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INVESTIGATING THE CONNECTION BETWEEN ACTING AND ACTION PERCEPTION IN INFANCY

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ABSTRACT

The ability to understand others’ actions is central in human interaction. Experience producing actions, including the experience that goes with advances in motor development and the experience associated with short-term training, is associated with action perception in the first year of life. To date, it is unclear how these two different aspects of action experience interact in supporting action perception. In this dissertation, I investigate the behavioral and neural responses that are associated with advances in motor development and that result from the effects of short-term action training. In Study 1, I explore the potential interplay between these two aspects of experience in relation to action understanding, by evaluating infants’ motor development and the effects of action training on their behavioral response to another person’s action. The results replicate prior findings associating motor skill and short-term training with action perception. They further indicate a compensatory interaction between action training and motor skills--action training improved action understanding, particularly for those infants who started out with lower motor skills. In Study 2, I investigate neural correlates associated with infants’ perception of actions that are within versus outside the repertoire of actions they are able to produce. Clarifying mixed findings from prior research, I find that actions within the infants’ developmental repertoire are associated with specific neural correlates, including functional connectivity between motor and visual processes. In Study 3, I ask whether similar patterns of connectivity are evident during infants’ perception of a newly trained action, following an intervention designed to support infants’ pointing. While I do not find motor-visual connectivity modulated by intervention experience, I find an increase in global connections across the brain as a function of intervention, suggesting that prolonged experience may be necessary to reliably build on specific network activations. Taken together, this work suggests that the connection

between action experience and action perception is associated with changes in dynamic network activity, and paves the way for developmental cognitive neuroscience research to investigate changes in functional neural networks that occur with experience and its implications on action perception.

Chapter 1: Introduction

Navigating the social world requires intelligent analyses of and responses to others' actions. The ability to make sense of others' actions is a critical foundation for early social cognition and social learning (Tomasello, 1999a; Woodward, 2009). Moreover, action perception is considered to be a building block of several social cognitive skills, such as communication, imitation, and empathy, and thus considered as an essential foundation for becoming a proficient social partner (Barresi & Moore, 1996; Gredebäck, 2018; Meltzoff, 2007a, 2007b; Meltzoff & Brooks, 2001; Tomasello, 1999b). Findings from developmental studies provide evidence that rudimentary forms of action understanding emerge early in life. It has been found that infants encode actions in terms of the relation between the agent and its goal (Luo & Johnson, 2009; Sodian & Thoermer, 2004; Woodward, 1998), anticipate the outcomes of others' goal-directed actions (Cannon & Woodward, 2012; Falck-Ytter et al., 2006; Gredeback & Falck-Ytter, 2015; Kanakogi & Itakura, 2011; Krogh-Jespersen & Woodward, 2014), and selectively imitate the goals of others' actions during the first year of life (Hamlin et al., 2008). Findings also suggest that action perception is tightly associated with and affected by infants' action experience in two senses: Advances in infants' motor development are associated with advances in action understanding (Cannon et al., 2012; Daum et al., 2011; Kanakogi & Itakura, 2011; Loucks & Sommerville, 2012; Melzer et al., 2012), and short-term training with a novel action leads to changes in infants' perception of the trained action when others produce it (Gerson, Mahajan, Sommerville et al., 2015; Gerson & Woodward, 2014a, 2014b; Skerry et al., 2013; Sommerville et al., 2008; Sommerville et al., 2005). Even so, relatively little is known about how these two different aspects of action experience may interact to support infants' understanding of others' actions, and little is known about whether these two aspects of action experience reflect similar or different underlying neurocognitive processes.

In this dissertation, I discuss research that explores these open questions. I explore whether variations in infant motor development interact with in-lab short-term trained experience in supporting action understanding. Moreover, despite consistent findings of behavioral data in infancy showing that both variations in motor skills and short-term training are linked to action perception, they leave open the question concerning the mechanism that underlies action experience and action perception. Thus, I investigate the neural correlates that underlie infants' perception of actions that are associated with their motor development, and the correlates that are associated with action training. I begin by outlining the empirical evidence demonstrating infants' action perception and the role of experience on action perception in the first year of life.

Action perception in the first year of life

The ability to discern the goal structure of others' simple action emerges in the first year of life (Biro & Leslie, 2007; Luo & Johnson, 2009; Woodward, 1998, 1999). A variety of methods have been developed to measure infants' action perception, utilizing measures of visual habituation, predictive looking, and imitation. Evidence shows that infants show selective attention to the goal structure of action (Hofer et al., 2007; Woodward, 1998), generate anticipatory saccades to others' action end-points (Ambrosini et al., 2013; Gredeback & Falck-Ytter, 2015; Kanakogi & Itakura, 2011), and respond selectively by imitating others' goals (Hamlin et al., 2008) in the first year of life. This is a specific response to well-formed goal-directed actions, distinct from how infants respond to the movements of inanimate objects, e.g., mechanical claws (Adam et al., 2016; Cannon & Woodward, 2012; Kanakogi & Itakura, 2011) or unusual movements of people, e.g., touching the toy with the back of the hand (Hamlin et al., 2008; Kanakogi & Itakura, 2011; Woodward, 1999).

In the second half of the first year, infants' ability to understand others' actions extends to more complex action with distal goals. By 12 months, infants begin to understand higher-order goals structure of action sequences that involves tool-use or intermediary objects (Henderson & Woodward, 2011; Hofer et al., 2005; Sommerville & Woodward, 2005). For instance, when they observe someone using a tool to retrieve an out-of-reach toy, they understand that the person's tool-use action is directed at the toy, rather than the tool itself (Sommerville & Woodward, 2005). Furthermore, this knowledge extends to communicative actions that do not involve physical contact between the agent and the object, such as pointing (Behne et al., 2012; Brune & Woodward, 2007; Daum et al., 2013; Liszkowski & Tomasello, 2011; Woodward & Guajardo, 2002).

Research suggests that infants' experiences contribute to their knowledge about others' actions. 'Experience' has been assessed largely in two ways: advances in infants' motor development and action production over a developmental time scale (in months) and short-term in-lab or home interventions (in minutes, days).

Motor development and action perception

During the first year of life, infants undergo dramatic changes in their capacity for action. For instance, around 4-to 6-months of age infants start to intentionally reach for objects and by 9-to 12-months, infants become efficient and proficient in their reaching and grasping actions (von Hofsten, 1989; von Hofsten, 2004; von Hofsten & Rönnqvist, 1988). Nine-to12-months is a special transitional period in infants' production of actions. As infants accrue multiple opportunities to maneuver their hands, they increasingly manipulate objects and their actions extend to more complex actions between 9-to-12 months, such as using another object as a means to obtain a desired goal toy beyond one's reach (Piaget, 1953; Willatts, 1984, 1999). This period also overlaps with infants' onset of a communicative action, i.e. pointing (Bates et al., 1975; Butterworth & Morissette, 1996; Leung & Rheingold, 1981).

Studies have shown tight relations between when infants gain the corresponding functional motor ability and the time when action perception for that action emerges (Gredebäck, 2018; Woodward, 2009). For instance, findings indicate that infants' proficiency in grasping was related to action prediction toward a target goal when observing reaching or grasping actions (Ambrosini et al., 2013; Cannon & Woodward, 2012; Cannon et al., 2012; Kanakogi & Itakura, 2011; Melzer et al., 2012). More specifically, faster latency to place a toy into a container (Cannon et al., 2012), better ability to produce bimanual reaches (Kanakogi & Itakura, 2011), more frequent production of contralateral reaches (Melzer et al., 2012), and more precise hand configuration in grasping (Ambrosini et al., 2013) predicted faster and accurate action prediction of others' action in infants. Moreover, infants' ability to produce pincer grasps (Daum et al., 2011; Loucks & Sommerville, 2013) was associated with infants' ability to discriminate functional consequences of another's grasp, and infants' ability to pre-shape their hands was found to be associated with better prediction of others' goal according to hand-configuration during a grasping action (Filippi & Woodward, 2016).

Similar links are found in the context of infants' development of means-end actions beginning around 9-to 12 months. As infants begin to recognize that objects can be used as an intermediary means to achieve the desired goal, they begin to produce spontaneous two-step means-end actions such as removing a cover (the means) to search for hidden objects (the goal) (Piaget, 1953; Willatts, 1984, 1999), or utilizing nearby utensils (e.g., hoop, crook, or stick) to drag an out-of-reach object closer (Bates et al., 1980; Bates et al., 1975). Studies have found connections between increases in infants' spontaneous means-end actions and changes in infants' perception of others' means-end action (Sommerville & Woodward, 2005). For instance, in Sommerville & Woodward, (2005), 10- and 12-month-old infants were habituated to an event in which an experimenter pulled one of two cloths, that each supported different toys, and retrieved the toy. In the test, infants were shown events where locations of the toys were reversed. The experimenter either reached for the cloth she had previously reached for that now supported a new toy, or the other cloth, which now supported the toy she had previously grasped for. 12-month-old infants looked longer to the new-toy event, suggesting that they construed the experimenter's cloth-pulling actions as directed toward the toy, and not on pulling the cloth itself (Sommerville & Woodward, 2005). The authors also measured infants' own performance on means-end cloth-pulling actions, and coded for instances that infants engaged in planful cloth-pulling action that resulted in successful retrieval of the toy. At 10 months, infants' own skill predicted their responses to the observed cloth-pulling actions: Infants who produced a high proportion of planful cloth-pulling actions showed evidence of interpreting the goal of others' cloth-pulling actions.

At 9-to 12 months infants also begin to produce communicative gestures, including pointing (Bates et al., 1980; Bates et al., 1975; Carpenter et al., 1998). At these ages, infants start to produce pointing directed at objects, e.g., to request a toy, or to share information or attention with a social partner (Bates et al., 1980; Cochet & Vauclair, 2010). Whether or not infants were categorized as pointers has been found to be associated with infants' understanding that others' pointing is directed towards a referent (Brune & Woodward, 2007; Woodward & Guajardo, 2002) and their behavioral responses to others' pointing (Behne et al., 2012; Liszkowski & Tomasello, 2011). For instance, Behne et al., (2012) assessed infants' production of pointing by measuring the proportion of instances that infants pointed toward the location of a hidden toy for another person. They also measured infants' comprehension of others' points by looking at whether infants searched for the location of a hidden toy that the experimenter had pointed toward using a pointing gesture. 12-month-old infants' tendency to point for others was related to their comprehension of others' pointing.

