn. Neurosci.* 1, 110–123. doi: 10.1016/j.dcn.2010.09.001

Marshall, P. J., Young, T., and Meltzoff, A. N. (2011). Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study. *Dev. Sci.* 14, 474–480. doi: 10.1111/j.1467-7687.2010.00991.x

Meltzoff, A. N. (1988). Infant imitation after a 1-week delay: long-term memory for novel acts and multiple stimuli. *Dev. Psychol.* 24, 470–476. doi: 10.1037/0012-1649.24.4.470

Muthukumaraswamy, S. D., Johnson, B. W., and McNair, N. A. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Brain Res. Cogn. Brain Res.* 19, 195–201. doi: 10.1016/j.cogbrainres.2003.12.001

Oostenveld, R., Fries, P., Maris, E., and Schoffelen, J. M. (2011). FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput. Intell. Neurosci.* 2011:156869. doi: 10.1155/2011/156869

Pace, A., Carver, L. J., and Friend, M. (2013). Event-related potentials to intact and disrupted actions in children and adults. *J. Exp. Child Psychol.* 116, 453–470. doi: 10.1016/j.jecp.2012.10.013

Paulus, M., Hunnius, S., van Elk, M., and Bekkering, H. (2012). How learning to shake a rattle affects 8-month-old infants' perception of the rattle's sound: electrophysiological evidence for action-effect binding in infancy. *Dev. Cogn. Neurosci.* 2, 90–96. doi: 10.1016/j.dcn.2011.05.006

Paulus, M., Hunnius, S., Vissers, M., and Bekkering, H. (2011a). Bridging the gap between the other and me: the functional role of motor resonance and action effects in infants' imitation. *Dev. Sci.* 14, 901–910. doi: 10.1111/j.1467-7687.2011.01040.x

Paulus, M., Hunnius, S., Vissers, M., and Bekkering, H. (2011b). Imitation in infancy: rational or motor resonance? *Child Dev.* 82, 1047–1057. doi: 10.1111/j.1467-8624.2011.01610.x

Pfurtscheller, G., and Da Silva, F. L. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin. Neurophysiol.* 110, 1842–1857. doi: 10.1016/S1388-2457(99)00141-8

Pineda, J. A. (2005). The functional significance of mu rhythms: translating "seeing" and "hearing" into "doing". *Brain Res. Brain Res. Rev.* 50, 57–68. doi: 10.1016/j.brainresrev.2005.04.005

Prinz, W. (1997). Perception and action planning. *Eur. J. Cogn. Psychol.* 9, 129–154. doi: 10.1080/713752551

Prinz, W. (2006). What re-enactment earns us. *Cortex* 42, 515–517. doi: 10.1016/s0010-9452(08)70389-7

Quandt, L. C., Marshall, P. J., Bouquet, C. A., Young, T., and Shipley, T. F. (2011). Experience with novel actions modulates frontal alpha EEG desynchronization. *Neurosci. Lett.* 499, 37–41. doi: 10.1016/j.neulet.2011.05.028

Reid, V. M., Csibra, G., Belsky, J., and Johnson, M. H. (2007). Neural correlates of the perception of goal-directed action in infants. *Acta Psychol. (Amst)* 124, 129–138. doi: 10.1016/j.actpsy.2006.09.010

Reid, V. M., Hoehl, S., Grigutsch, M., Groendahl, A., Parise, E., and Striano, T. (2009). The neural correlates of infant and adult goal prediction: evidence for semantic processing systems. *Dev. Psychol.* 45, 620–629. doi: 10.1037/a0015209

Rizzolatti, G., and Craighero, L. (2004). The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192. doi: 10.1146/annurev.neuro.27.070203.144230

Rizzolatti, G., Fogassi, L., and Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2, 661–670. doi: 10.1038/35090060

Rosander, K., and von Hofsten, C. (2011). Predictive gaze shifts elicited during observed and performed actions in 10-month-old infants and adults. *Neuropsychologia* 49, 2911–2917. doi: 10.1016/j.neuropsychologia.2011.06.018

Saby, J. N., Marshall, P. J., and Meltzoff, A. N. (2012). Neural correlates of being imitated: An EEG study in preverbal infants. *Soc. Neurosci.* 7, 650–661. doi: 10.1080/17470919.2012.691429

Schwier, C., von Maanen, C., Carpenter, M., and Tomasello, M. (2006). Rational Imitation in 12-month-old infants. *Infancy* 10, 303–311. doi: 10.1207/s15327078in1003_6

Shadmehr, R., and Holcomb, H. H. (1997). Neural correlates of motor memory consolidation. *Science* 277, 821–825. doi: 10.1126/science.277.5327.821

Sommerville, J. A., Woodward, A. L., and Needham, A. (2005). Action experience alters 3-month-old infants' perception of others' actions. *Cognition* 96, B1–B11. doi: 10.1016/j.cognition.2004.07.004

Southgate, V., Johnson, M. H., El Karoui, I., and Csibra, G. (2010). Motor system activation reveals infants' on-line prediction of others' goals. *Psychol. Sci.* 21, 355–359. doi: 10.1177/0956797610362058

Southgate, V., Johnson, M. H., Osborne, T., and Csibra, G. (2009). Predictive motor activation during action observation in human infants. *Biol. Lett.* 5, 769–772. doi: 10.1098/rsbl.2009.0474

Stapel, J. C., Hunnius, S., Meyer, M., and Bekkering, H. (2016). Motor system contribution to action prediction: temporal accuracy depends on motor experience. *Cognition* 148, 71–78. doi: 10.1016/j.cognition.2015.12.007

Stapel, J. C., Hunnius, S., van Elk, M., and Bekkering, H. (2010). Motor activation during observation of unusual versus ordinary actions in infancy. *Soc. Neurosci.* 5, 451–460. doi: 10.1080/17470919.2010.490667

Stets, M., Stahl, D., and Reid, V. M. (2012). A meta-analysis investigating factors underlying attrition rates in infant ERP studies. *Dev. Neuropsychol.* 37, 226–252. doi: 10.1080/87565641.2012.654867

Striano, T., and Reid, V. M. (2006). Social cognition in the first year. *Trends Cogn. Sci.* 10, 471–476. doi: 10.1016/j.tics.2006.08.006

van Elk, M., van Schie, H. T., Hunnius, S., Vesper, C., and Bekkering, H. (2008). You'll never crawl alone: neurophysiological evidence for experience-dependent motor resonance in infancy. *NeuroImage* 43, 808–814. doi: 10.1016/j.neuroimage.2008.07.057

Vogt, S., Buccino, G., Wohlschlager, A. M., Canessa, N., Shah, N. J., Zilles, K., et al. (2007). Prefrontal involvement in imitation learning of hand actions: Effects of practice and expertise. *NeuroImage* 37, 1371–1383. doi: 10.1016/j.neuroimage.2007.07.005

Wolpert, D. M., and Flanagan, J. R. (2001). Motor prediction. *Curr. Biol.* 11, R729–R732. doi: 10.1016/S0960-9822(01)00432-8

Woodward, A. L. (1998). Infants selectively encode the object of an actor's reach. *Cognition* 69, 1–34. doi: 10.1016/S0010-0277(98)00058-4

Woodward, A. L., and Sommerville, J. A. (2000). Twelve-month-old infants interpret action in context. *Psychol. Sci.* 11, 73–77. doi: 10.1111/1467-9280.00218

Zmyj, N., Buttelmann, D., Carpenter, M., and Daum, M. M. (2010). The reliability of a model influences 14-month-olds' imitation. *J. Exp. Child Psychol.* 106, 208–220. doi: 10.1016/j.jecp.2010.03.002

Zmyj, N., Daum, M. M., and Aschersleben, G. (2009). The development of rational imitation in 9- and 12-month-old infants. *Infancy* 14, 131–141. doi: 10.1080/15250000802569884

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

MANUSCRIPT II

Langeloh, M., Buttelmann, D., Pauen, S., & Hoehl, S. (2019). 12- to 14-month-olds expect unconstrained agents to act efficiently: ERP evidence from the head-touch paradigm. *Manuscript under review in Developmental Psychology.*

12- to 14-month-olds expect unconstrained agents to act efficiently: ERP evidence from the head-touch paradigm

Miriam Langeloh[1,2], David Buttelmann[3], Sabina Pauen[2] & Stefanie Hoehl[1,4]

[1]Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

[2]Department of Psychology, Heidelberg University, Heidelberg, Germany

[3]Department of Psychology, University of Bern, Bern, Switzerland

[4]Faculty of Psychology, University of Vienna, Vienna, Austria

Author Note

Miriam Langeloh, Early Social Cognition Research Group, Max Planck Institute for Human Cognitive and Brain Sciences.

This research was supported by grants from the Deutsche Forschungsgemeinschaft (DFG): PA691/10-1, HO4342/7-1, BU 2702/6-1.

Correspondence concerning this article should be addressed to Miriam Langeloh, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstrasse 1a, 04103 Leipzig, Germany. E-mail: langeloh@cbs.mpg.de

Abstract

Behavioral research has shown that 12- but not 9-month-olds imitate an unusual and inefficient action (turning on a lamp with one's forehead) more when the model's hands are free. Rational-imitation accounts suggest that infants evaluate actions based on the rationality principle, that is, they expect people to choose efficient means to achieve a goal. Accordingly, infants' expectations should be violated when observing inefficient actions. However, this has yet to be clearly tested. Here, we conducted three electrophysiological experiments to assess infants' neural indices of violation of expectation (VOE) when observing hand- and head-touch actions. We presented infants with video sequences showing a model whose hands were either free (Experiment 1 & 3) or restrained (Experiment 2). Subsequent images depicted a person turning on a lamp or a toy soundbox using her hand or head. We analyzed the Negative central (Nc) component, associated with the amount of attentional engagement, and the N400 component, reflecting semantic violations. In line with rational-imitation accounts, results revealed that 12- to 14-month-olds (Experiment 1) but not 9-month-olds (Experiment 3) were surprised while observing an inefficient, hands-free, head touch, as indicated by an increased Nc amplitude and an N400-like component. In contrast, infants did not show differences in our measures of VOE between head- and hand-touch outcomes when the model's hands were restrained (Experiment 2). Thus, 12- to 14-month-olds incorporate the action context when evaluating action outcomes.

Keywords: infants, event-related potentials, action perception, Nc, N400, rational imitation

12- to 14-month-olds expect unconstrained agents to act efficiently: ERP evidence from the head-touch paradigm

From early on, infants explore their environment and rapidly acquire novel information about the world through interactions with others. Imitation is one of the primary social mechanisms for young infants to learn about cultural practices, instrumental actions as well as their own similarities to other humans (Jones, 2009; Meltzoff & Marshall, 2018; Tomasello, 1999). Imitation can be defined as copying an action previously demonstrated by another person (Paulus, 2011; Zmyj & Buttelmann, 2014). Interestingly, infants do not blindly imitate every action they observe; rather, they do so selectively. Examining situations in which infants selectively imitate provides a useful approach to gain insights into their socio-cognitive abilities. However, many open questions regarding the underlying neuronal and cognitive mechanisms of selective imitation remain.

Past research has demonstrated that infants' selective imitation depends on factors regarding the model (i.e., the person performing the action), such as reliability (Zmyj, Buttelmann, Carpenter, & Daum, 2010), group membership (Buttelmann, Zmyj, Daum, & Carpenter, 2013), age (Zmyj, Daum, Prinz, Nielsen, & Aschersleben, 2012), the model's intentions (Buttelmann, Carpenter, Call, & Tomasello, 2008) and ostensive communication (Király, Csibra, & Gergely, 2013). Furthermore, external factors such as the necessity of the performed action (Nielsen, 2006) and the constraints of a given situation (Gergely, Bekkering, & Király, 2002) also influence infants' selective imitation. In particular, the effects of situational constraints and action efficiency on infants' selective imitation has led to a lively debate within the field of cognitive developmental psychology (Paulus, 2012; Zmyj & Buttelmann, 2014). Here, we apply electrophysiology to elucidate cognitive processes involved in infants' action observation in a widely applied imitation paradigm, which was introduced to test infants' selective imitation (Gergely et al., 2002).

The head-touch paradigm employed by Gergely et al. (2002) with 14-month-old infants features a model turning on a lamp with her head (head touch). One group of infants observed the unusual action while the model's hands were visible and free (hands-free condition) similar to the original setting by (Meltzoff, 1988). A second group observed the same action while the model's hands were occupied, holding a blanket (hands-occupied condition). One week later infants were given the opportunity to explore the lamp themselves. Infants imitated the irregular head action more often in the hands-free (69 %) than in the hands-occupied condition (21 %). Thus, 14-month-olds imitated an unusual and inefficient action far more frequently when the model had no discernible reason to perform the action in such a manner. This finding has been replicated multiple times within similar paradigms (Gellén & Buttelmann, 2017; Schwier, von Maanen, Carpenter, & Tomasello, 2006), younger age groups (Zmyj, Daum, & Aschersleben, 2009) and even with humans' closest relatives, chimpanzees (Buttelmann, Carpenter, Call, & Tomasello, 2007).

Whereas there is consensus concerning the existence of selective imitation, explanations differ regarding the level of infants' assumed cognitive abilities and the underlying mechanisms. On the one hand, rational-imitation accounts claim that selective imitation occurs because of infants' rational evaluation of the situation (Buttelmann et al., 2008; Gergely et al., 2002). These accounts suggest that infants interpret actions in accordance with the principle of rational action postulating that actions are executed in order to achieve a future goal-state with the most efficient means available. According to the teleological stance, the principle of rational action enables infants to relate and evaluate three components of another person's behavior: situational constraints (e.g., hands free or occupied), goal states (e.g., turn light on), and actions (Gergely & Csibra, 2003). Consequently, infants can predict the most efficient action based on the goal state and the situational constraints. Whether infants imitate a certain behavior or not depends on the evaluation of the model's behavior. When the model's hands are occupied, infants interpret the head touch as being the most efficient means to turn the lamp on. Since infants do not share this situational constraint when they interact with the lamp, they predominantly use their hands to turn it on. When the model turns on the lamp with her head even though her hands are free, infants are surprised and might infer that the unusual action offers some advantage. That is they may infer that this is the most efficient means in this situation (Gergely & Csibra, 2003). According to the teleological stance, infants do not necessarily ascribe intentions to the model during action evaluation. Rather, they base their evaluation solely on observable factors. However, the principle of rational action can also be applied to a mentalistic stance, stating that selective imitation is guided by the contents of a model's mental states. In this view, infants are more likely to imitate the unusual action, which the model freely chooses to perform, in order to figure out why the model acts in this peculiar way (Buttelmann et al., 2008).

To summarize, according to rational-imitation accounts, infants hold expectations on how the model should perform a specific action. If infants' expectations are violated, this results in increased imitation of the observed unusual action (here: head touch). Infants either imitate the unusual action because they assume this to have an advantage and be the most efficient means (teleological) or because they want to learn the reason why the model performed this action (mentalistic).