In sum, these findings indicate that infants' action development is associated with changes in how infants perceive others' actions, and raises the possibility that active experience plays an important role in shaping their interpretations of others' actions (Gredebäck, 2018; Woodward, 2009). However, further evidence conducting intervention experiments is needed to understand the causal connections that may be involved in this relation.

Short-term intervention and action perception

Action experience has also been assessed via brief laboratory interventions in which infants are given exposure to a novel action. These interventions provide infants with an opportunity to carry out and learn novel actions that are within "reach" of their current motor repertoire, providing experiences that could not be elicited or observed in a natural setting. These kinds of interventions offer a way to ask whether changes in infants' action experience cause changes in their action perception. One of the earliest pieces of evidence that intervention experience alters action perception comes from studies that provide 3-month-old infants, who are generally limited in their ability to reach for and grasp objects, with an opportunity to apprehend objects with their hands. At 3 months, infants cannot readily grasp objects nor do they attend differentially to changes in action goal structure. However, following a short-term (200s) training session where infants wear velcro-covered "sticky mittens" and play with Velcro covered toys, infants responded systematically to others' goal-directed actions (Gerson & Woodward, 2014a, 2014b; Skerry et al., 2013; Sommerville et al., 2005). While wearing the mittens, the infants had multiple opportunities to contact the toys. Then the experimenter removed the toy from the mitten and replaced it in front of the infant for them. This self-produced experience of coordinated actions with the mitten and the toy facilitated infants' sensitivity to the goal-structure of others' action (Sommerville et al., 2005; Gerson & Woodward, 2014a,b) and has been found to have an influence on infants' interpretation of the efficiency of observed actions (Skerry, Carey, & Spelke, 2013).

Means-end action intervention studies in older infants find consonant effects of short-term training (Gerson, Mahajan, Sommerville et al., 2015; Sommerville et al., 2008). For instance, infants under 12 months are limited in their ability to spontaneously and systematically recognize the relation between means-end tool-use actions on distant objects (Cannon & Woodward, 2010; Sommerville & Woodward, 2005; Gerson & Woodward, 2012). However, infants between 8-and 10-months who were trained to use a cane (Sommerville et al., 2008) or a cloth-pulling action (Gerson et al., 2015) to retrieve an out-of-reach toy, compared to observing an experimenter's means-end action, were found to respond systematically to others' means-end goals.

Together, there is strong support for the notion that infants' action experience is correlated with and plays a role in shaping their analysis of others' actions. Better competence and control in infants' own action is associated with how they process and perceive others' actions. Moreover, action training has a causal effect on inducing changes in infants analysis of others' actions.

Even so, there are open questions about how these two aspects of experience – the effects of motor development and the effects of short-term training – may relate to one another in supporting infants' action perception. Second, despite behavioral data from infants showing that both variations in motor development and induced short-term training experience are linked to changes in infants' analysis of others' actions, little is known about the mechanisms that underlie these relations between action experience and action perception. While research has begun to elucidate the neural correlates of action perception in infancy, little is known about the neural correlates associated with newly trained actions. Further, whether the same neural correlates are associated with the effects of motor development and the effects of training on infants' action perception is largely an open question. In this dissertation, I aim to investigate the effects associated with motor development and with short-term action training within the same study that parallels prior research paradigms with the goal to (1) understand how these two aspects of action experience may interact in their effects on action perception, and (2) to explore the neural correlates (during action perception) that are associated with each aspect of experience.

Overview of Dissertation

First, relatively little is known about how advances in infants' motor development (across months) and short-term in-lab interventions (across minutes) interact in supporting action understanding. While research documents independent contributions of motor development and short-term interventions, it is currently untested whether variability in infants' motor skills that they bring into the lab affect the degree in which they benefit from the intervention in supporting action understanding. It is possible that motor abilities relevant to the task at hand could pave the way for learning, which mediates infants' learning during training and subsequently enhances goal understanding. Alternatively, one-time short-term interventions may not generate changes in the way that long term motor development does. In Study 1, I explore the potential interplay between the types of experience in supporting action understanding by obtaining a metric of infants' motor development, conducting a tool-use training intervention, and measuring infants' action understanding, within the same experiment.

Second, while behavioral evidence illustrates a connection between production and perception in infants, the neural processes associated with this link are in question. In Study 2, I use an integration of neural and behavioral measures to investigate the neural processes that are associated with infants' perception of actions that are within their motor repertoires as compared to those that are not. I focus on an action that emerges in infants' behavior through a long term developmental timescale, namely grasping, compared to a novel cane-use action. I explore which aspects of neural processing are uniquely associated with actions that the infant can produce versus actions they have never produced before, and which aspects of neural processing correlate with motor competence of the action. In doing so, I implement a methodological approach that allows me to explore functional networks during action perception.

In Study 3, I seek to understand the neural correlates associated with action training, and whether novel training experiences exert the same pattern of changes in functional connectivity during action perception as motor development does. To do so, I conduct analysis on a pre-existing dataset from an intervention experiment designed to support 10- to 12-month-old infants' production of pointing. This study collected EEG as a measure of infants' neural activity during their observation of pointing and grasping action prior to and after intervention. I explore changes in neural networks during perception of pointing associated with pointing the intervention experience that was conducted for a 1-month period at home by the care-giver (different from the one-time in-lab interventions conducted in prior studies). In addition, examining these networks when infants are 10- to 12-months of age provides a special window to investigate changes in functional networks as infants experience a newly emerging communicative action (pointing), compared to actions that they have had prolonged experience producing (grasping). These are actions that are behaviorally similar in their form of presentation, but differ in their purpose (Novack & Goldin-Meadow, 2017). Thus, along with my main goal to address neural correlates associated with action training, I investigate whether infants recruit the same functional neural networks for perception of pointing as they do for perception of grasping.

Chapter 2: The roles of action training and motor development in supporting infants' action understanding

Every day, infants observe a wide range of actions—from simple goal-directed actions (e.g.,, reaching for a toy) to more complex actions where the goal is not the object being acted upon but using the object for another purpose (e.g.,, using a knife to slice an apple). To understand and respond to others' actions, infants need to rapidly deploy knowledge about the goal structure of actions (Krogh-Jespersen & Woodward, 2014). This capacity is shaped by action experience (Gredebäck, 2018; Hunnius & Bekkering, 2014; Woodward & Gerson, 2014). Despite considerable interest in the link between action experience and action understanding, questions remain about how infant's experiences across multiple timescales influence one another. The current study examines the interplay between infants' starting state means-end skills and the effects of short-term action training on their action understanding.

The ability to discern the goal structure of others' simple actions (e.g., reaching) emerges early in life (Woodward, 1998), as revealed by converging findings across visual habituation, predictive looking, and imitation studies. By 5-to 6-months of age, infants show selective attention to the goal structure of action (Hofer et al., 2007; Woodward, 1998), generate anticipatory saccades to others' action end-points (Ambrosini et al., 2013; Cannon & Woodward, 2012; Gredeback & Falck-Ytter, 2015), and respond selectively by imitating others' goals (Hamlin et al., 2008). For instance, Hamlin and colleagues (2008) showed 7-month-olds events in which an experimenter reached for one of two objects. When infants were given an opportunity to choose between the two objects, they systematically chose the experimenter's prior goal. In contrast, when the experimenter did not act in a goal-directed manner (e.g., touching the toy with the back of her hand), infants chose randomly between the two objects. By

12 months of age, infants can discern the higher-order goals that structure sequences of actions (Sommerville & Woodward, 2005). For instance, when they observe someone using a cane to retrieve an out-of-reach toy, they understand that the person’s tool-use action is directed at the toy, rather than the cane itself. Although infants under 12 months are limited in their ability to recognize the relation between tool-use actions on distant objects (Cannon & Woodward, 2012; Gerson & Woodward, 2012; Sommerville & Woodward, 2005) around their first birthday, this sensitivity to goals extends to means-end action sequences that involve tool-use or intermediary objects (Henderson & Woodward, 2011; Hofer et al., 2005; Sommerville & Woodward, 2005).

An extensive behavioral literature has provided evidence for the link between action experience and action understanding in infants (Gredebäck, 2018; Hunnius & Bekkering, 2014; Stapel, 2020; Woodward, 2009). In this literature, ‘action experience’ has been operationalized in two ways: (1) advances in infants’ motor skills (Ambrosini et al., 2013; Filippi & Woodward, 2016; Gredeback & Kochukhova, 2010; Kanakogi & Itakura, 2011; Loucks & Sommerville, 2012; Melzer et al., 2012; Sommerville & Woodward, 2005), and (2) training interventions that introduce infants to new actions (Gerson & Woodward, 2014a, 2014b; Skerry et al., 2013; Sommerville et al., 2005). In each case, findings have revealed connections between infants’ own skills or experience with an action and their sensitivity to the goal structure of that action in others. To start, considerable evidence shows that as infants become more proficient in their own actions, they also become more adept in understanding the goal structure in others' actions. For instance, Sommerville & Woodward, (2005) measured infants’ spontaneous proficiency to retrieve a toy by pulling on the cloth on which it rested. They found that 12-month-olds as a group responded systematically to the means-end structure of others’ cloth-pulling action, but 10-month-olds did not. However, at 10 months, individual variation in infants’ own cloth-pulling skills predicted their sensitivity to the goals of others’ cloth-pulling actions (Sommerville & Woodward, 2005). Other studies have revealed similar relations for pointing (Behne et al., 2012; Brune & Woodward, 2007; Woodward & Guajardo, 2002).

Other research has given infants brief training to provide them with the opportunity to learn novel actions that are within “reach” of their current motor skills. These intervention experiments show, for example, that infants who were trained to use a cane to retrieve a toy (Sommerville et al., 2008), compared to those who passively observed an experimenter’s actions with the cane, became sensitive to the goal structure of others’ cane-use actions. Similar effects have been observed for collaborative actions, in which two people play complementary roles to attain a joint goal. Infants who first were given the opportunity to engage in the collaborative action subsequently showed greater sensitivity to collaborative goals in others’ actions (Henderson et al., 2013; Krogh-Jespersen et al., 2020).

In some training studies, infants who were more proficient in learning to produce means-ends actions during training also showed more sensitivity to others’ means-end goals (Sommerville et al., 2008). Relatedly, Gerson, Mahajan, Sommerville et al. (2015) showed a similar effect of learning to engage in a cloth-pulling action to retrieve an out-of-reach toy where variation in how well infants learned during training predicted infants’ sensitivity to others’ means-end goals. This suggests that in addition to the in-lab experiences of acting on the tool, variation in proficiency of infants’ means-end motor skills may have paved the way for how ready they are to learn from training that supported infants’ understanding of goal structure in others’ actions. However, infant’s starting-state motor development was not evaluated in previous training studies, so it is difficult to disentangle this possibility.