On the other hand, non-rational imitation accounts have been brought forward relating infants' selective imitation to more basic, low-level processes such as motor resonance or attention (Beisert et al., 2012; Paulus, Hunnius, Vissers, & Bekkering, 2011a, 2011b). The two-stage model of infant imitation argues that two factors guide infants' imitation: First, as action observation and action execution are automatically linked (i.e., motor resonance), infants are more likely to imitate actions that are already represented in their own motor repertoire and hence, elicit high motor resonance (Paulus, Hunnius, & Bekkering, 2013; Paulus et al., 2011a). Second, salient action effects influence infants' imitative behavior in such actions eliciting effects (e.g., lamp lightens up) are imitated more than actions without effects (e.g., no light effect). In that perspective, infants need to physically support themselves by putting their hands on the table to turn on the lamp with their heads, similar to the adult model in the hands-free but not the hands-occupied condition (Paulus et al., 2011b). Consequently, only the demonstration in the hands-free condition elicited motor resonance and was thus imitated (for an evaluation of this account, see Buttelmann & Zmyj, 2012).

Finally, Beisert et al. (2012) proposed that selective imitation occurs because of differences in perceptual distraction and, thus, attention. Accordingly, the authors claim that infants were distracted by the unusual look of the blanket being wrapped around the model's torso and, therefore, imitated less in the hands-occupied condition (for findings inconsistent with this interpretation, see Buttelmann, Schieler, Wetzel, & Widmann, 2017; Elsner, Pfeifer, Parker, & Hauf, 2013; Kolling, Óturai, & Knopf, 2014). Both of these low-level non-rational imitation accounts differ from rational-imitation accounts in that infants' expectations about how a model should usually turn on a lamp do not play a role.

Non-rational imitation accounts might underestimate the pivotal role of violation of expectation (VOE) in infants' learning as infants take unexpected events as unique opportunities to learn. For instance, 11-month-olds learned better after observing an object that violated a physical core principle (e.g., a car that drove through a wall) and showed increased information-seeking and hypothesis-testing behavior (Stahl & Feigenson, 2015). Accordingly, researchers investigating the orienting response (OR) have suggested that the repeated presentation of a certain action/stimulus leads to a higher expectation of the occurrence of that action/stimulus. If forthcoming actions/stimuli deviate from the established representation, an OR is elicited indicating the detection of a mismatch. The OR amplifies processing of the attended action/stimulus (Kavsek, 2012; Sokolov, 1963, 1990). Consequently, when observing unusual action outcomes, infants show signs of increased attention, e.g. longer looking times or increased pupil dilation (Gergely, Nádasdy, Csibra, & Bíró, 1995; Gredebäck & Melinder, 2010). It follows that enhanced attention, in response to unexpected actions, may influence imitative behavior leading to an increase in imitation frequency.

A suitable method to investigate preverbal infants' attention and action expectations is electroencephalography (EEG). Recent electrophysiological evidence suggests that 12- to 14-month-old infants show increased motor activation, measured via a reduction in mu power, for the unexpected head-action condition compared to the expected hand-action condition in an adaptation of the head-touch paradigm (Langeloh et al., 2018). In line with the predictive processing framework (Kilner, Friston, & Frith, 2007), this effect was interpreted as reflecting infants' updating of their prior action predictions after observing unexpected actions leading to prediction errors (for similiar effects in eating actions, see Stapel, Hunnius, van Elk, & Bekkering, 2010). Beyond analyzing oscillatory responses in the EEG, event-related potentials (ERPs) have a high temporal resolution and consist of well-defined components associated with specific cognitive processes (Luck, 2005). To move the debate concerning infants' selective imitation forward, we measured their ERP responses to modeled actions to shed light on the underlying neuronal mechanisms. We focused on two well-known ERP components in particular: the N400 and the Negative central (Nc).

The N400 component has been associated with the violation of semantic context. For instance, the N400 amplitude is sensitive to linguistic manipulations that are semantically incongruent with, or unrelated to, specific task content (for a review, see Kutas & Federmeier, 2011). Related N400-like effects have been found for incongruent words in picture-word priming paradigms in 14- and 19-month-olds (Friedrich & Friederici, 2005a, 2005b). Even younger infants have responded with N400-like components to incongruent word picture pairs in an advanced language production subgroup (Friedrich & Friederici, 2010) or when infants' mothers verbally labeled the stimuli (Parise & Csibra, 2012). Research with adults indicates that language and action processing have similar neural mechanisms and underlying brain structures (Iacoboni, 2005). In line with this notion, action understanding at 9 months of age has been linked to language production at 18 months (Kaduk et al., 2016). Thus, the N400 component is also sensitive to actions that violate contextual expectations, such as combing one's hair with a toothbrush (Balconi & Caldiroli, 2011) or putting an empty spoon in one's mouth (Reid & Striano, 2008) (for a review on N400 in action contexts, see Amoruso et al., 2013).

There is limited but consistent evidence linking the N400 amplitude to the detection of unexpected action outcomes in infants, given the action context. Reid et al. (2009) conducted a study assessing the N400 component across development in 7- and 9-month-olds as well as adults. Participants were presented with short picture stories consisting of three images. The first image represented the action context (e.g., a person holding a pretzel). The second image illustrated the action initiation (e.g., the person opens his or her mouth while looking at the pretzel). Finally, the third image demonstrated either an expected action outcome (e.g., the pretzel in the person's mouth) or an unexpected action outcome (e.g., the pretzel at the person's ear). The first two images served as prompts to build up expectations, which were either violated or not by the third image, presenting the action outcome. An N400-like component was elicited in response to the unexpected outcomes in 9-month-olds and adults but not in 7-month-olds. Thus, 9-month-old infants anticipated action outcomes via semantic processing systems, similar to adults (Kaduk et al., 2016; Reid et al., 2009).

Further, 7- and 9-month-old infants discriminated between unexpected and expected action outcomes on an attentional level, indicated by an increased amplitude of the Nc component in response to expected eating outcomes (Kaduk et al., 2016; Reid et al., 2009). The Nc component is thought to index the amount of attentional engagement towards a stimulus (Reynolds, 2015; Reynolds & Richards, 2005). The direction of this effect is surprising with regard to the OR theory, which would rather predict that a mismatch between observed and expected actions should lead to an increase in attention, and, therefore, an increased Nc amplitude in response to the unexpected outcome. Reid et al. (2009) interpreted the increased amplitude of the Nc component in terms of successful food consumption, being highly salient and relevant for infants from an evolutionary point of view.

To summarize, two distinct processes can be measured on a neural level while observing unexpected action outcomes: the Nc (attention) and the N400 (semantic). Increased Nc amplitude is associated with a low-level mismatch detection and consequent orienting response (Vaughan Jr & Kurtzberg, 1992) and, thus, more allocation of attention towards the unexpected outcome (Reynolds & Richards, 2017; Richards, Reynolds, & Courage, 2010). In comparison, the N400-like component is related to a more sophisticated processing of semantic violations, in response to unexpected action outcomes (Amoruso et al., 2013; Kutas & Federmeier, 2011).

However, the cognitive mechanisms underlying infants' selective imitation are not yet clear. Contradicting rational- and non-rational imitation accounts have been proposed. Rational-imitation accounts imply that infants hold expectations about others' goal-directed actions which are violated in response to head-touch outcomes in the hands-free condition. Expectancy violations could then induce heightened attention, potentially supporting the learning of new actions through selective imitation. Yet, no study has directly investigated the neural processes underlying efficient and inefficient action observation, using ERPs in infants, that arise through situational constraints.

Present study

In the present study we aimed to elucidate the neural mechanisms underlying the observation of unexpected head-touch actions in an adaptation of the head-touch paradigm (Gergely et al., 2002; Langeloh et al., 2018; Zmyj et al., 2009). In Experiment 1 we explored whether, in accordance with rational-imitation accounts, infants' brains respond to unusual head-touch actions (hands-free, 12- to 14-month-olds) with VOE. In Experiment 2 (hands-restrained, 12- to 14-month-olds), we assessed whether this effect was context-dependent. Lastly, in Experiment 3 (hands-free, 9-month-olds), we examined whether the developmental onset of the underlying neural mechanisms was similar to the behavioral onset of selective imitation.

Experiment 1: hands-free, 12- to 14-month-olds

In Experiment 1, while measuring EEG, we presented 12- to 14-month-old infants with short video sequences of adult models demonstrating that their hands were free. Following action outcomes showed the same adult model either turning on a lamp or a soundbox with their hand (hand-touch condition) or their head (head-touch condition). If infants experience a VOE while observing an inefficient head touch, we expect an N400-like component in response to the unexpected action outcome only and not to the expected outcome (i.e., hand touch) (Kaduk et al., 2016; Reid et al., 2009). Second, we hypothesized an Nc component in both conditions, with increased amplitude in response to the unexpected head touch compared to the more familiar and thus expected hand touch (in line with OR theory, Sokolov, 1963; Sokolov, 1990).

Methods

Participants.

Infants in all studies were recruited from a midsized XXX [Nationality blinded for review] city and surrounding areas. They were from middle-class backgrounds, born full-term (37 – 41 weeks of gestation), Caucasian, and without any known neurological problems. In Experiment 1 the final sample consisted of twenty-two 12- to 14-month-old infants (11 girls, *M* age = 13 months 2 days, *SD* = 23 days, age range = 12 months 5 days to 14 months 24 days). Another 30 infants were tested but had to be excluded from the final sample due to fussiness (i.e., infants moved extensively or started crying before being presented with a required number of trials; 14 infants), failure to provide the minimum number of 10 artifact-free trials per condition despite completing a high number of trials (15 infants), or unsatisfactory contact of the reference electrodes (i.e., very spiky signal of all electrode channels; 1 infant). This attrition rate (about 58 %) is within the typical range for visual infant EEG studies of 50 – 75% (DeBoer, Scott, & Nelson, 2007; Hoehl & Wahl, 2012; Stets, Stahl, & Reid, 2012). Informed verbal and written consent were obtained from each participant's parent before conducting the experiment. Infants received a certificate with their photo for participation. All experimental procedures were approved by the ethics committee of XXX [blinded for review] (reference 3752-04/13).

Stimuli.

Infants were presented with video clips and photographs showing adult models performing head or hand actions (adapted from Gergely et al., 2002; Zmyj et al., 2009). Two different types of videos were used. To establish context and motivation at the beginning of the experiment, infants watched two pre-demonstration videos showing a female or a male adult sitting at a table demonstrating that their hands were free or restrained. Each participant watched both videos, in randomized order, establishing the models' sex and situational constraints.

Next, demonstration-phase video trials illustrated an action context depicting one of four adult models (two males, two females; different actors than in the pre-demonstration videos) sitting at a table with a touch-sensitive light in front of them. A line of duct tape was visible on the table but the model's hands were clearly free (hands-free). Subsequent test frames depicted either expected (turning on the lamp using the hand) or unexpected action outcomes (turning on the lamp using the head) (Figure *1*). In half of the trials, a round lamp (12 cm diameter) mounted on a black box (27 x 20 x 6 cm) was illuminated while the model was touching it (Gergely et al., 2002; Meltzoff, 1988). To increase infants' attention towards the presentation, in the other half of trials a toy-squeezing sound was generated by a blue and green soundbox (i.e., toy that makes a sound when being touched) (13 x 13 x 11.5 cm) while the model was touching it (similar to Buttelmann et al., 2007). The sound was presented with a maximum intensity of 75 dB. In the test frames, the lamp was presented with a size of 4.6 x 8.4 cm (visual angle of 4.79° x 8.73°) and the soundbox with a size of 4 x 4.5 cm (visual angle of 4.17° x 4.69°). The model was presented on screen with a width of approximately 9.13 cm (visual angle of 9.49°) and a height of 10.34 cm (visual angle of 10.74°) measured from head to table. We balanced the test frames for brightness and contrast with Adobe Photoshop CS4 extended (all ps > .05).

Procedure.

During EEG recording, infants sat on their parent's lap in a dimly lit testing area in front of a 75 Hz 19-inch stimulus monitor with a viewing distance of about 55 cm. The testing area was separated from the rest of the laboratory by dark blue room dividers to minimize infants' distraction. Parents were instructed not to interact with their infant during data collection. The experiment consisted of one block of a maximum of 120 trials (60 hand-touch and 60 head-touch outcomes). The videos were displayed in semi-randomized order via the software Presentation (Neurobehavioral Systems, Albany, USA) with the constraint that the same modality (light/sound), gender (male/female) or outcome (hand touch/head touch) was not presented three times consecutively and that all 16 possible combinations (light/sound, head touch/hand touch, for each of the four models) were displayed within the first 48 trials. In addition, equal numbers of hand and head actions were used as the first trial stimulus to avoid a systematic confounding effect of the first observed action type.

Figure *1* illustrates examples of the stimulus presentation sequence in which the model turns on the light or produces a sound by using either his or her hand or head. Every trial started with a central attractor (white star on black background) for an average of 1000 ms to attract infants' attention to the screen. The subsequent video sequence depicted the model showing that their hands were free (by wiggling them) for 5000 ms, followed by a blank screen presented for a random period between 800 and 1000 ms. Lastly, the test frame demonstrating a hand- or head-touch outcome was presented for 1500 ms. Each trial lasted 8500 ms leading to a maximum total testing time of 17 min. Whenever an infant became tired or fussy, the experimenter paused the presentation and resumed the experiment when the infant was in a calm and attentive state again. The session ended when the infant's attention could no longer be directed to the presentation or when the infant completed all the trials. EEG activity was recorded continuously and infants were video-recorded throughout the experiment for offline coding of looking behavior.

EEG Recording and Analyses.

EEG was recorded with an ActiCap System (Brain Products, Gilching, Germany) with 32 active silver/silver chloride (Ag/AgCl) electrodes arranged according to the 10-10 system and a right mastoid reference. Sampling rate was set at 250 Hz and the EEG signal was amplified via a BrainAmp amplifier (Brain Products, Gilching, Germany). Horizontal and vertical electrooculograms were recorded bipolarly. Impedances were controlled at the beginning of the experiment and accepted when below 20 kΩ.

For additional EEG data editing, BrainVision Analyzer 2 (Brain Products, Gilching, Germany) was used. Offline filters were set from 0.3 to 30 Hz to remove frequencies not related to cortical processing and data were re-referenced to the average mastoids (TP9, TP10). Data were scanned for artifacts with an automatic artifact detection algorithm implemented in BrainVision Analyzer 2. Data were automatically excluded if the amplitude of the channels of interest (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4) exceeded a voltage threshold of 200 µV within a 200 ms interval (Michel, Wronski, Pauen, Daum, & Hoehl, 2017). Data were then segmented into epochs that comprised 200 ms before stimulus onset of the test frame to 1500 following stimulus onset. Infants' behavior was video-coded and only trials in which infants did not blink and paid attention during the presentation of the test frame were included in further analyses. An independent rater blind to hypotheses coded 27 % of the behavioral videos. An excellent degree of inter-rater reliability was found between 446 measures with an average measure intraclass correlation of .99. EEG data were then baseline-corrected using 200 ms prior to the onset of the test frame and subsequently categorized as hand- or head-touch outcomes across lamp and sound modality. Individual averages were computed for each of the two conditions. A minimum of 10 artifact-free trials per condition was required for an infant to be included in the grand average. Each infant contributed 13 to 56 trials (*M* = 21.23, *SD* = 9.88) to the head-touch condition and 11 to 56 trials (*M* = 19.18, *SD* = 9.81) to the hand-touch condition.

The number of trials contributed to the head-touch condition (*M* = 21.23, *SD* = 9.88) was significantly higher than the number of trials contributed to the hand-touch condition (*M* = 19.18, *SD* = 9.81), $t(21) = 2.045$, $p = .001$. However, a subsequent *F*-test indicated that variances of the measured ERP components did not differ significantly between conditions, $F(21,20) = 0.567$, $p > .05$. Thus, trial numbers were not artificially reduced to the level of the other condition (Peykarjou, Pauen, & Hoehl, 2014).

To compare head- and hand-touch conditions statistically on the ERP components of interest, two-way, repeated measures analysis of variances (rmANOVA) or *t*-tests were conducted with the within-subjects factor condition (hand touch, head touch). Greenhouse-Geisser corrections for non-sphericity and Bonferroni corrections were employed if applicable for conservative corrections. The significance level was set to $p = .05$ (two-tailed) for all statistical analyses.

Results

Time windows and electrodes of interest were selected based on visual inspection and previous research (Kaduk et al., 2016; Michel, Kaduk, Ni Choisdealbha, & Reid, 2017; Reid et al., 2009). Grand averages of the electrode channels of interest (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4) are displayed in Figure *2*. Relevant components were most pronounced on central channels (C3, Cz, C4).

Nc.

Across all trials a negative deflection in the mid-latency range was observed on central channels (C3, Cz, C4). This negative deflection is commonly referred to as the Nc component and is thought to indicate the amount of attentional engagement towards a stimulus (Reynolds, 2015). Visual inspection indicated an effect of condition on the Nc, as the negativity amplitude was greater for head-touch outcomes in comparison to hand-touch outcomes (see Figure *2A* for grand averages). In line with other studies investigating this waveform (Kaduk et al., 2016; Michel, Kaduk, et al., 2017; Reid et al., 2009), we analyzed mean amplitude differences on the Nc component in a time window between 400 and 600 ms.

A paired *t*-test indicated significantly greater negativity for central electrodes in response to head-touch outcomes (M = -20.57, SD = 10.86) compared to hand-touch outcomes (M = -16.23 µV, SD = 10.68 µV), $t(21) = 2.470$, $p = .022$, 95%CI [-7.99 µV, -0.69 µV], $d = 0.53$. Means and standard deviations of the Nc mean amplitude for single central channels in both conditions are reported in supplementary material *1*. Thus, we found greater negativity on central electrode positions in the head-touch condition likely indicating increased allocation of attention during the observation of unexpected action outcomes.

N400.

Following the Nc component, a clear negative peak was observed indicating an N400-like component on central channels (C3, Cz, C4). This was observed in a much more salient way for the head-touch condition (see Figure *2A* for grand averages). As a defined peak of interest was predominantly present in only one condition, we applied the windows analysis technique by Hoormann, Falkenstein, Schwarzenau, and Hohnsbein (1998) (see also Kaduk et al., 2016; Michel, Kaduk, et al., 2017; Reid et al., 2009). The window analysis technique extracts values of the amplitude of the ERP wave within a chosen time window at several time points for both conditions and compares conditions in a rmANOVA, with condition and time as within-subjects factors. A significant interaction between time and condition reveals that ERP waves differ in their morphology. For the window analysis, we chose a time window of 736 to 868 ms after stimulus-onset, very similar to previous studies on action understanding (Kaduk et al., 2016; Reid et al., 2009). In the present study the time course of the N400-like component was shorter than in previous studies, which conducted the analysis with 17 time windows (Kaduk et al., 2016; Reid et al., 2009). However, we included only 12 time windows to appropriately analyze the current ERP waveforms. Consequently, a 2 x 12 rmANOVA with the within-subjects factors condition (hand touch, head touch) and time (12 samples at one sample per 12 ms) was performed. The rmANOVA revealed the critical significant interaction of condition and time, $F(3.22,67.67) = 2.862$, $p = .040$, $\eta^2_p = 0.120$. In addition, a significant main effect of time, $F(3.16,66.362) = 7.068$, $p < .001$, $\eta^2_p = 0.252$ was found indicating that across conditions ERP amplitudes differed between time windows. The analysis yielded no significant main effect of condition, $F(1,21) = 0.230$, $p = .636$. Thus, waveforms differed significantly between brain responses to expected hand-touch outcomes and unexpected head-touch outcomes. The variation of the ERP amplitude within the tested time window was only present in the head-touch condition indicating an N400-like response towards unexpected action outcomes (see Figure *2B*).

Discussion

Results of Experiment 1 are in line with our hypothesis that infants would experience a VOE when observing an unusual and inefficient head touch while the models' hands were free. We first showed that 12- to 14-month-olds discriminated between expected hand-touch and unexpected head-touch actions with differences on the Nc component. The increased Nc amplitude in response to the unusual head touch might indicate an OR, a fast mismatch detection (Sokolov, 1963, 1990; Vaughan Jr & Kurtzberg, 1992). Second, the N400-like response to the unusual head touch implies that infants had difficulties in integrating the action outcome into the semantic action context (Reid et al., 2009).

Our results suggest that infants were surprised when observing an unusual head action. However, it is important to test whether they take the action context into account, especially the action constraints posed on the model that proved critical in previous behavioral research on selective imitation (i.e., restrained hands) (Gergely et al., 2002; Zmyj et al., 2009). In Experiment 2 we therefore changed the action context to rule out unspecific OR and VOE responses to head-touch actions irrespective of situational action constraints.

Experiment 2: hands-restrained, 12- to 14-month-olds

In Experiment 2 we presented an additional sample of 12- to 14-month-old infants with the same stimuli as in Experiment 1 (hands-free, 12-month-olds) with the only difference that we changed the context such that the model's hands were taped to the table (hands-restrained). Stimuli were adapted from Zmyj et al. (2009), which demonstrated that 12-month-olds imitated the head touch significantly more in the hands-free condition compared to the hands-restrained condition. If infants' brains consider the action context when evaluating the outcomes in this scenario, we would not expect an increased Nc component or N400-like components in response to the head touch. Rather, a VOE would be expected in response to hand-touch actions, as it would be physically impossible to use the hands when they are restrained.

Methods

Participants.

Twenty 12- to 14-month-old infants (9 girls, *M* age = 12 months 25 days, *SD* = 22 days, age range = 12 months 1 day to 14 months 29 days) were included in the final sample. Another 47 infants were tested but had to be excluded from the final sample due to fussiness (18 infants), failure to provide the minimum number of 10 artifact-free trials per condition (24 infants), unsatisfactory contact of the reference electrodes (3 infants) or technical/experimental errors (2 infants). This attrition rate (about 70 %) is high but still within the typical range for infant EEG studies of 50 – 75% (DeBoer et al., 2007; Hoehl & Wahl, 2012; Stets et al., 2012).

Stimuli.

Infants were presented with the same two pre-demonstration videos as in Experiment 1 showing a female or a male demonstrating that their hands were free or restrained. Stimuli of the demonstration phase were also identical to Experiment 1 except for the action context: the hands of the adult model were now tied to the table with duct tape and could not be moved freely (in adaptation to the hands-restrained condition by Zmyj et al., 2009). Consequently, infants observed an adult model demonstrating that his or her hands were restrained in each trial. Subsequent test frames depicted the model turning on the lamp or soundbox either by head or by hand (Figure *3*). Again, we presented infants with sound and lamp stimuli to keep infants interested in the presentation (for more details, see Experiment 1). We balanced the test frames for brightness and contrast with Adobe Photoshop CS4 extended (all *p*s > .05).

Procedure and EEG Recording and Analyses.

Both the procedure and EEG and statistical analyses were identical to Experiment 1. Infants' looking behavior was reliability-coded by an independent rater, blind to hypotheses. For

25 % of the videos, a high degree of inter-rater reliability was found between 319 measurements with an average measure intraclass correlation of .71. Each infant contributed 10 to 34 trials (M = 17.25, SD = 5.87) to the head-touch condition and 10 to 34 trials (M = 16.05, SD = 5.45) to the hand-touch condition. The number of trials contributed to the final analysis did not differ significantly between conditions, $t(19) = 1.447$, $p = .164$.

Results

The morphology of the components of interest was highly comparable to Experiment 1. Thus, the same time windows and electrodes were chosen in Experiment 2. Grand averages of the electrode channels of interest (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4) are displayed in Figure *4*.

Nc.

Visual inspection indicated a negative deflection on central channels – the Nc component – in both conditions (see Figure *4A*). Thus, the mean amplitude of the Nc component was assessed on central electrode channels (C3, Cz, C4) in a time window between 400 and 600 ms after stimulus onset. Again, we conducted a paired *t*-test, which revealed no significant difference between head- (M = -19.90 µV, SD = 17.13) and hand-touch outcomes (M = -19.35 µV, SD = 16.11), $t(19) = -.141$, $p = .889$. Means and standard deviations of the Nc mean amplitude for single central channels, in both conditions, are reported in supplementary material *2*. We reasoned that infants' initial action expectations, of the models using their heads to operate the lamp and soundbox may have been overwritten by repeatedly observing them using their hands, despite being restrained by the duct tape. To examine this idea, we performed the same analysis on the Nc component for the first half of presented trials only. Infants contributed 4 to 12 valid trials (M = 7.74, SD = 2.28) to the head-touch condition and 5 to 14 trials (M = 7.87, SD = 2.32) to the hand-touch condition. No significant differences were found between head- (M = -

22.67, *SD* = 19.91) and hand-touch outcomes (*M* = -23.13, *SD* = 19.33), $t(19) = -.105$, $p = .918$. Thus, when the model's hands were restrained infants did not seem to discriminate between head- and hand-touch conditions with regard to the negative component thought to reflect attentional engagement.

N400.

Although Experiment 1 and previous literature (e.g., Kaduk et al., 2016; Reid et al., 2009) suggest an N400-like component in response to unexpected action outcomes, no evidence for an N400-like component was observed in Experiment 2. This includes both the expected and the unexpected conditions (see Figure *4A*). To verify the visual inspection we applied the windows analysis technique of Hoormann et al. (1998) with 12 time points in a time window of 736 – 868 ms post stimulus onset. We conducted a 2 x 12 rmANOVA with the within-subjects factors condition (head touch, hand touch) and time (12 samples at one sample per 12 ms). A significant time x condition interaction would indicate differences in morphology between conditions. The rmANOVA yielded no significant interaction between time and condition, $F(4.02,76.32) = .498$, $p = .738$, and no main effect of time, $F(2.83,53.69) = 1.023$, $p = .387$ or condition, $F(1,19) = .647$, $p = .431$. In sum, the ERP waveforms in Experiment 2 did not differ in morphology, suggesting that infants did not distinguish the two action outcomes on a semantic level (see Figure *4B*).

Discussion

Contrary to our expectations, in Experiment 2 infants neither discriminated between hand- and head-touch action outcomes in terms of attentional engagement nor on a semantic level. One explanation why this effect was not found in the present study is that infants may not have noticed the restraining duct tape due to a lack of visual salience. Alternatively, they may not have understood the constraining nature of the tape on the model's actions. However, both explanations are quite unlikely as Zmyj et al. (2009) demonstrated that 12-month-olds imitated selectively using the same external physical constraint, also presented via computer. Further, if infants did not notice or understand the consequences of the duct tape, results should have been similar to Experiment 1 (hands-free, 12- to 14-month-olds). Thus, even though results of Experiment 2 deviate from our hypotheses, they show that infants' VOE response towards unusual head-touch outcomes is rather context-dependent and does not reflect a general response towards an unusual head-touch action.

At this point we conclude that 12- to 14-month-old infants experience VOE when observing an unusual head touch, but only when the hands are free. We conducted Experiment 3 to explore the developmental onset of infants' action expectations in the head-touch paradigm.

Experiment 3: hands-free, 9-month-olds

In Experiment 3 we tested infants at the age of 9 months with the same paradigm as in Experiment 1 (hands-free, 12- to 14-month-olds). Zmyj et al. (2009) demonstrated that 12- but not 9-month-old infants considered non-voluntary, physical restraints (i.e., hands are tied to the table) when selectively imitating unusual head-touch actions. However, previous research suggests that 9-month-olds possess a quite sophisticated action understanding (Gredebäck & Daum, 2015), being able to predict and evaluate action outcomes based on their efficiency (e.g., eating actions Gredebäck & Melinder, 2010; Kaduk et al., 2016; Reid et al., 2009). We aimed to elucidate whether neural processing of unusual actions in the head-touch paradigm develops earlier than explicit selective imitation behavior. If 9-month-olds also experience VOE in response to the unusual head touch, in a hands-free condition, we should observe an increased

Nc amplitude and an N400-like component in response to the head- compared to the hand-touch action.

Methods

Participants.

In Experiment 3, the final analysis was comprised of the data of twenty-three 9-month-old infants (15 girls, *M* age = 9 months 16 days, *SD* = 8 days, age range = 9 months 0 days to 9 months 28 days). An additional 51 infants were not included in the final analysis due to fussiness (26 infants), failure to provide the minimum number of 10 artifact-free trials per condition (19 infants), unsatisfactory contact of the reference electrodes (4 infants) or technical error (2 infants). This exclusion rate (about 69 %) is still within the typical range for infant EEG studies of 50 – 75% (DeBoer et al., 2007; Hoehl & Wahl, 2012; Stets et al., 2012).

Stimuli and Procedure and EEG Recording and Analyses.

The stimuli and procedure as well as EEG recordings and statistical analyses were identical to Experiment 1. A second coder, blind to the purpose of this study, coded 26 % of the videos for infants' looking behavior. The inter-rater reliability between 384 measurements was high with an average measure intraclass correlation of .92. The final analyses consisted of 10 to 20 trials (M = 13.91, SD = 2.97) in the head-touch condition and 10 to 23 trials (M = 12.91, SD = 3.26) in the hand-touch condition. The number of trials infants contributed to the final analysis did not differ significantly between conditions, $t(22) = 1.294$, $p = .209$.