Taken together, these findings indicate connections between infants’ own motor experience and their understanding of other people’s actions. Even so, they raise questions about how these two aspects of experience – the effects of motor development and the effects of short-term training – may relate to one another in supporting infants’ action understanding. That is, previous studies have not yet explored whether the extent to which infants benefit from training depends on their existing motor skills they have accrued over development. This is an intriguing unanswered question as infants’ experience via motor development and short-term training differ in many aspects. First, changes in motor skills occur over a prolonged developmental time scale, with new skills becoming robust and stable over many months, whereas the training in the relevant studies usually involves a single, brief exposure to the new action. Moreover, the two kinds of experiences also likely relate to different underlying neurocognitive processes. For instance, the prefrontal and motor areas play an important role during execution of stable and well-practiced skills, while the cerebellum is suggested to play a critical role during the early stages of learning a new skill (Doyon et al., 2002; Halsband & Lange, 2006; Nishiyori, 2016). Thus, it is yet an open question to explore the contributions of different types of experience on action understanding.

These points highlight the need for a closer look at infants’ motor development and training in one study, which could shed light on whether and how motor skills and training interact to affect action understanding. Due to the challenges in assessing several infant capacities in a short time given infants’ limited attention spans, parent report questionnaires such as the Early Motor Questionnaire (Libertus & Landa, 2013) are fruitful to assess a broad range of skills, which may not be captured in a single lab session (including gross motor, fine motor and visual receptive skills). For instance, infants’ means-end skills can be assessed directly via a set of questions on the visual-reception scale within the EMQ. Moreover, the breadth of EMQ allows examination of whether general improvements in motor development may facilitate means-end action understanding. The current study takes this approach.

The current study

The present study investigated the effects of action training and means-end skills, within the same experiment. To do so, we assessed infants' starting-state means-end problem solving skills with a validated parent report questionnaire (EMQ), conducted an in-lab training to teach infants to retrieve out-of-reach toys with a novel cane (modeled after Sommerville et al., 2008), and evaluated action understanding using a goal imitation paradigm (Hamlin et al., 2008).

We aimed to investigate whether there is an interaction between short-term training and motor skills on infants' action understanding. One possibility is that there is an additive interaction between training and motor skills, such that those infants who arrive at the lab more proficient in the relevant motor skills would benefit more from the training. In this case, motor skills might serve as an index of infant's "readiness to learn" (Gerson, Mahajan, Sommerville et al., 2015; Keen, 2011; Lockman, 2000; Piaget, 1955), and may mediate learning during training and subsequently enhance action understanding. Alternatively, there may be a compensatory interaction--infants who come in with less advanced motor skills benefit more the from training in terms of its effects on action understanding. A final possibility is that the effects of motor skill and training could be independent, such that training improves infants' goal understanding independent of their starting skill level.

Along with our main questions, we expected to replicate prior findings illustrating that 1) training alters infants' understanding of novel goal-directed actions 2) the more proficient an infant is at producing the trained action, the more adept they are in recognizing this action as goal-directed (Sommerville et al., 2008; Gerson et al., 2015), and 3) infants' own action competence in a specific action is associated with recognizing the action as goal-directed (Kanakogi & Itakura, 2011; Cannon et al., 2012; Melzer et al., 2012). In addition, we had two exploratory questions regarding infants' motor skills. First, as variations in motor skills affect learning and cognition (Adolph & Joh, 2007) we explored whether motor skills measured via the EMQ predicted infants' degree of learning during training. Second, no study has asked how specific the relation between motor skills and action understanding is, as aforementioned studies have examined variability in infants' own actions in a single domain (often using the exact task that children will see during the action observation assessment). Therefore, we explored whether means-end skill is a specific predictor of means-end understanding or whether general motor maturity also contributes to means-end understanding, using the subscales within the EMQ.

Method

Participants

Eighty full-term (minimum 37 weeks gestation) 9-month-old infants (M_{age}=8 months 27 days; range= 8 months 0 days –10 months 0 days, 39 female) participated in this study. Participants were recruited from a database of families in a large Midwestern city interested in participating in Child Development research, and represented a diverse racial background (44% White, 13% African American, 6% Asian, 5% Hispanic, and 33% more than one race). Parent/guardian consent was obtained for all infants. Forty infants were randomly assigned to the training-first condition (20 females; M_{age} = 8 months 24 days) and 40 to the imitation-first condition (19 females; M_{age} = 8 months 27 days). An additional 23 infants were tested but not included in final analyses due to failure to complete either imitation or training session (N = 10), inattention during the task (N = 3), side bias (choosing the same side across all 6 trials) during imitation procedure (N = 7), technical issues (N = 2), or parents not consenting to session being filmed (*N* = 1). The conditions did not vary in terms of average age or sex composition (all *p's* > .8). Data loss, age, and sex of the child did not differ as a function of condition (all *p'*s > 0.8).

Procedure

Infants participated in a tool-training paradigm (i.e., cane training task) and a goal imitation task (used to evaluate action understanding) in one lab visit. Infants were either randomly assigned to undergo tool training before (training-first condition) or after (imitation-first condition) the goal imitation procedure. For both tasks, infants sat on a parent's lap at a table and parents were asked not to influence their infant's actions in any way.

Cane Training Task

The cane training task was modeled after Sommerville, Hildebrand, & Crane (2008). During the task, infants pulled a cane to retrieve a series of out-of-reach toys. All infants were given pre-training and post-training trials in which the experimenter did not help the infant in any way. The pre-training trials indexed infant's knowledge of how to use the cane prior to the intervention and the post-training trials indexed learning over the training session. Between pre-training and post-training, the experimenter provided infant-directed training that supported the infants' success in retrieving the out-of-reach toy themselves (using the cane). During all three phases of the training task, the experimenter gave the toy back to the infant after each trial was over, even if the infant was not able to retrieve the toy independently, to keep infants motivated. Infants acted on a red cane during pre-training and training, and a blue cane (which was identical to the red in every way except for color) for post-training trials (The blue cane was used as a test of how well the infant was able to generalize what they learned when working with a new cane).

Experimental Set-Up. Infants were seated within reach of the cane with enough room to pull the cane (length of cane: 48cm, width of crook: 13.5cm). The experimenter sat beside the infant so that the infant and the experimenter were both facing the toy and the cane (See Figure 1). A camera was placed in front of both the experimenter and infant to record the training session. Recordings were then used for offline coding.

Figure 1. Schematic depiction of the cane training task.

Pre- and Post-training Trials. Infants received three pre-training and three post-training trials in which the experimenter placed the toy (animal shaped bath toys) out of the infants' reach in the crook of the cane. Infants acted on a different toy on each trial, and toys were presented in random order. Each trial began with the experimenter placing a toy in the crook of the cane. Pre- and post-training trials ended after infants either successfully retrieved the toy or 30 seconds elapsed. If an infant was successful at retrieving the toy, the experimenter provided positive encouragement (i.e., "Good job" or "Yay"). If an infant was unsuccessful, the experimenter provided a positive comment and gave the toy to the infant (i.e., "Let's try this one."). If an infant was successful at using the cane to retrieve the out-of-reach toy on all 3 pre-training trials, the experimenter proceeded directly to post-training (skipping training trials; training-first: N = 4; imitation-first: N = 8).

Training Trials. Immediately following pre-training, infants were taught how to retrieve toys using the cane. During training, the experimenter helped the infants pull the cane to retrieve the toy themselves. Types of assistance included tapping on the toy, tapping on the cane, helping infants pull the cane, modeling cane-pulling, and praising infants after they obtained the toy. Assistance was adjusted depending on the infants' behaviors (e.g.,, if the infant did not reach for the cane, the experimenter tapped on the cane's handle). Thus, the number of training trials varied from 0 to 8 trials. Each training trial ended after infants either successfully retrieved the toy or 30 seconds elapsed. Infants proceeded to post-training if they either (1) used the cane to retrieve the out-of-reach toy on at least 3 trials (this included successful trials during the pre-training and the 3 trials need not be consecutive) or (2) reached a maximum of 8 training trials.

Goal Imitation Task

A modification of the goal imitation task developed by Hamlin and colleagues (2008) was used as a measure of infant's action understanding. This task has been utilized at several ages to evaluate infants' action understanding (Gerson & Woodward, 2012; Hamlin et al., 2008; Mahajan & Woodward, 2009).

Experimental Set-Up. Infants sat on their parent's lap in front of a table and the experimenter sat across from the infant facing them. Two cameras were used to record this task; one camera was placed behind the experimenter to record the infant's behavior and another camera was placed behind the infant to capture the experimenter's demonstration. These recordings were used for offline coding.

Familiarization Phase. Infants were first familiarized with the twelve bath toys (which differed from the toys used in cane training task) that would be featured during the goal imitation procedure. Each toy was presented one at a time in randomized order, on alternating sides of a board (76 cm X 23 cm). Trials ended when infants manually touched the toys. If the infant did not touch the toy, the experimenter handed the toy to the infant so the infant knew they could pick up the toys.

Test Phase. Following familiarization, the experimenter placed a pair of toys 28 cm apart on the tray (See Figure 2) behind an occluder. Once set up, the experimenter removed the occluder and monitored the infants' gaze to ensure the infant looked toward both toys. If infants did not look toward to the toys, the experimenter snapped or clapped behind each toy to direct the infant's gaze to it. She then brought the infants' gaze to the center by saying, ‘‘Hi! Look!’’ She then shifted her gaze toward the goal toy as she placed the crook of the red cane (i.e., the cane used during training trials) around one of the two toys to indicate her toy choice. She gazed at the toy throughout and said ‘‘Oooh!’’ twice but did not pick up or move the toy. The experimenter then withdrew the cane and established eye contact with the infant, bringing the infant's attention back to center. She then looked down at the table (to ensure her gaze could not influence the infant's subsequent choice), pushed the tray to the infant, and said, ‘‘Now it's your turn!’’ The experimenter ended the trial when the infant selected a toy or, if the infant did not act on either toy, after 30 seconds elapsed. This procedure was repeated six times with a new pair of toys presented at each trial. The order of the pairs was pseudo-randomized. Within each condition, each toy was selected by the experimenter equally, and side of presentation and side of first reach was counterbalanced across infants.