Results

The morphology of the components of interest was highly similar to Experiment 2 (hands-restrained, 12- to 14-month-olds). For comparability, the same time windows and electrodes were chosen in Experiment 3. Grand averages of the electrode channels of interest

(F3, Fz, F4, C3, Cz, C4, P3, Pz, P4) are displayed in Figure *5*. According to visual inspection, existing literature (Kaduk et al., 2016; Reid et al., 2009) and results of Experiment 1 and 2, components were analyzed on central channels (C3, Cz, C4).

Nc.

The mean amplitude of the Nc component was assessed on central electrode channels (C3, Cz, C4) in a time window between 400 and 600 ms after stimulus onset (Figure *5A*). We conducted a paired *t*-test revealing no significant differences between head- (M = -12.28 µV, SD = 16.13) and hand-touch outcomes (M = -12.45 µV, SD = 13.27), $t(22)$ = -.050, p = .961. Means and standard deviations of the Nc mean amplitude for single central channels in both conditions are reported in supplementary material *3*. We performed the same analysis on the Nc component for the first half of presented trials to determine whether we would find evidence for initial action expectations that might have vanished across the course of the experiment. Infants contributed 4 to 15 valid trials (M = 9.65, SD = 2.87) to the head-touch condition and 6 to 13 trials (M = 9.10, SD = 2.25) to the hand-touch condition. Mean amplitude did not differ significantly between head- (M = -17.42, SD = 17.28) and hand-touch outcomes (M = -10.90, SD = 19.22), $t(22)$ = 1.329, p = .198. Taken together, infants did not respond differently to head-touch or hand-touch actions on the level of the Nc component and thus presumably allocated the same amount of attention towards both outcomes.

N400.

Based on Experiment 1 (hands-free, 12- to 14-month-olds) and the existing literature on 9-month-olds action processing (e.g., Kaduk et al., 2016; Reid et al., 2009), we expected an N400-like component in response to the unexpected head touch. However, visual inspection did not provide any evidence for an N400-like component in any of the two conditions (see Figure

5A). To test for an N400 effect in the present sample, similar to Experiment 1 and Experiment 2, we conducted a 2 x 12 rmANOVA with the within-subjects factors condition (head touch, hand touch) and time (12 samples at one sample per 12 ms in a time window of 736 – 868 ms after stimulus onset). No time x condition interaction was found, $F(3.887,85.512) = .246$, $p = .907$. The statistical analysis did not reveal significant main effects (all other *p*s > .05). Thus, ERP waveforms of the head-touch and hand-touch outcomes did not differ in Experiment 3. No indication for an N400-like component was found (see Figure *5B*).

Discussion

The results of Experiment 3 suggest that 9-month-old infants did not discriminate between the unusual head touch and the familiar hand touch on either an attentional or a semantic level. Our findings, with an adapted head-touch paradigm, are in line with behavioral evidence indicating that the developmental onset of selective imitation takes place between 9 and 12 months of age (Zmyj et al., 2009). Still, our results are surprising with regard to the literature on early action understanding (Gredebäck & Daum, 2015). Actions in the current scenario may have been less familiar than eating actions in previous studies and were more difficult to evaluate for young infants.

General Discussion

While infants imitate selectively and show more frequent imitation of an unusual head action when the model's hands are free, theoretical explanations differ with regard to the assumed level of infants' cognitive abilities (Beisert et al., 2012; Buttelmann et al., 2007; Gergely et al., 2002; Paulus et al., 2011a, 2011b). Rational-imitation accounts posit that 1-year-olds hold expectations about another person achieving a goal by the most efficient means. These expectations should be violated after observing an unusual or inefficient means to achieve a desired action outcome. Non-rational imitation accounts do not make specific predictions about VOE effects and can, thus, neither be supported nor completely refuted in the current study.

In the three experiments reported here we investigated infants' electrophysiological responses in an adaptation of the well-established head-touch paradigm (Gergely et al., 2002; Zmyj et al., 2009). We analyzed the Nc and N400-like components associated with VOE, in particular attentional orienting and semantic processing, respectively. We predicted an increased Nc amplitude as well as an N400-like component for inefficient and unexpected action outcomes. Results revealed that 12- to 14- but not 9-month-olds show evidence for VOE when observing unexpected head-touch actions when the model's hands are free, as indicated by an increased Nc amplitude and an N400-like component (Experiments 1 and 3). In contrast, 12- to 14-month-old infants did not show an indication of VOE in response to head-touch actions when the model's hands were restrained (Experiment 2).

Previous research has associated the Nc component with the allocation of attentional engagement towards a stimulus (Reynolds, 2015). We found an increased Nc amplitude across central channels, between 400 and 600 ms, in response to the unexpected head touch compared to the expected hand touch, specifically when the models' hands were free (Experiment 1: hands-free, 12- to 14-month-olds). Thus, more attentional resources were used to process unexpected action outcomes. Both the topography of the Nc component and the latency are in accordance with literature on Nc effects in similar age groups (Kaduk et al., 2016; Reid et al., 2009; Webb, Long, & Nelson, 2005). However, previous ERP studies investigating eating actions have demonstrated increased Nc amplitudes in response to expected outcomes (food to the mouth) compared to unexpected outcomes (food to the head). Directing food to the mouth may have been of higher importance to infants than directing food to other parts of the head (Kaduk et al., 2016; Reid et al., 2009). In contrast, in the present case we interpret the increased Nc amplitude in response to unexpected action outcomes as reflecting an OR (Sokolov, 1963, 1990; Vaughan Jr & Kurtzberg, 1992). When observing an unexpected action and, thus, a stimulus that deviates from the prior action representation, a mismatch response occurs. The mismatch detection leads to increased attention, as indicated by an enhanced Nc amplitude. This process puts infants in a receptive state and sets up the preconditions for subsequent learning to take place when observing a head touch while the model's hands are free.

Our interpretation is in line with research on infants' arithmetic knowledge, which has demonstrated a higher negativity on frontocentral channels in response to incorrect solutions of basic equations (e.g., 1 + 1 dolls = 2 dolls (correct) or = 1 doll (incorrect)). Berger, Tzur, and Posner (2006) explained the greater negativity in response to incorrect outcomes as error detection when perceiving expectancy violations, similar to the theory of the OR (Sokolov, 1963, 1990). Infants in their first year of life seem to focus more on unusual or unexpected action outcomes possibly because they may learn from them. In line with the directed attention model (Reid & Striano, 2007), infants are able to identify actions from which they can acquire novel information within social contexts.

Intriguingly, 12- to 14-month-olds did not only discriminate between the unexpected head touch and the expected hand touch on an attentional level but also processed the unexpected action on a semantic level as indicated by an N400-like component. The N400 component has been associated with constructing semantic meaning with previous experiences and contextual information in the language and action domain in adults (Amoruso et al., 2013; Kutas & Federmeier, 2011) and in infants (Friedrich & Friederici, 2004, 2006; Reid et al., 2009). In accordance with the latter work on infants, the N400-like response to unexpected head-touch actions was delayed in time in the present study compared to adults' N400 component. However, the localization of the N400-like component to central regions differs from that of previous infant studies on semantic action processing, which observed the component over parietal regions in 9-month-olds (Kaduk et al., 2016; Reid et al., 2009). A more frontally or centrally distributed N400 component could be related to less effortful processing and/or decreasing stimulus demand in 12- to 14-month-olds compared to younger infants. The central location of the N400-like component in the present study could thus indicate that the detection of a semantic violation is less demanding for 1-year-olds than for 9-month-olds, similar to adults (Bach, Gunter, Knoblich, Prinz, & Friederici, 2009; Wu & Coulson, 2005) and older children (Coch, Maron, Wolf, & Holcomb, 2002). The present results are also consistent with N400-like responses to eating actions (Kaduk et al., 2016; Reid et al., 2009). This implies that 1-year-old infants can even build up semantic action expectations for actions performed with novel objects (i.e., touch light and soundbox). Importantly, differences in neurophysiological responses towards action outcomes cannot be explained by low-level differences as we controlled for luminance and contrast and varied only whether the hand or the head touched the lamp.

Detecting unexpected action outcomes involves quite sophisticated action understanding abilities (for an overview, see Gredebäck & Daum, 2015). Infants need to identify an agent and adjust their focus of attention within the direction of the other person. Further, infants need to build up action predictions by taking into the account agent, future goal states and contextual features. Finally, infants need to evaluate whether their action predictions are confirmed or violated after having observed an action outcome. We argue accordingly that the N400-like response towards the unexpected head touch in Experiment 1 indicates a surprise reaction after evaluating the rationality of the experimenters' actions.

VOE responses in 12- to 14-month-olds may support their learning and enhance imitation behavior. This is in line with recent research demonstrating increased exploration and hypothesis-testing behavior in 11-month-olds, after observing objects behaving in an unexpected way (Stahl & Feigenson, 2015). Consequently, results of Experiment 1 are consistent with rational-imitation accounts (Buttelmann et al., 2008; Gergely et al., 2002): Based on the principle of rational action (Gergely & Csibra, 2003), infants assume that agents achieve a goal (here: turning on a lamp) by the most efficient means (here: hand). These expectations were violated when an inefficient action was performed (here: head). Whereas results of Experiment 1 fit neatly into previous research on early action understanding, findings of Experiment 2 (hands-restrained, 12- to 14-month-olds) and 3 (hands-free, 9-month-olds) contrast with our expectations and some reports in the literature. In Experiment 2, when the model's hands were restrained, 12- to 14-month-olds did not discriminate between head- and hand-touch outcomes on an attentional or semantic level.

Several different explanations might account for this finding. First, infants may not have detected the restraining duct tape and therefore did not perceive the experimenter's hands as being restrained at all. If that had been the case, however, we would have expected the same results as in Experiment 1, i.e. indices of VOE in response to the head touch. Second, it is possible that infants did in fact process the restrained hands, but the head touch was still more salient and caught infants' attention. Supporting this idea, recent eye tracking data suggests that infants pay a similar, and substantial, amount of attention to a model's head touch, irrespective of the situational constraints (Buttelmann et al., 2017). Third, across the course of the experiment, infants may have learned that both action outcomes (head or hand) are equally likely in this scenario. Yet, infants did not discriminate between action outcomes even within the first half of observed trials. Hence, it seems unlikely that infants' prior expectations were gradually overwritten by observing many repetitions of the same action. Finally, in Experiment 2 we did not measure VOE based on predictions of the principle of rationality (Gergely & Csibra, 2003), but rather on physical principles. Although past research suggests that infants understand basic physical principles from early on (Baillargeon, 2004; Spelke & Kinzler, 2007), applying this knowledge to a novel social context with unknown objects might have been too difficult. Alternatively, two distinct parallel processes might have cancelled each other out: 1) VOE for unusual head actions and 2) VOE for physically impossible hand actions. In sum, based on the data of Experiment 2, we suggest that VOE in response to the unusual head touch is context-dependent as infants were not surprised in response to the head touch when the models' hands were restrained (but they were surprised when the model's hands were free, Experiment 1).

In addition, 9-month-olds did not distinguish hand- and head-touch outcomes on an attentional or semantic level when the model's hands were free (Experiment 3). Why did we not replicate results of previous studies on food consumption (Kaduk et al., 2016; Reid et al., 2009)? In the present case, actions and objects were novel and unknown and thus fundamentally different from feeding actions. Outcomes of eating actions, on the other hand, are highly familiar and might have been easier for infants to anticipate and evaluate, even at nine months of age. Alternatively, the action sequences in the present study might have challenged 9-month-olds' working memory capacities (Ross-Sheehy, Oakes, & Luck, 2003). This could have inhibited semantic processing and, thus, rational evaluation of action outcomes. Reducing the stimulus complexity by only presenting action outcomes may reveal semantic action processing in the present paradigm even in 9-month-olds (Michel, Kaduk, et al., 2017). Finally, our preferred interpretation of Experiment 3 is that at the age of 9 months, infants are not actually surprised when observing an unexpected head touch. This would be the case if they were unable to form action expectations that are generalizable to novel situations, such as the current paradigm. This is in accordance with behavioral studies showing that the developmental onset of selective imitation occurs between 9 and 12 months of age (Zmyj et al., 2009).

The fact that we did not measure a behavioral outcome in the present study limits the conclusions we can draw about neural mechanisms of selective imitation itself. In order to fully understand the relation between neural mechanisms and imitation behavior, future research should focus on paradigms including both neurophysiological and behavioral measures (Köster, Langeloh, Kliesch, Kanngiesser, & Hoehl, 2019). Analyzing individual differences of the occurrence of the N400-like component (Kaduk et al., 2016) may provide additional insights about neural mechanisms discriminating between imitators and non-imitators. Further, adding the simultaneous application of eye tracking to the EEG recording could reveal information on predictive gaze shifts, pupil dilation, and looking time measures to further understand processes taking place while observing VOE in action contexts (Gredebäck & Melinder, 2010; Hunnius & Bekkering, 2010).

To summarize overall, our data suggest that 12- to 14-month-olds experience VOE when observing unusual and inefficient head touches compared to more familiar and efficient hand touches. We found evidence for this both in terms of attentional orienting and semantic integration. However, the effect was restricted to conditions when the model’s hands were free (Experiment 1) as opposed to when their hands were restrained (Experiment 2). The increased Nc amplitude in response to the unusual head touch likely illustrates stronger attentional engagement and should put infants in a more receptive state. Such a state would influence learning and detection of a semantic violation, reflected by the subsequent N400-like component.

No discrimination between the unusual head touch and the familiar hand touch was found in 9-month-olds (Experiment 3). Our results are in line with rational-imitation accounts suggesting the developmental onset of selective imitation occurs between 9 and 12 months of age.