Figure 2. Depiction of the goal imitation paradigm. Left: Screenshot of experimenter using the cane to indicate the goal toy. Right: Screenshot of an infants' subsequent goal response.

Early Motor Questionnaire (EMQ)

To assess infants' motor development, we administered the Early Motor Questionnaire (EMQ) developed by Libertus & Landas, (2013). The EMQ is a parent report measure that has been validated using the Mullen Scales of Early Learning (MSEL) and Peabody Developmental Motor Scales (PDMS-2) (see Appendix A). The items included on the EMQ describe motor behaviors typically emerging within the first 2 years of life (0–24 months). Parents report their infant's gross motor, fine motor, and visual receptive (formally known as perception-action scale). Examples of prototypic EMQ items (taken directly from the questionnaire) relevant to the age range assessed in the current study are shown in Table 1. The EMQ uses a 5-point scale ranging from −2 to +2. The score -2 indicates if the parent is sure the child does not show the behavior yet, and +2 if the parent remembers a particular instance where the child exhibited the behavior. Parents filled out the EMQ online prior to their visit to the lab and if parents were unable to complete the EMQ prior to the visit, they filled it out in the waiting room during consent prior to the experiment.

Coding

Cane Training Task

Planful Toy Retrieval. To assess learning over the course of the training session, we coded for the proportion of trials that the infant used the cane to retrieve the out-of-reach toy in a goal-directed or planful manner during pre-training and post-training. Trials were scored as planful if infants looked at the toy, pulled the cane while maintaining attention to the toy, and grasped the toy within three seconds (see Sommerville & Woodward, 2005, Sommerville et. al., 2008; Gerson & Woodward, 2012 for comparable coding scheme). Reliability coding was completed for the whole sample for the pre- and post-training trials. A high degree of reliability was found for both planful scores in pre-training (ICC- 0.79, with 95% confidence interval from 0.69 to 0.84) and post-training (ICC- 0.78, with 95% confidence interval from 0.67 to 0.85) trials.

Experimenter assistance. To evaluate the extent to which the experimenter assisted the infant during training, we coded the training trials to identify the frequency of each method of training support that the experimenter could provide. Coders identified instances of: tapping on the toy, assisting the infant in pulling the cane, and changing the cane's angle. These data were used to determine whether any of these experimenter variables accounted for infants' improvement from pre- to post-training trials.

Goal Imitation Task

Goal Imitation. In this procedure, goal imitation refers to choosing the same goal object as the experimenter (Hamlin et al., 2008; Gerson & Woodward, 2012). Coders, who were unaware of infants' condition or the experimenter's goal on each trial coded infants' toy selection offline using video. The infant's choice was coded as the first toy touched so long as the infant visually attended to the toy before the touch (Gerson & Woodward, 2012). If the infant touched a toy without looking or touched the toy by accident, this was coded as a mistrial. If the infant did not choose a toy, the trial was coded as no choice. All mistrials and no choice trials were excluded from subsequent analyses. A second independent coder scored 25% of the infants, and the two coders' judgments were highly correlated (Cronbach's alpha (a) = 0.97).

Infant Attention. Infants' visual attention during the goal imitation task was also coded to assess whether attention differed as a function of condition. Coders identified the duration of the time that the infant attended to the goal toy, non-goal toy, and experimenter using a digital coding program (Mangold, 1998). A second independent coder coded 25% of the infants' test-trials and the two coders' judgments were highly correlated (Attention to goal toy: ICC- 0.94 with 95% confidence interval from 0.82 to 0.98; experimenter: ICC- 0.86 with 95% confidence interval from 0.6 to 0.96; other toy: ICC- 0.90 with 95% confidence interval from 0.72 to 0.97). The relative time to aspects of the events (goal toy, non-goal toy, and experimenter) were calculated by each aspect of the event divided by the total duration of attention.

Table 1

Examples of prototypic EMQ items.

Gross Motor Scale
When placed into a sitting position on the floor, your child is able to…
a) use hands and legs to scoot forward on his/her bottom?
b) maintain a stable sitting position while turning head and torso to look around?
Fine Motor Scale
When sitting on your lap or in a high chair while playing with toys, your child is able to…
a) successfully hold on to a small object such as a ring or stick?
b) purposefully bang toys on the table or tray?
Visual Reception Scale (Perception-Action Scale)
When your child is sitting on the floor on his/her own without support, your child will...
a) pull an object to reveal another object that was hidden underneath?
b) find a hidden object when given multiple choices to search?

Preliminary analyses

Preliminary analyses were conducted to evaluate the relation between all measures of interest (goal imitation, planful scores, and EMQ scores), age, and sex. Results indicated that neither infants' goal responses (during the goal imitation task) nor planful scores (Pre- and Post-training) were related to age (all p's > .3) or sex (all p's > .1). EMQ scores did not differ as a function of sex (all p's > .5), though scores were related to age (GM: $r = 0.4$, $p < .001$; FM: $r = 0.25$, $p < .05$; VR: $r = 0.23$, $p < .05$). However, since we see no differences between age (p

> .815) nor EMQ scores (all *p's* > .3) between conditions, we did not include age and sex as covariates in further analyses.

Goal imitation. Preliminary analyses indicated that infants' responses did not vary across trials (*F*(5,57) = .99, *p* = .42) thus average goal imitation across all six test trials was used in all analyses. There were no condition differences in the number of mistrials (*p* > .831) or no choice trials (all *p's* > .599).

Learning during cane training task. The number of training trials infants received did not differ between conditions (training-first condition: *M* = 2.2; range: 0 - 7 trials; imitation-first condition: *M* = 2.0; range: 0 - 7 trials). On average, the training session lasted 3 minutes and 32 seconds (range: 30 seconds to 6 minutes and 40 seconds). The level of experimenter's assistance did not differ between condition (all *p's* > .2). We next tested whether infants learned over the course of the cane training session by comparing infants' planful scores at pre-training to post-training. Results indicated that infants improved from pre-training to post-training in their ability to retrieve the toy using the cane in the training-first condition but not in imitation-first condition (training-first condition: pre-training (*M* = .48, *SD* = .35), post-training (*M* = .65, *SD* = .36); *t*(38) = -3.18, *p* = *.003*; imitation-first condition: pre-training (*M* = .51, *SD* = .39), post-training (*M* = .52, *SD* = .42); *t*(34) = .58, *p* = .562). This unexpected result demonstrates that the effect of training was greater for those in the training-first condition, and we checked whether it could be due to differences in experimenters' assistance.

A multivariate regression model with condition and total number of assistance in predicting planful score at post-test(R^2 = .18, *F*(7, 65) = 3.24, *p* = .005) revealed a main effect of assistance (ß = -0.03, SE = 0.01, *p* > .001), suggesting that the less amount of experimenter's assistance was associated with infants' post-test planful score, and this was not different between condition. Thus, the unexpected result that the effect of training was greater for those in the training-first condition was not due to differences in experimenter's assistance. It could be that infants got tired faster after the imitation paradigm. Importantly, the lack of evidence of learning in the imitation-first condition did not create a problem because the aim of our study was to directly test the effect of receiving training prior to the imitation task versus not.

EMQ. For our main analysis, we took a subset of the visual receptive scale (VR) as an indicator of infants' means-end problem solving skills. These were the items that particularly assessed individual variation in infants' means-end motor skills related to the cane training task and goal imitation task (referred to as 'EMQ-Means End score' from now on; #7~13 within the VR sub-scale; e.g., pull on a string or cloth to obtain a connected object). The mean of EMQ-Means End score did not differ between conditions ($t(70) = .04$, $p > .965$; Training-first: M = 11.03, SD = 2.25; Imitation-first: M = 10.9, SD = 2.96). See Table 2 for a summary of raw EMQ scores and

Table 3 on for the details on the selected items for the EMQ-Means End score within the visual receptive scale.

Table 2

Summary of EMQ raw sub-scales scores.

Condition	**Visual-reception (VR)**	**Gross Motor (GM)**	**Fine Motor (FM)**
	Mean (*SD*)	**Mean (*SD*)**	**Mean (*SD*)**
Training-first	2.84 (10.27)	-11.81 (14.07)	-12.16 (12.58)

Imitation-first	1.11 (12.25)	-15.27 (15.27)	-12.67 (12.64)

Table 3

Selected items for the EMQ-Means End score.

Selected items(#7-13) for the EMQ-Means End scores within the VR scale
While sitting on you lap or fully supported in a high chair or car seat, you have noticed your child…
7) shift eye gaze back and forth between your face and an object?
8) focus on a far-away object (e.g., toy across the room?)
9) orient to noises and visually search for the cause of the noise?
10) extend his/her arms towards an object that is close by?
11) pull on a string or cloth to obtain a connected object?
When your child is sitting on the floor on his/her own without support, your child will…
12) pull an object to reveal another object that was hidden underneath?
13) find a hidden object when given multiple choices to search?

Results

Focal analyses: Interplay between motor development and training on goal imitation

Our main goal was to explore the interplay between infants’ action learning and motor ability on action understanding. We conducted a multiple regression analysis with condition (training-first, imitation-first) and EMQ-Means End scores (individual variation in infants’ means-end motor skills) as factors in predicting action understanding (proportion of goal imitation).

The model reached significance (R^2 = 0.16, *F*(3, 72) = 4.56, *p* = .005), indicating a significant main effect of condition (ß = -0.54, SE = 0.17, *p* = .002) and a significant interaction of condition and EMQ-Means End scores (ß =0.04, SE = 0.15, *p* < .001). A closer look at the main effect of condition revealed that infants in the training-first (*M* = .63, *SD* = .18) condition chose the goal significantly more often than infants in imitation-first (*M* = .52, *SD* = .16) condition (mean difference = .11; *t*(78) = 2.92, *p* < .001; Figure 3). Furthermore, infants in the training-first condition imitated the goal more often than would be expected by chance (*t*(39) = 4.56, *p* < .001). This was not found in the imitation-first condition (*t*(39) = .61, *p* = .545).

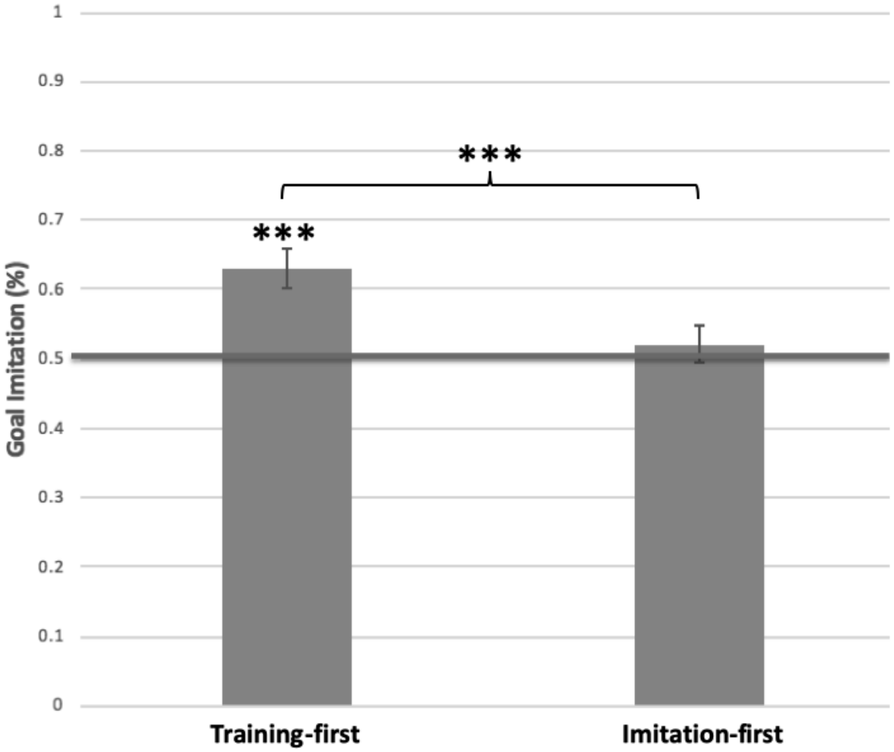

Figure 3. Proportion of infants' goal imitation between conditions. Horizontal line indicates the change level of 50%. Error bars indicate ± 1 standard error. ***p<.001.

Follow-up analyses were performed separated by condition to determine where the interaction effect originated. In the training-first condition, there was no evidence of a relation between EMQ-Means End scores and goal imitation (*r* = -0.26, *p* = .121). In the imitation-first condition, EMQ-Means End scores were significantly correlated with goal imitation (*r* = .36, *p* = .026). More specifically, infants with better means-end skills were more likely to generate goal responses to the experimenter's cane-use action. Among infants who came into the lab with lower EMQ-Means End scores, those in the training-first condition exhibited higher goal imitation (see Figure 4) than those in the imitation-first condition. This suggests that motor skills did not synergistically boost the effect of training on infants' action understanding. Rather, training seemed to benefit infants who had lower means-end skills, showing a compensatory relation between training and infants' baseline means-end skills.

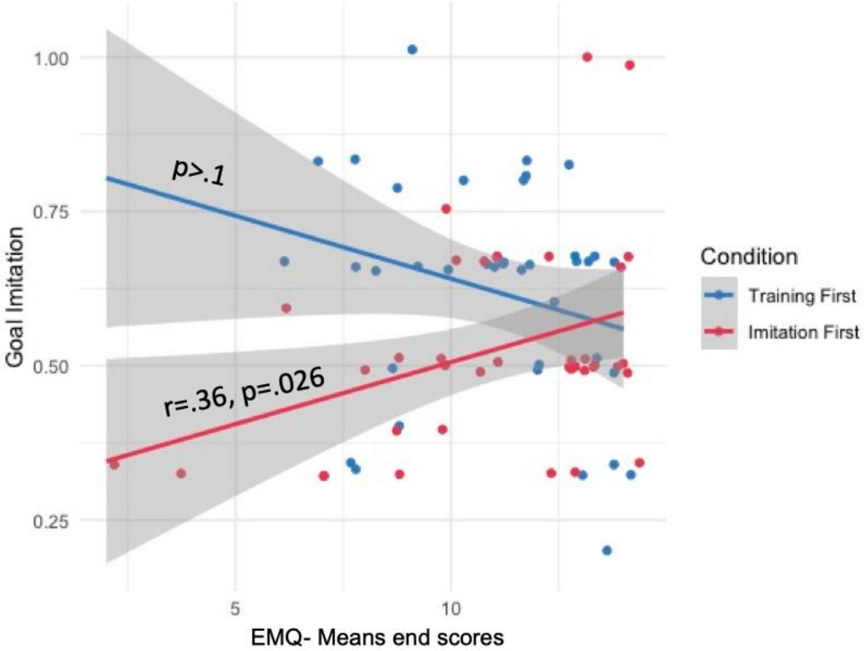

Figure 4. Scatterplot of infants' goal imitation and EMQ-Means End scores separated by condition.

We evaluated how granular the association between motor development and action understanding was. That is, we wanted to explore whether infants' means-end skills that they brought into the lab were a specific predictor of understanding of others' means-end action (goal imitation), or whether motor maturity more generally predicted understanding of others' means-end action. We conducted the same model as the focal analysis with the raw scores of GM, FM, and VR scores respectively, resulting in three independent models. We found no evidence of a relation between infants' action understanding, training, and gross motor (all *p's* > .1) and fine motor skills (all *p's* > .2). Interestingly, when using the sum of visual receptive scales, the model reached significance (R^2 = 0.13, $F(3, 71) = 3.48$, $p = .02$), and we found a significant main effect of condition (ß =-0.12, SE=0.05, $p < .001$), though a marginal interaction of condition and means-end score (ß =0.01, SE=0.01, $p = .078$). When we followed up with the marginal interaction, the correlation between VR scores and goal imitation failed to reach significance in both training-first and imitation-first conditions (all *p's* >.2). Thus, with raw VR scores, it was difficult to conclude where the interaction originated. These analyses provide supportive evidence that particularly means-end skills, rather than general metrics of motor maturity, was a specific predictor of infants' means-end understanding.

Replication of prior findings

In conducting this focal analysis, we replicated two findings from the prior literature. We replicated the finding that training alters infants' understanding of novel goal-directed actions (Sommerville et al., 2005, 2008; Gerson et. al., 2015) by demonstrating that infants who experienced cane training prior to the imitation paradigm subsequently imitated the goal of the experimenter's tool use actions. Moreover, we replicated that infants' level of motor skill with an action is associated with recognizing the action as goal-directed (Kanakogi & Itakura, 2011; Cannon et al., 2012; Melzer et al., 2012). When no prior experience was provided beforehand, infants depended on the means-end motor skills that they have accrued through development (imitation-first condition).

Next, we evaluated whether we replicated the prior findings of a relation between infants' planful means-ends actions during training and infants' ability to recognize others' action as goal-directed (Sommerville et. al., 2008; Gerson et. al., 2015). In doing so, we also explored whether variations in motor skills affected infants' learning, and thereby, affected changes in infants' action understanding. To answer these questions, we conducted an analysis with the training-first group since these infants demonstrated robust evidence of learning via training (see preliminary analyses). First, Pearson correlations was calculated with post-training planful scores and the EMQ-Means End scores. The same analysis was conducted with post-training planful scores and the three raw scores of the EMQ (GM, FM, and VR) in order to evaluate whether domains other than means-end skills related to infants' action learning. Results indicated that EMQ-Means End scores were marginally related to post-training scores ($r = .31$, $p = .062$). This relation was not found with any of the raw EMQ scores (all *p's* > .2). Thus, there was preliminary evidence that infants' own means-end skills were specifically related to the extent to which infants learned to produce a new means-end action during training, which is not accounted by global enhancement in motor development. Although marginal effects should be interpreted with caution, this suggests that EMQ-Means End scores was a potentially valuable indicator of how much infants will learn from training.

Second, we conducted a multivariate regression with post-training scores and EMQ-Means End scores as independent variables and proportion of goal imitation as a dependent variable within the training-first condition. Results revealed no evidence of an effect of planful scores during post-training ($p = .204$), effect of EMQ-Means End scores ($p = .975$), nor interaction ($p = .261$) on goal imitation. There was no evidence that the amount of planful strategies that infants produced during the training task nor infants' own means-end skills accounted for infants' subsequent goal imitation in the training-first condition. Thus, we did not replicate the pattern that was found in prior studies.

Attention during goal imitation

Follow-up analyses examined whether attentional differences during the imitation session could explain the condition differences on training. There were no condition differences in the proportion of duration of attention the goal, experimenter, or the non-goal toy during goal imitation paradigm (all *p's* > .3; Figure 5); indicating that on average infants in both conditions attended to the scene similarly. Therefore, the training effect on goal imitation was not due to changes in low-level attentional patterns to others' means-end action.

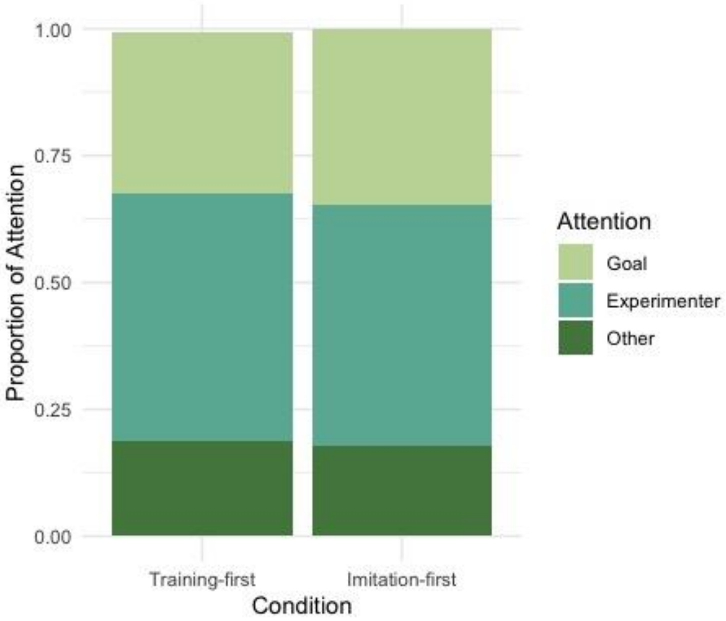

Figure 5**.** Proportion of visual attention allocation during the goal imitation paradigm.

Discussion

To identify how action training and an infant's starting state of motor development interact to shape action understanding, we conducted a cane training session, gained a metric of infants' means-end skills using the EMQ, and assessed action understanding using a goal imitation paradigm. This study provides evidence that action understanding is shaped both by training and related to infant's starting state means-end capacity. In particular, training improved action understanding, particularly for those infants who started out with lower means-end skills.