References

Amoruso, L., Gelormini, C., Aboitiz, F., Alvarez Gonzalez, M., Manes, F., Cardona, J. F., & Ibanez, A. (2013). N400 ERPs for actions: Building meaning in context. *Front Hum Neurosci, 7*, 57. doi:10.3389/fnhum.2013.00057

Bach, P., Gunter, T. C., Knoblich, G., Prinz, W., & Friederici, A. D. (2009). N400-like negativities in action perception reflect the activation of two components of an action representation. *Social Neuroscience, 4*(3), 212-232. doi:10.1080/17470910802362546

Baillargeon, R. (2004). Infants' physical world. *Current Directions in Psychological Science, 13*(13), 89-94. doi:10.1111/j.0963-7214.2004.00281.x

Balconi, M., & Caldiroli, C. (2011). Semantic violation effect on object-related action comprehension: N400-like event-related potentials for unusual and incorrect use. *Neuroscience, 197*, 191-199. doi:10.1016/j.neuroscience.2011.09.026

Beisert, M., Zmyj, N., Liepelt, R., Jung, F., Prinz, W., & Daum, M. (2012). Rethinking 'Rational Imitation' in 14-month-old infants: A perceptual distraction approach. *PLoS ONE, 7*(3), e32563. doi:10.1371/journal.pone.0032563.g001

Berger, A., Tzur, G., & Posner, M. I. (2006). Infant brains detect arithmetic errors. *PNAS, 103*(33), 12649-12653. doi:10.1073/pnas.0605350103

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Dev Sci, 10*(4), F31-38. doi:10.1111/j.1467-7687.2007.00630.x

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2008). Rational tool use and tool choice in human infants and great apes. *Child Dev, 79*(3), 609-626. doi:10.1111/j.1467-8624.2008.01146.x

Buttelmann, D., Schieler, A., Wetzel, N., & Widmann, A. (2017). Infants' and adults' looking behavior does not indicate perceptual distraction for constrained modelled actions - An eye-tracking study. *Infant Behav Dev, 47*, 103-111. doi:10.1016/j.infbeh.2017.04.001

Buttelmann, D., & Zmyj, N. (2012). Evaluating the empirical evidence for the two-stage-model of infant imitation: A commentary on Paulus, Hunnius, Vissers, and Bekkering (2011). *Front Psychol, 3*, 512. doi:10.3389/fpsyg.2012.00512

Buttelmann, D., Zmyj, N., Daum, M., & Carpenter, M. (2013). Selective imitation of in-group over out-group members in 14-month-old infants. *Child Dev, 84*(2), 422-428. doi:10.1111/j.1467-8624.2012.01860.x

Coch, D., Maron, L., Wolf, M., & Holcomb, P. J. (2002). Word and picture processing in children: an event-related potential study. *Dev Neuropsychol, 22*(1), 373-406. doi:10.1207/S15326942dn2201_3

DeBoer, T., Scott, L. S., & Nelson, C. A. (2007). Methods for acquiring and analyzing infant event-related potentials. In M. de Haan (Ed.), *Infant EEG and event-related potentials* (pp. 5-38). New York: Psychology Press.

Elsner, B., Pfeifer, C., Parker, C., & Hauf, P. (2013). Infants' perception of actions and situational constraints: An eye-tracking study. *J Exp Child Psychol, 116*(2), 428-442. doi:10.1016/j.jecp.2012.11.014

Friedrich, M., & Friederici, A. D. (2004). N400-like semantic incongruity effect in 19-month-olds: Processing known words in picture contexts. *J Cognitive Neurosci, 16*(8). doi:10.1162/0898929042304705

Friedrich, M., & Friederici, A. D. (2005a). Lexical priming and semantic integration reflected in the event-related potential of 14-month-olds. *NeuroReport, 16*(6), 653-656. doi:10.1097/00001756-200504250-00028

Friedrich, M., & Friederici, A. D. (2005b). Phonotactic knowledge and lexical-semantic processing in one-year-olds: Brain responses to words and nonsense words in picture contexts. *J Cognitive Neurosci, 17*(11), 1785-1802. doi:10.1162/089892905774589172

Friedrich, M., & Friederici, A. D. (2006). Early N400 development and later language acquisition. *Psychophysiology, 43*(1), 1-12. doi:10.1111/j.1469-8986.2006.00381.x

Friedrich, M., & Friederici, A. D. (2010). Maturing brain mechanisms and developing behavioral language skills. *Brain Lang, 114*(2), 66-71. doi:10.1016/j.bandl.2009.07.004

Gellén, K., & Buttelmann, D. (2017). Fourteen-month-olds adapt their imitative behavior in light of a model's constraints. *Child Development Research, 2017*, 1-11. doi:10.1155/2017/8080649

Gergely, G., Bekkering, H., & Király, I. (2002). Rational imitation in preverbal infants. *Nature, 415*(6873), 755. doi:10.1038/415755a

Gergely, G., & Csibra, G. (2003). Teleological reasoning in infancy: The naïve theory of rational action. *Trends Cogn Sci, 7*(7), 287-292. doi:10.1016/s1364-6613(03)00128-1

Gergely, G., Nádasdy, Z., Csibra, G., & Bíró, S. (1995). Taking the intentional stance at 12 months of age. *Cognition, 56*(2), 165-193. doi:10.1016/S0010-0277(98)00058-4

Gredebäck, G., & Daum, M. (2015). The microstructure of action perception in infancy: Decomposing the temporal structure of social information processing. *Child Development Perspectives, 9*(2), 79-83. doi:10.1111/cdep.12109

Gredebäck, G., & Melinder, A. (2010). Infants' understanding of everyday social interactions: A dual process account. *Cognition, 114*(2), 197-206. doi:10.1016/j.cognition.2009.09.004

Hoehl, S., & Wahl, S. (2012). Recording infant ERP data for cognitive research. *Dev Neuropsychol, 37*(3), 187-209. doi:10.1080/87565641.2011.627958

Hoormann, J., Falkenstein, M., Schwarzenau, P., & Hohnsbein, J. (1998). Methods for the quantification and statistical testing of ERP differences across conditions. *Beh Res Methods, 30*(1), 103-109. doi:10.3758/BF03209420

Hunnius, S., & Bekkering, H. (2010). The early development of object knowledge: A study of infants' visual anticipations during action observation. *Dev Psychol, 46*(2), 446-454. doi:10.1037/a0016543

Iacoboni, M. (2005). Understanding others: Imitation, language, and empathy. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science* (Vol. 1, pp. 77-99). Cambridge, MA: MIT Press.

Jones, S. S. (2009). The development of imitation in infancy. *Philos Trans R Soc Lond B Biol Sci, 364*(1528), 2325-2335. doi:10.1098/rstb.2009.0045

Kaduk, K., Bakker, M., Juvrud, J., Gredebäck, G., Westermann, G., Lunn, J., & Reid, V. M. (2016). Semantic processing of actions at 9 months is linked to language proficiency at 9 and 18 months. *J Exp Child Psychol, 151*, 96-108. doi:10.1016/j.jecp.2016.02.003

Kavsek, M. (2012). The comparator model of infant visual habituation and dishabituation: recent insights. *Dev Psychobiol, 55*(8), 793-808. doi:10.1002/dev.21081

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. *Cogn Process, 8*(3), 159-166. doi:10.1007/s10339-007-0170-2

Király, I., Csibra, G., & Gergely, G. (2013). Beyond rational imitation: Learning arbitrary means actions from communicative demonstrations. *J Exp Child Psychol, 116*(2), 471-486. doi:10.1016/j.jecp.2012.12.003

Kolling, T., Óturai, G., & Knopf, M. (2014). Is selective attention the basis for selective imitation in infants? An eye-tracking study of deferred imitation with 12-month-olds. *J Exp Child Psychol, 124*, 18-35. doi:10.1016/j.jecp.2014.01.016

Köster, M., Langeloh, M., Kliesch, C., Kanngiesser, P., & Hoehl, S. (2019). Motor cortex activity during action observation predicts infants' subsequent imitation behavior. *Manuscript submitted for publication*.

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annu Rev Psychol, 62*(1), 621-647. doi:10.1146/annurev.psych.093008.131123

Langeloh, M., Buttelmann, D., Matthes, D., Grassmann, S., Pauen, S., & Hoehl, S. (2018). Reduced mu power in response to unusual actions is context-dependent in 1-year-olds. *Front Psychol, 9*, 36. doi:10.3389/fpsyg.2018.00036

Luck, S. J. (2005). An introduction to event-related potentials and their neural origins. In S. J. Luck (Ed.), *An introduction to the event-related potential technique* (pp. 1-50). Cambridge, Mass.: MIT Press.

Meltzoff, A. N. (1988). Infant imitation after a 1-week delay: Long-term memory for novel acts and multiple stimuli. *Dev Psychol, 24*(4), 470-476. doi:10.1037/0012-1649.24.4.470

Meltzoff, A. N., & Marshall, P. J. (2018). Human infant imitation as a social survival circuit. *Current Opinion in Behavioral Sciences, 24*, 130-136. doi:10.1016/j.cobeha.2018.09.006

Michel, C., Kaduk, K., Ni Choisdealbha, A., & Reid, V. M. (2017). Event-related potentials discriminate familiar and unusual goal outcomes in 5-month-olds and adults. *Dev Psychol, 53*(10), 1833-1843. doi:10.1037/dev0000376

Michel, C., Wronski, C., Pauen, S., Daum, M. M., & Hoehl, S. (2017). Infants' object processing is guided specifically by social cues. *Neuropsychologia*. doi:10.1016/j.neuropsychologia.2017.05.022

Nielsen, M. (2006). Copying actions and copying outcomes: Social learning through the second year. *Dev Psychol, 42*(3), 555-565. doi:10.1037/0012-1649.42.3.555

Parise, E., & Csibra, G. (2012). Electrophysiological Evidence for the Understanding of Maternal Speech by 9-Month-Old Infants. *Psychological Science, 23*(7), 728-733. doi:10.1177/0956797612438734

Paulus, M. (2011). Imitation in infancy: Conceptual considerations. *Theory & Psychol, 21*(6), 849-856. doi:10.1177/0959354310395990

Paulus, M. (2012). Is it rational to assume that infants imitate rationally? A theoretical analysis and critique. *Hum Dev, 55*(3), 107-121. doi:10.1159/000339442

Paulus, M., Hunnius, S., & Bekkering, H. (2013). Neurocognitive mechanisms underlying social learning in infancy: Infants' neural processing of the effects of others' actions. *Soc Cogn Affect Neurosci, 8*(7), 774-779. doi:10.1093/scan/nss065

Paulus, M., Hunnius, S., Vissers, M., & Bekkering, H. (2011a). Bridging the gap between the other and me: The functional role of motor resonance and action effects in infants' imitation. *Dev Sci, 14*(4), 901-910. doi:10.1111/j.1467-7687.2011.01040.x

Paulus, M., Hunnius, S., Vissers, M., & Bekkering, H. (2011b). Imitation in infancy: Rational or motor resonance? *Child Dev, 82*(4), 1047-1057. doi:10.1111/j.1467-8624.2011.01610.x

Peykarjou, S., Pauen, S., & Hoehl, S. (2014). How do 9-month-old infants categorize human and ape faces? A rapid repetition ERP study. *Psychophysiology, 51*(9), 866-878. doi:10.1111/psyp.12238

Reid, V. M., Hoehl, S., Grigutsch, M., Groendahl, A., Parise, E., & Striano, T. (2009). The neural correlates of infant and adult goal prediction: Evidence for semantic processing systems. *Dev Psychol, 45*(3), 620-629. doi:10.1037/a0015209

Reid, V. M., & Striano, T. (2007). The directed attention model of infant social cognition. *European Journal of Developmental Psychology, 4*(1), 100-110. doi:10.1080/17405620601005648

Reid, V. M., & Striano, T. (2008). N400 involvement in the processing of action sequences. *Neurosci Lett, 433*(2), 93-97. doi:10.1016/j.neulet.2007.12.066

Reynolds, G. D. (2015). Infant visual attention and object recognition. *Behav Brain Res, 285*, 34-43. doi:10.1016/j.bbr.2015.01.015

Reynolds, G. D., & Richards, J. E. (2005). Familiarization, attention, and recognition memory in infancy: An event-related potential and cortical source localization study. *Dev Psychol, 41*(4), 598-615. doi:10.1037/0012-1649.41.4.598

Reynolds, G. D., & Richards, J. E. (2017). Infant Visual Attention and Stimulus Repetition Effects on Object Recognition. *Child Development*. doi:10.1111/cdev.12982

Richards, J. E., Reynolds, G. D., & Courage, M. L. (2010). The neural bases of infant attention. *Curr Dir Psychol Sci, 19*(1), 41-46. doi:10.1177/0963721409360003

Ross‐Sheehy, S., Oakes, L. M., & Luck, S. J. (2003). he development of visual short‐term memory capacity in infants. *Child Dev, 74*(6), 1807-1822. doi:10.1046/j.1467-8624.2003.00639.x

Schwier, C., von Maanen, C., Carpenter, M., & Tomasello, M. (2006). Rational Imitation in 12-month-old infants. *Infancy, 10*(3), 303-311. doi:10.1207/s15327078in1003_6

Sokolov, E. N. (1963). *Perception and the conditioned reflex*. Oxford: Pergamon Press.

Sokolov, E. N. (1990). The orienting response, and future directions of its development. *Pavlov J Biol Sci, 25*(3), 142-150. doi:10.1007/BF02974268

Spelke, E. S., & Kinzler, K. D. (2007). Core knowledge. *Dev Sci, 10*(1), 89-96. doi:10.1111/j.1467-7687.2007.00569.x

Stahl, A. E., & Feigenson, L. (2015). Observing the unexpected enhances infants' learning and exploration. *Science, 348*(6230), 91-94. doi:10.1126/science.aaa3799

Stapel, J. C., Hunnius, S., van Elk, M., & Bekkering, H. (2010). Motor activation during observation of unusual versus ordinary actions in infancy. *Soc Neurosci, 5*(5-6), 451-460. doi:10.1080/17470919.2010.490667

Stets, M., Stahl, D., & Reid, V. M. (2012). A meta-analysis investigating factors underlying attrition rates in infant ERP studies. *Dev Neuropsychol, 37*(3), 226-252. doi:10.1080/87565641.2012.654867

Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, Mass.: Harvard Univ. Press.

Vaughan Jr, H. G., & Kurtzberg, D. (1992). Electrophysiologic indices of human brain maturation and cognitive development. In M. R. Gunnar & C. A. Nelson (Eds.), *Minnesota Symposia on Child Psychology* (pp. 1-36). Hillsdale, NJ: Erlbaum.

Webb, S. J., Long, J. D., & Nelson, C. A. (2005). A longitudinal investigation of visual event-related potentials in the first year of life. *Dev Sci, 8*(6), 605-616. doi:10.1111/j.1467-7687.2005.00452.x

Wu, Y. C., & Coulson, S. (2005). Meaningful gestures: Electrophysiological indices of iconic gesture comprehension. *Psychophysiology, 42*(6), 654-667. doi:10.1111/j.1469-8986.2005.00356.x

Zmyj, N., & Buttelmann, D. (2014). An integrative model of rational imitation in infancy. *Infant Behav Dev, 37*(1), 21-28. doi:10.1016/j.infbeh.2013.10.001

Zmyj, N., Buttelmann, D., Carpenter, M., & Daum, M. M. (2010). The reliability of a model influences 14-month-olds' imitation. *J Exp Child Psychol, 106*(4), 208-220. doi:10.1016/j.jecp.2010.03.002

Zmyj, N., Daum, M. M., & Aschersleben, G. (2009). The development of rational imitation in 9- and 12-month-old infants. *Infancy, 14*(1), 131-141. doi:10.1080/15250000802569884

Zmyj, N., Daum, M. M., Prinz, W., Nielsen, M., & Aschersleben, G. (2012). Fourteen-month-olds' imitation of differently aged models. *Infant Child Dev, 21*(3), 250-266. doi:10.1002/icd.750

Figures

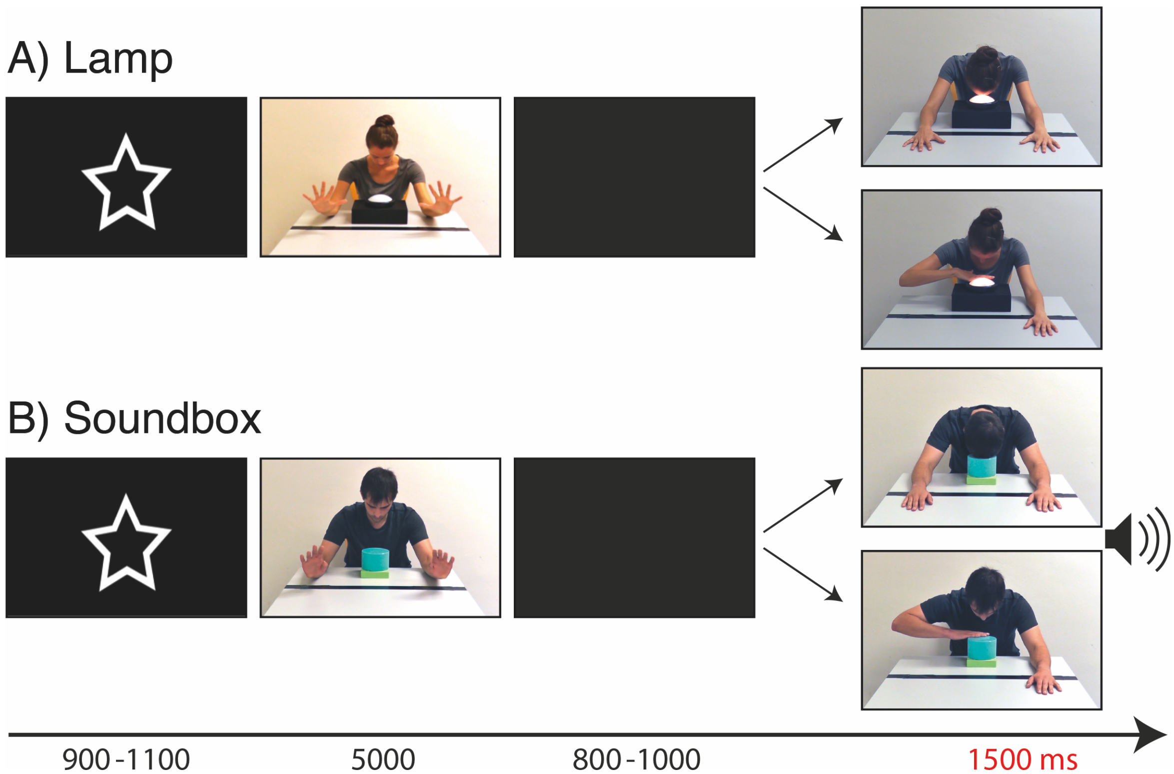

Figure 1. Stimulus examples of lamp (A) and sound (B) modality used for Experiment 1 (hands-free, 12- to 14-month-olds) and Experiment 3 (hands-free, 9-month-olds). The model's hands are free while turning on a lamp/soundbox using either his/her hand (expected) or head (unexpected). Models did not establish eye contact with infants. Action outcomes represent test frames used for ERP analyses. Persons appearing in this figure consented to the publication of these images.

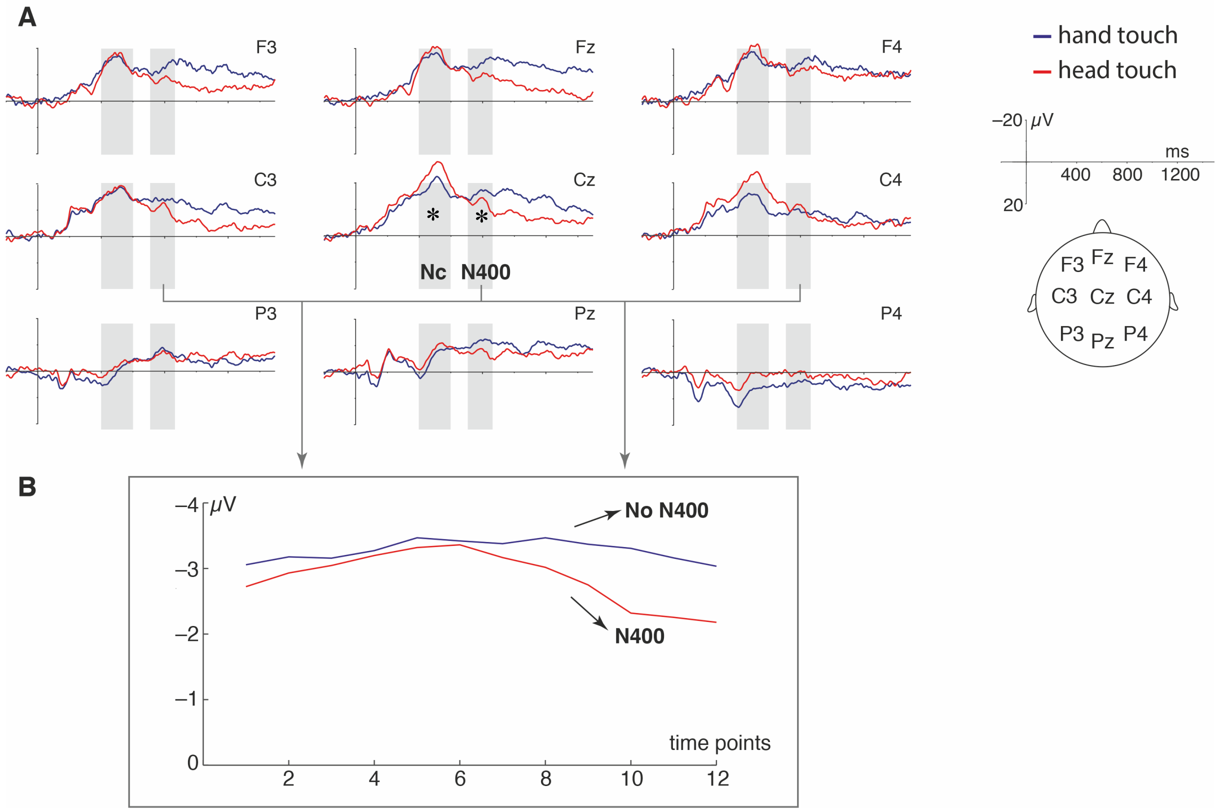

Figure 2. A) Grand average ERP responses to hand- (blue) and head-touch (red) outcomes in 12- to 14-month-olds in Experiment 1. Statistical analyses on the Nc and N400-like component were conducted on central channels (C3, Cz, C4). Note that negative is plotted up. Asterisks depict significant differences with $p < .05$. B) Zoomed-in time window of interest (736 – 868 ms) with 12 time points (each 12 ms) indicating an N400-like component in response to the head-touch outcomes but not to the hand-touch outcomes.

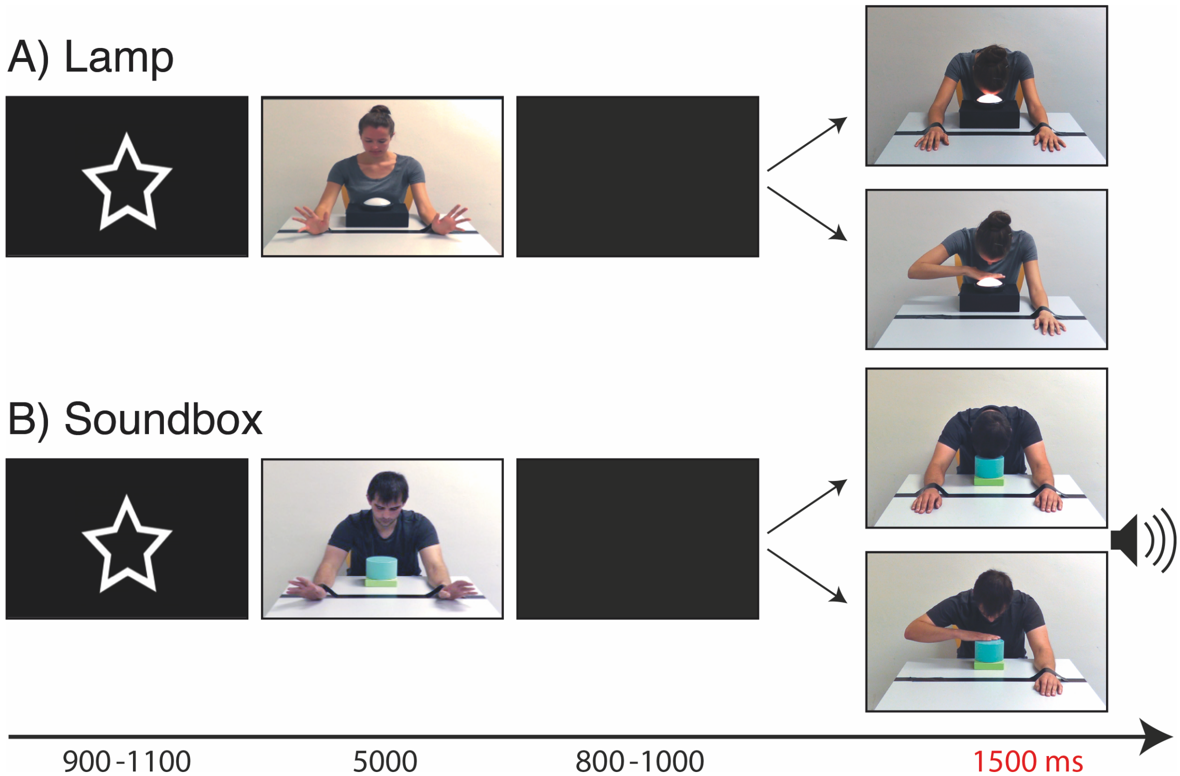

Figure 3. Stimulus examples of lamp (A) and sound (B) modality used for Experiment 2 (hands-restrained, 12- to 14-month-olds). The model's hands are tied to the table while turning on a lamp using either his/her hand (unexpected) or head (expected). Models did not establish eye contact with infants. Action outcomes represent test frames used for ERP analyses. Persons appearing in this figure consented to the publication of these images.

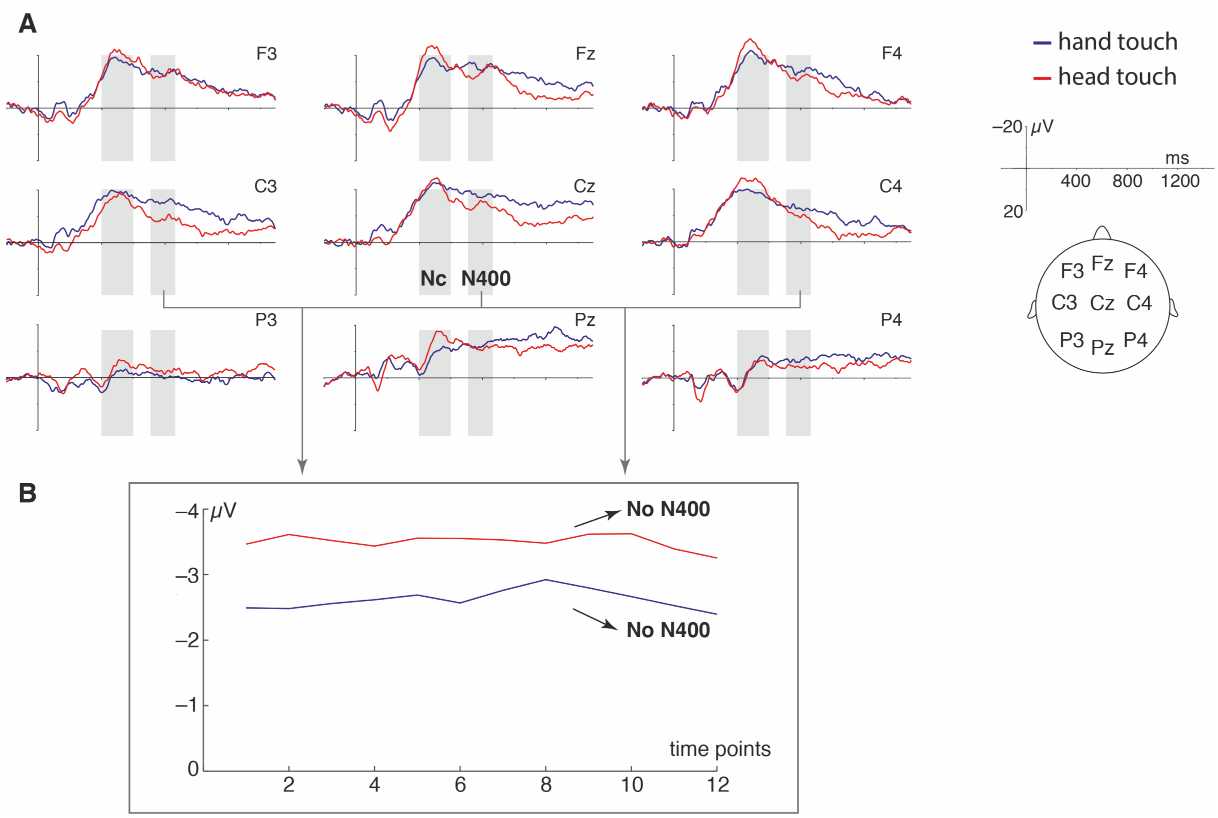

Figure 4. A) Grand average ERP responses to hand- (blue) and head-touch (red) outcomes in 12- to 14-month-olds in Experiment 2. Statistical analyses on the Nc and N400-like component were conducted on central channels (C3, Cz, C4). Note that negative is plotted up. B) Zoomed-in time window of interest (736 – 868 ms) with 12 time points (each 12 ms) indicating no N400-like component in response to either head-touch or hand-touch outcomes.