Results further indicated that infants who did not receive any training experience in the lab drew on their existing means-end skills. Specifically, those who came into the lab with higher means-end abilities showed better action understanding. This pattern was specific to means-end skills—no relation was found with gross and fine motor skill.

First, we contribute to the large body of literature on unique effects of training by demonstrating that training on novel tool-use action alters on action understanding of others' tool-use action (Gerson, Mahajan, Sommerville et al., 2015; Gerson & Woodward, 2014a, 2014b; Skerry et al., 2013; Sommerville et al., 2008; Sommerville et al., 2005). The infants who received training in a cane-pulling task benefited subsequently generated selective goal responses to the experimenter's cane-use action. Moreover, we also replicate that infants' own action capacities relates to action understanding (Sommerville & Woodward, 2005; Ambrosini et al, 2013; Kanakogi & Itakura, 2011; Loucks & Sommerville, 2012). There was a positive association between means-end skills and goal imitation in those who did not receive training; such that those who came in with higher means-end abilities showed higher goal responses. Importantly, this was not predicted by other metrics of global motor development. This suggests that the relation between infants' own action experience and action understanding is action specific rather than influenced by general improvements in motor development.

The current findings go beyond prior work in demonstrating that infants' means-end skills interact with training experience in their analysis of others' actions. Our results provide evidence of a compensatory effect of training and motor skills: infants in the training first condition benefitted from the training, and those who came in with less advanced means-end skills seemed to benefit the most from training. This suggests that training presents differential opportunities that are modulated by infants' starting-state skills. For infants coming in with less advanced motor skills, training provides an opportunity to use the cane in a coordinated manner and to direct their attention to goals, which they could not yet glean on their own, that supports their understanding of others' action. However, for those coming in with advanced motor skills, training experience may be priming them on what they already know.

While previous studies have found that infants' variability in means-ends actions after training was associated with action understanding (Sommerville et. al., 2008; Gerson et. al., 2015), we did not replicate this association. Interestingly so, even though there was preliminary evidence that those who came in with better means-end skills produced more planful coordinated actions after training, this did not exert a boosting effect on their action understanding in the current study. This suggests that there could be another factor that accounted for a change in infants' action understanding, beyond information from engaging in goal-directed action. One possibility is that minor differences in our training procedure impacted our ability to detect this effect. In the current study during training, the infant was given the toy at the end of each trial regardless of whether they had successfully pulled the cane. In prior studies (Sommerville et. al., 2008; Gerson et. al., 2015), the toys were not given to the infants following a non-successful action. This procedural difference may explain why infants in the training condition who were less successful in the training condition still benefitted from training. Having multiple instances to acquire a desired toy after attempts of pulling (not dependent on the successfulness of the pull) may have led infants to understand goal of the trained action despite limited proficiency with the action itself. Research has shown that highlighting a salient action-effect (even for unfamiliar events such as mechanical claw or back-of-hand toy-touching events) supported action understanding (Adam & Elsner, 2018; Elsner & Adam, 2021; Jovanovic et al., 2007); although see Sommerville et al, 2008; Gerson et al 2015 for evidence that observational experience with action-effects is not sufficient for action encoding). Alternatively, it could be that infants interpreted the training session as a collaborative context—one in which the infant and experimenter act together to retrieve the toy (e.g.,, if the infant touched the cane and the experimenter gave the toy—as was typical during training). Henderson et al., (2013) have found that 10-month-old infants who engaged in a collaborative activity represented others' actions in terms of a collaborative goal (see Krogh-Jespersen et al., 2020 for similar results). This may be another explanation for why even the infants who engaged in training but did not necessarily succeed in producing planful actions showed changes in action understanding. Future work should replicate this paradigm without giving the infant the toy during training to determine whether this impacts replication of our effects.

Future Directions

The current findings replicate prior work that both infants' motor skills accrued over developmental time scale and short-term training impacts infants' sensitivity to the goal structure of others' actions. Although beyond the scope of this current study, it is an open question regarding the neurocognitive representations that support infants' analysis of goals. Neuroscientific methods have the advantage over behavioral methods providing information about the processes that underlie perception of actions (Stapel, 2020). Studies investigating the neural correlates during action perception that are associated with motor experience and the correlates associated with action training may shed light on this question.

For instance, many studies provide evidence in support of the notion that variation in infants' motor skills is associated with sensorimotor activity during observation of action that infants have prolonged experience with (Cannon et al., 2016; Filippi et al., 2016; Upshaw et al., 2016; van Elk et al., 2008). Furthermore, recent infant EEG studies showed that that visual and motor areas were more connected than other control circuits during observation of familiar grasping action in infants (Chung et al., 2022; Debnath et al., 2019), but not during observation of an unfamiliar cane-use action (Chung et al., 2022). In a follow-up study, it was found that infants more competent in grasping objects showed higher levels of motor-visual coupling during action anticipation of both grasping and cane-use action (Colomer et al., under review). These findings suggest that the neural activity underlying processing and encoding of others' actions that infants have prolonged experience with may involve an integration of functional connectivity between motor and visual processes, and that this connectivity scales with infants' motor development. It is an open question whether training of novel action subsequently induces changes in functional connectivity between motor and visual processes or is governed via a different set of networks.

Moreover, while our work indicates that there were no significant differences in overt attention, prior findings indicate that as infants gain proficiency in producing actions themselves, they shift their attention to the goal rather than focusing on the means (Willatts, 1999). The same shift in attention occurs in infants' perception of others' means-end actions (Gerson & Woodward, 2013, 2014a). It is possible that training gives rise to differential attention processing that highlights the relation between the agent and the goal, which cannot be accounted by overt attention alone. Neuroscientific methods (e.g.,, EEG, fNIRS, or fMRI) may provide more sensitive measures of attentional processing (Begus & Bonawitz, 2020; Ellis et al., 2021; Filippi et al., 2020; Stapel, 2020) and may inform whether active training generates changes in attentional processes which in turn modulates action understanding.

Future work should also consider extensions of this work to clinical populations where motor experience may be altered early in life (e.g., cerebral palsy, autism). Research comparing typical and atypical development in the relation between motor and social-cognitive abilities is also needed, as it may shed light on how these domains influence each other, and how neural patterns and connectivity play a role in observed behaviors. If active motor experience engenders functional changes in processing and understanding others' actions, this could pave new insights for interventions that target motor training in clinical populations.

Conclusion

Together this work not only replicates prior findings on the effects of both infants' own motor skills and direct in-lab intervention experience on infants' action understanding, but also suggests that the effects of training may differ depending on infants' motor skills. More specifically, findings highlight a complementary role of infants' in-lab experience and their own motor skills, particularly showing that the effect of training was most beneficial for infants coming in with less means-end skills. This work also demonstrates the value of measuring infant motor development in addition to assessing in-lab trained task performance and provides several avenues for future research examining the relation between active experience and action understanding.

Chapter 3: Neural correlates of familiar and unfamiliar action in infancy[1]

There is a close connection between action production and action perception that emerges early in development. Behavioral studies have demonstrated that as infants gain experience with new actions, there are also changes in their anticipation and understanding of other's actions (Ambrosini et al., 2013; Cannon et al., 2012; Filippi & Woodward, 2016; Kanakogi & Itakura, 2011; Krogh-Jespersen et al., 2020; Krogh-Jespersen & Woodward, 2018; Sommerville et al., 2008; Sommerville & Woodward, 2005). Neural mirroring, the recruitment of similar neural activity during the production and perception of action, has been suggested as a mechanism that links action experience and action perception (Gallese et al., 1996; Hunnius & Bekkering, 2014; Marshall & Meltzoff, 2014; Pineda, 2005; Woodward & Gerson, 2014). Research into this possibility has made use of the EEG mu rhythm, which is oscillations in the alpha band (adults 8-13Hz, infants 6-9Hz) recorded over the sensorimotor cortex, as a potential index of neural mirroring (Cochin et al., 1999; Fox et al., 2016; Lepage & Theoret, 2006; Muthukumaraswamy & Johnson, 2004). The mu rhythm is found to be suppressed in power (also called mu suppression) during both action execution and action observation, and cortical source localization studies provide supportive evidence that the mu rhythm is associated with activity in the sensorimotor cortex in adults (Hari et al., 1997; Toro et al., 1994). However, deploying measures of the mu rhythm in infant EEG studies has led to seemingly contradictory findings on the unique role of one's motor expertise on the level of mu suppression. That is, research with infants has demonstrated an association between infants' motor experience and the level of mu

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[1] This work is a published paper. See Chung, Meyer, Debnath, Fox, & Woodward (2022). Neural correlates of familiar and unfamiliar action in infancy. Journal of Experimental Child Psychology, 220C. https://doi.org/10.1016/j.jecp.2022.105415.

power suppression during action observation. Yet, other studies have revealed similar patterns in mu suppression not only for motorically familiar actions such as grasping actions, but also for actions that are completely outside of infants' motor repertoire such as tool-use actions. This calls into question whether the mu rhythm is modulated by the motoric familiarity of an action or not. In the current study, we aimed to investigate the neural underpinnings of observing familiar and novel actions within the same sample of infants and to identify the neural processes that are uniquely associated with observing motorically familiar actions.

A growing body of studies indicates that mu suppression is associated with and affected by infants' experience producing actions (Cannon et al., 2016; Gerson, Bekkering, & Hunnius, 2015; Paulus et al., 2012; van Elk et al., 2008; Yoo et al., 2016). For instance, Cannon et al. (2016) found that 9-month-old infants who were more proficient graspers showed stronger mu suppression when observing others' grasping actions. In an experimental intervention, Gerson, Bekkering et al., (2015) reported that active experience with a novel action, but not passive observational experience, engendered changes in mu power when 10-month-old infants subsequently heard the sound associated with that action. Moreover, Filippi et al. (2016) found that 7-month-old infants' likelihood of imitating the goals of others' action was correlated with variations in mu suppression during their own reaching and during observation of others' reaching actions. Together, these findings highlight the potential role of motor experience in modulating mu suppression during action observation.

However, another body of studies with infants at the same age (9 months) and analyzing neural activity in the same frequency range (6-9Hz) recorded over the sensorimotor cortex (central sites), found mu suppression when infants observe actions and events that they have not had active experience with (de Klerk et al., 2016; Southgate & Begus, 2013; Virji-Babul et al., 2012). In a between-subjects design, Southgate and Begus (2013) reported that 9-month-old infants showed mu suppression during anticipation of grasping as well as novel tool-use actions and even while viewing the movements of self-propelled objects. Similar findings were reported by Virji-Babul et al., (2012), in 4-to-11 month-old infants in a within-subjects design. These findings challenge the assumption that mu suppression is a unique neural correlate of the motor familiarity of observed actions.