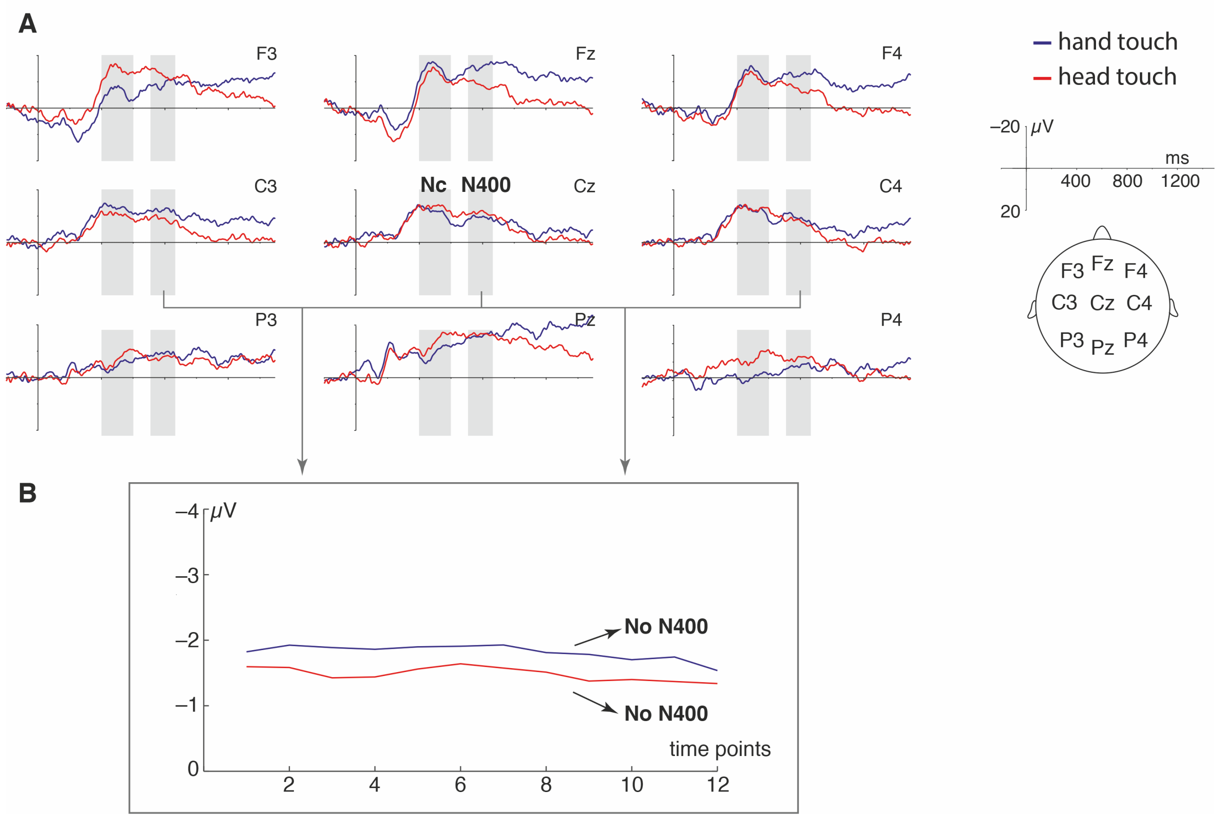

Figure 5. A) Grand average ERP responses to hand- (blue) and head-touch (red) outcomes in 9-month-olds in Experiment 3. Statistical analyses on the Nc and N400-like component were conducted on central channels (C3, Cz, C4). Note that negative is plotted up. B) Zoomed-in time window of interest (736 – 868 ms) with 12 time points (each 12 ms) indicating no N400-like component in response to either head-touch or hand-touch outcomes.

MANUSCRIPT III

Langeloh, M., Pauen, S., Buttelmann, D., Hoehl, S. (2019). One-year-olds' event-related potentials differentiate expected from unexpected action outcomes without context information. *Manuscript under review in Infancy.*

One-year-olds' event-related potentials differentiate expected from unexpected action outcomes without context information

Miriam Langeloh[1,2], Sabina Pauen[2], David Buttelmann[3], & Stefanie Hoehl[1,4]

[1]Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

[2]Department of Psychology, Heidelberg University, Heidelberg, Germany

[3]Department of Psychology, Bern University, Bern, Switzerland

[4]Faculty of Psychology, University of Vienna, Vienna, Austria

Author Note

Correspondence concerning this article should be addressed to Miriam Langeloh, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstrasse 1a, 04103 Leipzig, Germany. Phone: +49 341 9940 2234. E-mail: langeloh@cbs.mpg.de.

Abstract

From early on, infants evaluate other people's actions. Past research suggests that infants distinguish expected from unexpected action outcomes with regard to attention allocation and semantic integration. Adults do not require context information to evaluate action outcomes semantically. Crucially, in previous studies, infants were presented with information concerning action context. Yet, little is known about the role of context information in infants' action evaluation. In the absence of extra contextual information, we measured 12-month-old infants' (N = 23) electrophysiological responses to expected hand- and unexpected head-touch action outcomes (i.e., a person turning on a lamp or a soundbox using her hand or head). Event-related potential components, associated with attentional engagement (Negative central; Nc) and semantic integration (N400), were analyzed. Infants responded with an increased negativity on the Nc component towards unexpected head-touch outcomes. No N400 component was observed for unexpected action outcomes. Thus, our data suggest that, in the absence of contextual information, one-year-olds discriminate between expected and unexpected outcomes in attentional but not semantic terms. In comparison to adults, infants may still require context information for semantic action processing.

Keywords: action perception, infants, event-related potentials, Nc, N400

One-year-olds' event-related potentials differentiate expected from unexpected action outcomes without context information

When engaging in a social interaction, we constantly try to make sense of the other person's actions in order to respond appropriately. This ability is highly complex, incorporating the evaluation of the other person's action goal, the means to accomplish it, and the contextual information. In this respect, it is fascinating that infants within their first year of life begin to process and interpret other people's actions (for overviews, see Ni Choisdealbha & Reid, 2014; Gredebäck & Daum, 2015).

Infants' action understanding has mainly been studied with behavioral paradigms, which suggest that at the age of 4 months infants are sensitive to unexpected action outcomes when contextual information is provided (Gredebäck & Melinder, 2011). In addition, neurophysiological studies examined cognitive processes underlying infants' action understanding by analyzing oscillatory dynamics (Langeloh et al., 2018) and event-related potentials (ERPs; Langeloh, Buttelmann, Pauen, & Hoehl, 2019; Reid et al., 2009). Two ERP components related to the evaluation of unexpected action outcomes and thus, to the violation of expectation (VOE), have been brought forward. The Negative central (Nc) component is associated with the amount of attentional engagement (Reynolds, 2015), whereas the N400 reflects the detection of violations of semantic action contexts (Amoruso et al., 2013). For example, in an adaptation of the head-touch paradigm (Gergely, Bekkering, & Király, 2002), 12- to 14-month-olds displayed VOE when observing an adult who performed an inefficient action (i.e., turning on a lamp with her head while her hands were free) (Langeloh et al., 2019). Specifically, infants showed an increased Nc amplitude as well as an N400-like component during the unexpected actions (for similar N400 effects during unexpected eating actions, see Kaduk et al., 2016; Reid et al., 2009).

Interestingly, adults are able to process semantic violations without receiving prompts concerning the action context (Michel, Kaduk, Ni Choisdealbha, & Reid, 2017; Mudrik, Lamy, & Deouell, 2010). Crucially, the previously discussed ERP-studies presented infants with information on the action context. Thus, this may have facilitated the detection of the unexpected action outcomes. Still, it remains unclear whether infants process action outcomes semantically, as adults do, when no contextual information is provided.

In the current study we aimed to clarify the role of action context during the processing of action outcomes in infants and to replicate recent findings (Langeloh et al., 2019). We showed 12-month-olds action outcomes that were demonstrated by adult models. The models turned on either a lamp or a soundbox with their hand (hand-touch condition) or their head (head-touch condition) while their hands were otherwise free. However, contextual information was not provided prior to each trial, as it was originally (Langeloh et al., 2019). That is, only the action outcome (expected or unexpected) was presented. If infants discriminate action outcomes in attentional terms, we expected an increased Nc amplitude for unexpected action outcomes compared to more familiar and expected action outcomes. Second, we hypothesized that – should infants experience VOE even without prior context information – their brains would respond with an N400 component in response to the unexpected action outcomes only.

Methods

Participants

Required sample size (*N* = 22) was predetermined based on an a priori power analysis (G*Power: Faul, Erdfelder, Lang, & Buchner, 2007) given a level of significance of 0.05, a power of 0.8, and an expected medium effect size of f = 0.25. The final sample consisted of *N* = 23 infants (11 girls, *M* age = 12 months 11 days, *SD* = 8 days, age range = 12 months 1 day to 12 months 29 days)[1]. Another *N* = 25 infants were tested but had to be excluded from the final sample because of failure to reach the minimum number of artifact-free trials per condition (*n* = 18), bad data quality (*n* = 4), poor contact of the reference electrode (*n* = 2), or experimental error (*n* = 1). All infants were born full-term (37 – 41 weeks of gestation) and without any known neurological problems. Informed verbal and written consent were obtained from each participant's parent. The experiment was carried out in line with institutional protocols and the Declaration of Helsiniki. The preregistration of this study can be accessed via https://aspredicted.org/tf6q4.pdf.

Stimuli

We presented infants with static images[2] depicting action outcomes showing one of four adult models turning on a lamp or a soundbox (i.e., a toy that makes a sound when being touched) (Gergely et al., 2002; Buttelmann, Carpenter, Call, & Tomasello, 2007). Action outcomes were presented in an *expected* (i.e., using the hand) or in an *unexpected* manner (i.e., using the head). Figure *1* illustrates the complete stimulus set used in the present study. Whenever an action outcome of an adult touching the soundbox was shown, a toy-squeezing sound was generated at a maximum intensity of 65 dB. Stimuli were presented at the center of a 60-Hz 17-inch monitor at a viewing distance of about 55 cm at a visual angle of 11.52° x 15.91°. Action outcomes were matched with Adobe Photoshop CS4 extended for luminance and contrast (all *p*s > .05).

Procedure

During EEG recording infants sat on their parent's lap in an electrically-shielded and sound-attenuated cabin. Parents were instructed not to interact with their infant during data collection. Infants' electrical brain activity was measured in two within-subjects conditions, the hand-touch and the head-touch condition. The experiment consisted of one block of a maximum of 120 trials (60 hand-touch and 60 head-touch outcomes). The two conditions were presented in a semi-randomized order via the software Presentation (Neurobehavioral Systems, Albany, USA). The same outcome (hand touch/head touch), same modality (lamp/sound), and same sex (male/female) was not presented in more than two consecutive trials. All 16 possible action outcomes (head touch/hand touch, lamp/sound, for each of the four adults) were presented within the first 48 trials. Furthermore, we counterbalanced between infants whether the first action presented was a hand touch or a head touch to avoid a confounding effect of the first observed action type.

Every trial started with an attention getter (900 – 1100 ms), followed by an expected or unexpected action outcome (1500 ms; see Figure *2* for an example of a trial sequence). Whenever the infant became fussy, the experimenter paused the experiment and resumed when the infant was in an attentive state again. The testing session ended when the infant's attention could no longer be attracted to the screen or when the infant completed all the trials. EEG was recorded continuously during the experiment and infants' behavior was video-recorded for offline coding of looking behavior.

EEG Recording and Analyses

EEG was recorded from 29 scalp locations according to the 10-20 system using Ag/AgCl ring electrodes and referenced online to Cz. Data were recorded with a Twente Medical Systems

32-channel REFA amplifier at a sampling rate of 500 Hz. Horizontal and vertical electrooculograms were recorded bipolarly. Impedances were controlled at the beginning of the experiment and accepted when below 10 kΩ. EEG data were preprocessed in Brain Vision Analyzer 2 (Brain Products, Gilching, Germany), in the same manner as in recent research (Langeloh et al., 2019). Offline filters were set from 0.3 to 30 Hz and data were re-referenced to the average mastoids (TP9, TP10). Data were automatically excluded if the amplitude of any channel exceeded a voltage threshold of 200 µV within a 200 ms interval. Data were time-locked to the action outcomes and thus segmented into epochs of waveforms that comprised 200 ms prior to 1500 ms after stimulus onset. Infants' looking behavior was coded offline and only trials in which infants did not blink during the onset and watched the entire presentation of the action outcome were included in further analyses. An independent rater, blind to hypotheses, rated 26 % of the videos leading to a high inter-rater reliability of ICC = .93. For the baseline correction, we used the 200 ms before the stimulus onset. An individual average was calculated per participant across lamp and soundbox stimuli for each of the two within-subjects conditions (hand touch, head touch). Subsequently, grand averages were estimated across all subjects for each condition. A minimum of 10 artifact-free trials per condition was required for an infant to be included in the grand average. On average each infant contributed 10 to 43 trials ($M = 23.34$, $SD = 9.61$) to the head-touch condition and 10 to 41 trials ($M = 22.04$, $SD = 10.12$) to the hand-touch condition. The number of trials did not differ significantly between conditions, $t(22) = 1.219$, $p = .236$.

For statistical analyses, two-way repeated measures analysis of variances (rmANOVA) or paired *t*-tests were conducted with the main within-subjects factor condition (hand touch, head touch). Greenhouse-Geisser correction was employed if applicable. The level of significance was set to 0.05 for all statistical analyses.

Results

Following recent findings (Langeloh et al., 2019), components of interest were analyzed on central channels (C3, Cz, C4). Final analyses differed slightly from the preregistered analyses (see supplemental material for details and justification). Grand averages of frontocentral electrodes are displayed in Figure *3*.

Nc

The mean amplitude of the Nc component was assessed on an average of central electrode channels (C3, Cz, C4) in a time window between 400 and 600 ms after stimulus onset, similar to Langeloh et al. (2019) (Figure *3*). A paired *t*-test revealed significant differences between action outcomes with greater negativity in response to head-touch outcomes (M = -18.44 µV, SD = 10.56) compared to hand-touch outcomes (M = -13.66 µV, SD = 12.30), $t(22)$ = 2.159, p = .042, 95 % CI [0.19 µV, 9.38 µV], d = .49. Means and standard deviations of the Nc mean amplitude for single frontocentral channels, in both conditions, are reported in Table *1*. The greater negativity in response to head-touch actions suggests that infants allocated more attention towards unexpected action outcomes.

N400

Visual inspection did not indicate an N400-like component in response to head- or hand-touch action outcomes (Figure *3*). To statistically test for the possibility that ERP waves differ in morphology with an N400-like component being present in only one condition, we applied the windows analysis technique (Hoormann, Falkenstein, Schwarzenau, & Hohnsbein, 1998). We extracted amplitude values for several time points for both conditions and compared them in a rmANOVA with the within-subjects factors condition and time. A significant interaction between time and condition would indicate that the ERP waveform differed between conditions. We conducted the same analysis across central channels (C3, Cz, C4) as in Langeloh et al. (2019) in a time window of 736 to 868 ms after stimulus onset by extracting 12 samples. The rmANOVA with the within-subjects factors condition (head touch, hand touch) and time (12 samples at one sample per 12 ms) revealed no significant interaction of condition and time, $F(3.00,65.96) = 1.684$, $p = .179$. No main effects were found (all other *p*s > .05). In sum, ERP waveforms in the time window previously associated with an N400-like component did not differ between conditions. This suggests that infants did not distinguish head- from hand-touch action outcomes on a semantic level.

Discussion

In the present study, we aimed to elucidate whether 12-month-olds require context information to detect semantic violations in action outcomes. As hypothesized, infants responded with increased negativity on the Nc component towards unexpected head-touch outcomes (i.e., a person turning on a lamp or a soundbox using her head, although her hands were free). Replicating previous research (Langeloh et al., 2019), we suggest that the enhanced Nc amplitude indicates an orienting response triggered by a VOE. When observing an unexpected action outcome, a mismatch response occurs leading to increased attention (Sokolov, 1990; Vaughan Jr & Kurtzberg, 1992). Similarly, the N2 in adults, a potential successor of the Nc (Rothenberger, Banaschewski, Siniatchkin, & Heinrich, 2007; Vaughan Jr & Kurtzberg, 1992), has been associated with attended mismatch (Folstein & Van Petten, 2008).

In contrast, no N400 component was observed for unexpected action outcomes. Hence, 12-month-old infants, similar to 5-month-olds in past research (Michel et al., 2017), may not use semantic systems when observing action outcomes unless action context is presented beforehand.

Thus, prior information on action initiation and context may have facilitated infants' semantic processing in previous studies (Kaduk et al., 2016; Reid et al., 2009; Langeloh et al., 2019).

Our results support the idea that two distinct cognitive mechanisms may be involved in infants' action processing: a fast discrimination on an attentional level (enhanced Nc amplitude) and a more specific mismatch processing on a semantic level (N400) (for a similar distinction in adults, see Szucs, Soltesz, Czigler, & Csepe, 2007). These mechanisms are not mutually exclusive. They may emerge from a rudimentary familiarity distinction (Michel et al., 2017) and develop to a discrimination in attentional terms in older infants, up to a full-fledged semantic action processing in adults. In future research, infants' neural responses towards a broader range of actions should be tested across their first years of life and linked to behavioral outcomes, such as imitation scores (Filippi et al., 2016).

To summarize, our data suggest that 1-year-olds discriminate between expected and unexpected action outcomes in attentional terms. Consequently, for a fast detection of unusual action outcomes, even in an unfamiliar situation such as the head-touch paradigm, infants do not need specific context information. A deeper semantic processing of unexpected actions may require prior information concerning action initiation and context.

References

Amoruso, L., Gelormini, C., Aboitiz, F., Alvarez Gonzalez, M., Manes, F., Cardona, J. F., & Ibanez, A. (2013). N400 ERPs for actions: Building meaning in context. *Front Hum Neurosci, 7*, 57. doi:10.3389/fnhum.2013.00057

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Dev Sci, 10*(4), F31-38. doi:10.1111/j.1467-7687.2007.00630.x

Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav Res Methods, 39*, 175-191. doi:10.3758/BF03193146

Filippi, C. A., Cannon, E. N., Fox, N. A., Thorpe, S. G., Ferrari, P. F., & Woodward, A. L. (2016). Motor System Activation Predicts Goal Imitation in 7-Month-Old Infants. *Psychol Sci, 27*(5), 675-684. doi:10.1177/0956797616632231

Folstein, J. R., & Van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: a review. *Psychophysiology, 45*(1), 152-170. doi:10.1111/j.1469-8986.2007.00602.x

Gergely, G., Bekkering, H., & Király, I. (2002). Rational imitation in preverbal infants. *Nature, 415*(6873), 755. doi:10.1038/415755a

Gredebäck, G., & Daum, M. (2015). The microstructure of action perception in infancy: Decomposing the temporal structure of social information processing. *Child Development Perspectives, 9*(2), 79-83. doi:10.1111/cdep.12109

Gredebäck, G., & Melinder, A. (2011). Teleological reasoning in 4-month-old infants: pupil dilations and contextual constraints. *PLoS ONE, 6*(10), e26487. doi:10.1371/journal.pone.0026487

Hoormann, J., Falkenstein, M., Schwarzenau, P., & Hohnsbein, J. (1998). Methods for the quantification and statistical testing of ERP differences across conditions. *Beh Res Methods, 30*(1), 103-109. doi:10.3758/BF03209420

Kaduk, K., Bakker, M., Juvrud, J., Gredebäck, G., Westermann, G., Lunn, J., & Reid, V. M. (2016). Semantic processing of actions at 9 months is linked to language proficiency at 9 and 18 months. *J Exp Child Psychol, 151*, 96-108. doi:10.1016/j.jecp.2016.02.003

Langeloh, M., Buttelmann, D., Matthes, D., Grassmann, S., Pauen, S., & Hoehl, S. (2018). Reduced mu power in response to unusual actions is context-dependent in 1-year-olds. *Front Psychol, 9*, 36. doi:10.3389/fpsyg.2018.00036

Langeloh, M., Buttelmann, D., Pauen, S., & Hoehl, S. (2019). 12- to 14-month-olds expect unconstrained agents to act efficiently: ERP evidence from the head-touch paradigm. *Manuscript submitted for publication*.

Michel, C., Kaduk, K., Ni Choisdealbha, A., & Reid, V. M. (2017). Event-related potentials discriminate familiar and unusual goal outcomes in 5-month-olds and adults. *Dev Psychol, 53*(10), 1833-1843. doi:10.1037/dev0000376

Mudrik, L., Lamy, D., & Deouell, L. Y. (2010). ERP evidence for context congruity effects during simultaneous object-scene processing. *Neuropsychologia, 48*(2), 507-517. doi:10.1016/j.neuropsychologia.2009.10.011

Ni Choisdealbha, A., & Reid, V. M. (2014). The developmental cognitive neuroscience of action: Semantics, motor resonance and social processing. *Exp Brain Res, 232*(6), 1585-1597. doi:10.1007/s00221-014-3924-y

Reid, V. M., Hoehl, S., Grigutsch, M., Groendahl, A., Parise, E., & Striano, T. (2009). The neural correlates of infant and adult goal prediction: Evidence for semantic processing systems. *Dev Psychol, 45*(3), 620-629. doi:10.1037/a0015209

Reynolds, G. D. (2015). Infant visual attention and object recognition. *Behav Brain Res, 285*, 34-43. doi:10.1016/j.bbr.2015.01.015

Rothenberger, A., Banaschewski, T., Siniatchkin, M., & Heinrich, H. (2007). Entwicklungsneurophysiologie. In F. Herpertz-Dahlmann, M. Resch, A. Schulte-Markwort, & A. Warnke (Eds.), *Entwicklungspsychiatrie* (pp. 50-84). Stuttgart: Schattauer.

Sokolov, E. N. (1990). The orienting response, and future directions of its development. *Pavlov J Biol Sci, 25*(3), 142-150. doi:10.1007/BF02974268

Szucs, D., Soltesz, F., Czigler, I., & Csepe, V. (2007). Electroencephalography effects to semantic and non-semantic mismatch in properties of visually presented single-characters: the N2b and the N400. *Neurosci Lett, 412*(1), 18-23. doi:10.1016/j.neulet.2006.08.090

Vaughan Jr, H. G., & Kurtzberg, D. (1992). Electrophysiologic indices of human brain maturation and cognitive development. In M. R. Gunnar & C. A. Nelson (Eds.), *Minnesota Symposia on Child Psychology* (pp. 1-36). Hillsdale, NJ: Erlbaum.

Footnotes

[1]During data acquisition we could only roughly estimate whether an infant might be included in the final analyses. Therefore, our final sample included one participant more than the a priori power analysis suggested.

[2]To establish context at the beginning of the experiment before the presentation of action outcomes, infants were presented with two pre-demonstration videos showing a female or male adult sitting at a table demonstrating that their hands were free or restrained. Adult models were different actors than in the photographs depicting action outcomes during the experiment. Each infant watched two videos, in randomized order, establishing the models' sex and situational constraints (for details, see Langeloh et al., 2019).

Tables

Table 1

Means (M) and standard deviations (SD) of the Nc amplitude for frontocentral electrodes

	Head touch		Hand touch	
Electrode	*M*	*SD*	*M*	*SD*
F3	-16.53	15.10	-10.98	13.48
Fz	-15.30	13.96	-9.05	10.49
F4	-18.50	13.97	-11.58	12.56
C3	-18.64	13.10	-13.18	12.30
Cz	-17.12	10.28	-13.31	13.49
C4	-19.56	13.66	-14.48	15.51

Note: Amplitude size is reported in µV.

Figures

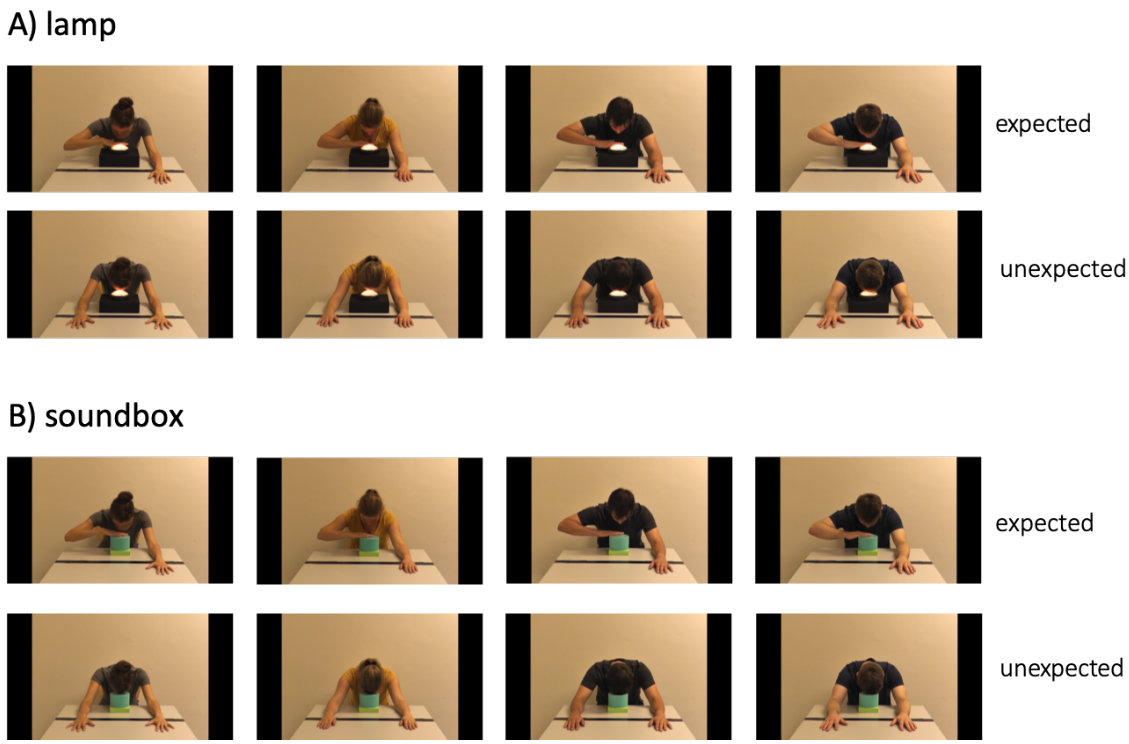

Figure 1. Complete stimulus sets showing four adult models (two males, two females) turning on A) a lamp or B) a soundbox with their hand (expected) or their head (unexpected). Persons appearing in this figure consented to the publication.

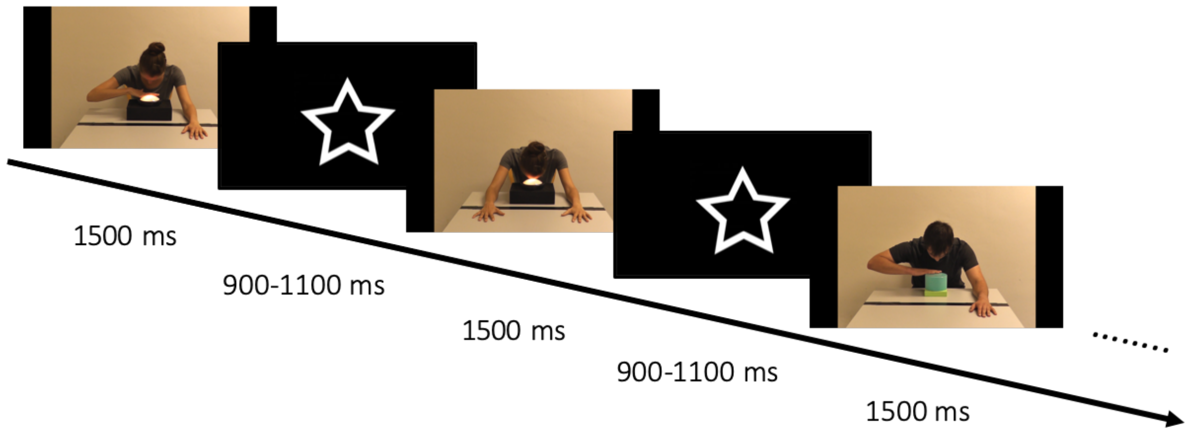

Figure 2. An example stimulus sequence presented to infants. From top left to bottom right: expected hand touch lamp (1500 ms), inter-stimulus-interval (900 – 1100 ms), unexpected head touch lamp (1500 ms), inter-stimulus-interval (900 – 1100 ms), expected hand touch soundbox (1500 ms). Persons appearing in this figure consented to the publication.

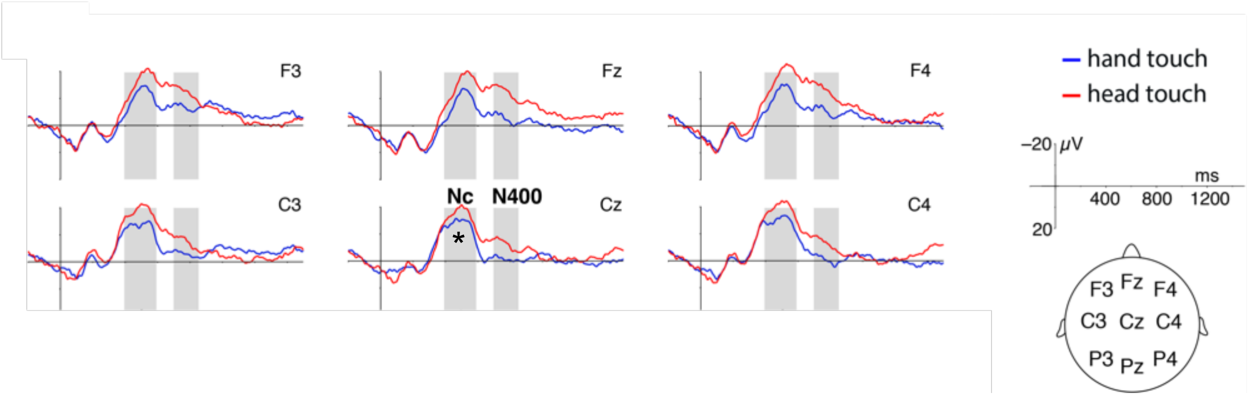

Figure 3. Grand average ERP responses to hand- (blue) and head-touch (red) outcomes in 12-month-olds. Statistical analyses on the Nc and N400-like component were conducted on central channels (C3, Cz, C4). Note that negativity is plotted up. Asterisk depicts significant difference with $p < .05$.