Thus, while behavioral evidence illustrates a connection between production and perception in infants, the neural processes associated with this link are in question. Mu suppression has been a valuable candidate, extensively used as an index of neural processes associated with action production and perception. However, mu suppression as an isolated neural signal, may not unambiguously reflect motor familiarity of the observed action. One reason could be related to the potential influence of occipital (visual) alpha, which occurs in response to the presentation of a visual stimulus (Fox et al., 2016; Hobson & Bishop, 2016). Reliable separation of mu from occipital alpha is critical for adequate interpretation of visual and motor effects on action perception (Hobson & Bishop, 2016). Yet, it remains a methodological challenge to parse apart mu from occipital alpha (Hobson & Bishop, 2016). To resolve this issue, reporting alpha activity recorded over multiple brain regions (at least including activity over visual areas) has been recommended (Bowman et al., 2017; Cuevas et al., 2014; Fox et al., 2016; Perry & Bentin, 2010). This is a helpful starting point, though reporting multi-region activity is not sufficient to parse apart whether mu suppression is reliably discernable from visual alpha. Others explore the relation between central and occipital alpha (Tangwiriyasakul et al., 2013) or encourage researchers to use methodological controls (e.g., using baselines that control for attentional demands) as an additional approach to distinguish action-specific processes from visual processes (Fox et al., 2016). Infant researchers have reported alpha activity recorded over multiple regions (Cannon, et al., 2016; de Klerk et al., 2016; Filippi et al., 2016; Southgate & Begus, 2013; Yoo et al., 2015); however, it is rarely the case that additional approaches are endorsed to ensure that activity recorded over central and occipital sites are reliably independent (but see Filippi et al., 2016; de Klerk et al., 2016).

In addition, it is not only important to reliably distinguish between motor and visual processes, but also understanding how motor and visual processes are coordinated together during action perception is crucial, as visual processes may be inherent during action processing (Fox et al., 2016). Using mu suppression in isolation as a neural marker of action processing may overlook potentially important network connectivity. Understanding the dynamic inter-regional communications among networks in the brain can provide insights to the basis of infants' behavioral repertoire (Gao et al., 2017). However, the functional relation of motor and visual processes on action perception in infancy remains unclear. Debnath and colleagues (2019) demonstrated enhanced connectivity between EEG signal recorded at central and occipital scalp locations during infants' observation of a familiar grasping action. It is an open question whether this functional connectivity is also evident during the observation of novel actions. Exploring functional connectivity between mu and occipital alpha, rather than mu as an isolated neural marker, could be the key in reconciling the discrepancy across findings (Bowman et al., 2017). That is, functionally related neural systems may better index the underlying mechanism that uniquely governs perception of motorically familiar action. It could be that active experience in an action builds on and strengthens communication between network processes (Johnson, 2000), which may not be evident during observation of novel action.

Current Study

In the current study, we aimed to better understand the neural correlates of perceiving motorically familiar and unfamiliar actions, beyond changes in mu power. For this purpose, we collected EEG while 9-and 12-month-old infants viewed a familiar action (grasping) and a novel action (tool use) in a within-subjects design. Infants begin to produce reaches by 5 months and become highly skilled by 9 months (Bertenthal & Clifton, 1998). The ability to engage in tool-use actions becomes robust during the second year when infants become able to spontaneously engage with novel tools (Keen, 2011). Thus at both 9 and 12 months of age, reaching is a motorically familiar action, while engagement with a novel tool is unfamiliar. Therefore, our main analyses were conducted across these two ages. We drew on several recent methodological approaches to more clearly capture distinct EEG mu measured at the central electrodes from EEG alpha measured at the occipital electrodes (see Bowman et al., 2017; Fox et al., 2016; Hobson & Bishop, 2016). Importantly, we assessed mu suppression relative to a baseline that was visually similar to the action videos. This was done to reduce the extent to which mu activity might be confounded with occipital alpha response to visual novelty (Nystrom et al., 2011). Then, offering a tighter comparison with a within-participant design, we compared whether suppression of mu / occipital alpha is modulated by motor familiarity. We also assessed infants' skills in grasping and capacity to engage in the novel tool use action so that we could evaluate correlations between motor competence and mu / occipital alpha suppression during action observation. Lastly, we explored functional connectivity between central and occipital neural activity during perception of familiar and unfamiliar action to evaluate coordination of motor and visual processes.

Method

Participants

Forty-nine full-term 9-month-olds (21 infants; *M* = 9 months 21 days, *SD*= 10; range: 9;0 – 10;15; 13 males) and 12-month-old infants (28 infants; *M* = 12 months 21 days, *SD*= 17.8; range: 11;15 – 13;15; 11 males) participated in this study[2]. Participants were recruited in an urban Midwest region in the United States. Infants represented a diverse racial background (52% European, 15% Hispanic, 16% African-American, 5% Asian, and 12% mixed-racial) and were from relatively highly educated families (91% caregivers reported receiving bachelor's or higher degrees). Thirteen infants were excluded from analyses due to being distressed shortly after application of the EEG electrode net (*N* = 2), unusable EEG data prior to data analysis (*N* = 6), and for not having at least three artifact-free EEG trials per condition after all EEG processing steps (*N* = 5). The final dataset consists of 36 infants (17 9-month-olds, 19 12-month-olds). This study was approved by the campus Institutional Review Board at the University of Chicago.

Procedure

Upon arrival in the laboratory, infants' caregivers were first informed about the testing procedure by Experimenter 1 (E1) and filled out a written consent form. During this process, Experimenter 2 (E2) measured the infants' head circumference and prepared the best-fit net in the EEG testing room. Then, the infants and caregivers were accompanied to the EEG testing room. The infants sat in an infant-friendly high-chair or on the caregiver's lap and were fitted with a 128-sensor HydroCel Geodesic Sensor Net (Electrical Geodesics [EGI], Eugene, OR, USA). Impedances were kept below 100 kΩ where possible. The EEG was recorded at 1000Hz (Net Station software, Version 4.5.7; EGI) and Cz electrode was used as an online reference.

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[2] We based the sample size on the studies that have utilized similar experimental designs (Cannon et al., 2016 analyzed 21 participants, and Southgate & Begus, 2013 analyzed 33 participants with 11 in each condition).

Once infants wore the EEG net, E1 took pictures and a video to document individual net placement, and these pictures were sent to caregivers after their visit. Infants faced a computer screen on a table at approximately 70cm distance on which stimuli videos were presented via E-prime 2.0 (Schneider et al., 2012). When videos were presented via E-prime, triggers indicating the onset and end of videos were simultaneously sent to the EEG recording software Net Station. See Figure 6 for room set up. E1 sat behind a screen throughout the video presentation hiding from the infants' view and monitored the infant during the experimental procedure. Parents were asked to avoid interacting with their infants as much as possible, except when the infants were in distress. E2 was in the next room monitoring the recordings of EEG and videos of the session. Videos of the sessions were recorded from two different camera views. One camera was placed in front of the infant to capture a close-up view of the infant, and another camera was placed behind the infant to record the computer monitor presenting the video stimulus during observation. These recordings in the experimental session were video-coded offline so that it can be time-locked to the EEG recording. The EEG session consisted of an action observation and an action execution phase.

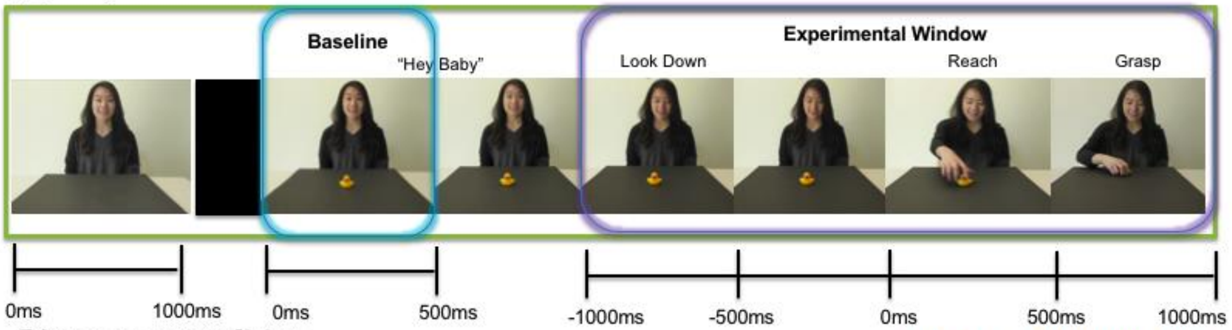
Action observation

During the action observation phase, two types of actions were presented: a familiar action (i.e. grasping a toy to bring it closer) and a novel tool-use action (i.e. using a cane to bring a toy closer; see Figure 6). Both action observation conditions were presented with 4000-4500ms long videos. To make the transition of the videos look more natural, we put a dissolve filter in the video editing software (Adobe Premiere Pro) that introduced a gradation of brightness for 500ms (dark to bright) at the start and end of each video for both conditions. Each video began with the experimenter sitting still and facing the center of the screen and saying “Hey, Baby!” or

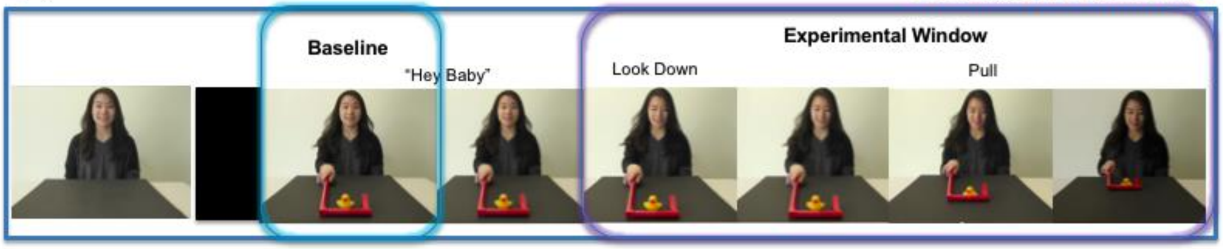
Observation phase

A. Schematic time-line of Observation trial

(a)Grasp Condition



(b)Cane-use Condition



B. Experimental set up during Observation phase

Figure 6. A. Schematic time-line of an observation trial. (a) grasp condition; (b) cane-use condition. B. Experimental room set-up of the observation phase.

"Hi there!", presented in a pseudo-random order with no more than 3 repetitions in order. The toy for the grasp condition and the toy and cane for the cane-use condition were present in the scene from the start of the videos. In the grasp condition, the experimenter looked down at the toy, grasped it and brought the toy closer. In the cane-use condition, the experimenter looked down at the toy and then pulled the cane to bring the toy closer. Before each action observation video, a still image of the experimenter sitting in front of an empty table was presented for 1000ms. Trials were presented in a semi-randomized order of grasping and cane-use action videos, such that infants were presented with a maximum of 20 trials per set, up to 40 trials in total. The order of the conditions was pseudorandomized so that infants did not observe more than three trials of the same type of action in a row. Ten unique toys were used for the two types of action conditions such that all toys appeared twice for each trial type. Infants completed a mean of 33.4 trials (*SD*= 7.1, Range: 16-40), (9m: 32.7 trials, *SD*= 6.7; 12m: 34.1 trials, *SD*= 7.5). After 40 trials or once the infants lost interest, the observation phase ended and infants participated the action execution phase.

Action execution

We collected infants' execution of grasping and cane use action to A) confirm whether the neural response during action observation indeed reflects the neural response during the execution of action and B) to examine whether individual variance in motor competence affects infants' processing of action. During the action execution phase, infants sat in front of a table (see Figure 7). Across the table, E1 positioned herself behind curtains and E2 sat next to the caregiver, outside of the infants' visual scene. The execution phase began with two warm-up trials, where E1 (the same person infants observed in the videos during the action observation phase) opened the curtains, saying "Hi, baby. Are we ready?" and closed the curtains. These warm-up trials were to ensure that the infants were attending and ready to proceed with the session. Every infant received 5 grasp trials and 5 cane-use trials in a fixed order, first grasp followed by cane-use trials. We utilized a fixed order of grasp and cane-use execution trials to be sure to get at least infants' execution of grasps. The execution grasp condition began with E1 opening the curtains, not moving for 1000ms (baseline), and then closing the curtains. Then, E1 opened the curtain again and said “Hey baby, look!” showing the toy to the infant. E1 placed the toy in front of the infant, making sure that the toy was placed within the infants’ reach. The execution grasp condition ended when the infant grasped the toy. If the infant did not attempt to grasp the toy within 10 seconds, E1 pointed or tapped the toy so that the infant attended to the toy. Once infants reached for and grasped the toy, or after 3 repetitions of the prompt, E1 retracted the toy and closed the doors. Every trial ended with E1 providing positive encouragement (i.e. “Good job” or “All right”). Infants completed a mean of 4.74 trials (*SD*= 0.94, Range: 1-5), (9m: 4.8 trials, *SD*= 0.91; 12m: 4.68 trials, *SD*= 0.98).

The execution cane-use condition also began with the same baseline prompt as the grasp execution condition. Then, E1 opened the curtain and said “Look” showing the toy to the infant, and placed the toy at the end of the table, beyond infants’ reach. E2 then placed the cane (length of cane: 48cm, width of crook: 13.5cm) around the toy. If the infant did not attempt to grasp the toy within 10 seconds, E1 pointed or tapped the toy so that the infant attended to the toy. E1 did not point to the cane nor provided any assistance. The cane-use trial ended after infants either successfully retrieved the toy by pulling the cane or 60 seconds elapsed. Every trial ended with E1 providing positive encouragement (i.e. “Good job” or “All right”). Infants completed a mean of 4.07 trials (*SD*= 1.2, Range:1-5), (9m: 4.14 trials, *SD*= 1.2; 12m: 4 trials, *SD*= 1.3).

At the end of the testing session, caregivers were debriefed about the goal of the study and families received a small gift (toy or t-shirt) and 20 US dollars as compensation.

Analysis

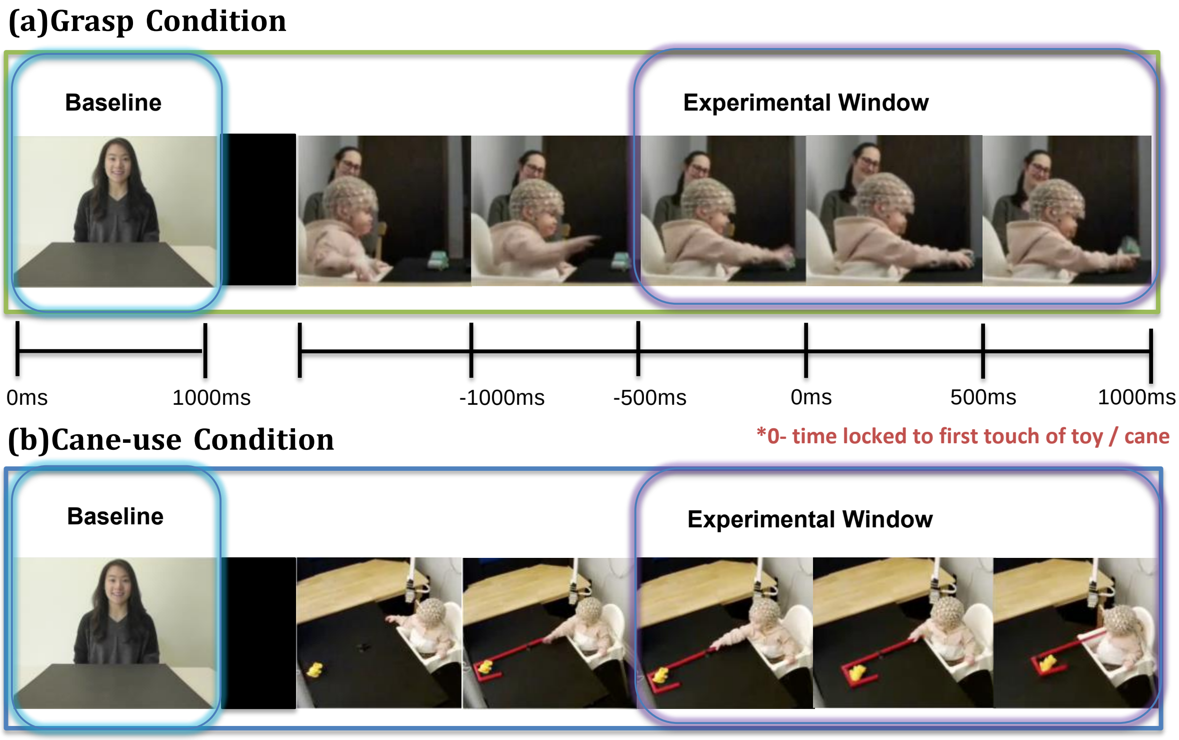
Video-coding analysis

An open-source video coding software Datavyu (Datavyu, 2014) was used for coding videos offline. It was important that we utilize a baseline that closely matches the visual scenes of the action observation experimental window of each condition in order to reduce the influence of visual differences. The baseline for action observation phase was coded as the first frame after change of brightness (from dark to bright), and when E1 was visible with objects (toy and cane) present, but not moving for 500ms (Figure 6). The baseline period included the experimenter sitting still and greeting the child without further movement.

The baseline did not include any arm or hand movements and this was the same across conditions. The experimental time window in the action observation phase was coded from the first frame of E1's movement onset (started to reach in grasp condition or started pulling the cane in cane-use condition). E1's onset of movement was time-locked to 0ms, and data of 1000ms before and 1000ms after this mark were taken as the experimental time window for the analyses. For execution trials, since it was impossible to match the visual scene of the baseline and experimental windows for execution trials, the baseline was coded as the first frame that the curtains were fully open, and when E1 was visible to the infant for 1000ms. The experimental time window for the grasp and cane-use condition was coded based on the first frame that the infant touched the toy and the contact led to grasping the toy / that led to pulling the cane. Infants' touch was time-locked to 0ms, and data of 500ms before and 1000ms after this mark was taken as the time window for EEG execution analyses (Figure 7). In order to capture infants' processing of others' actions in the action observation phase and not the coincidental execution of their own actions, we coded moments of infants' own grasping actions, which included grasping (e.g.,, arm of the chair, or mother's hand) or grasping movements without an object (e.g.,, making a grasping movement in the air) in the action observation phase. All action observation and baseline EEG segments that overlapped with parental interference (e.g.,, bouncing the infant), crying, infant not-looking, or infants' grasping were excluded.

Execution phase

A. Schematic time-line of Execution trial



B. Experimental set up during Execution phase

Figure 7. A. Schematic time-line of an execution trial. (a) grasp condition; (b) cane-use condition. B. Experimental room set-up of the execution phase. Left: View of infant and E1 during an execution grasp trial (E1 left to the curtain). Right: View of infant and parent during execution grasp trial.

Behavioral Analysis

Grasping latency. Based on Cannon et al. (2016) and Yoo et al. (2016), we examined infants' grasping competence during execution trials. We assessed the latency with which infants grasped the toys as a marker of their grasping competence. The amount of time was calculated from the touch that resulted in a grasp until the completion of the grasp. Grasp completion was coded as the beginning of the toy pick up or infants' fingers wrapped around the toy if there was no pick up. Only trials with touches that led to a toy grasp were included to calculate the grasp latency measure. An independent coder coded 73% of the data. A high degree of reliability was found (ICC- 0.78) with 95% confidence interval from 0.57 to 0.9 for grasping latency. Infants had to provide at least two codable trials to be included in the analysis.

Cane pulling latency. In order to use a measure comparable to the grasp latency measure, we defined infants' cane-use competence during execution trials as latency to pull the cane. The average amount of time was calculated from the pull that resulted with the toy within infants' reach. A successful pull in the cane-use condition was defined as 1) looked at the toy 2) initiated one clear pull without removal of hand from cane and 3) maintained eye-gaze throughout the pull. An independent coder coded 70% of the data. A high degree of reliability was found (ICC- 0.95) with 95% confidence interval from 0.86 to 0.98 for cane-pulling latency. Infants had to provide at least two codable trials to be included in the analysis.

EEG data analysis

The EEG data preprocessing was performed by the Maryland analysis of developmental EEG (MADE) pipeline (Debnath et al., 2020). Recordings were converted and exported to a Matlab-compatible format (The Mathworks, Natick, MA) using Net Station software. EEG data (pre)processing was conducted using EEGLAB (v14.0.0) toolbox (Delorme & Makeig, 2004).

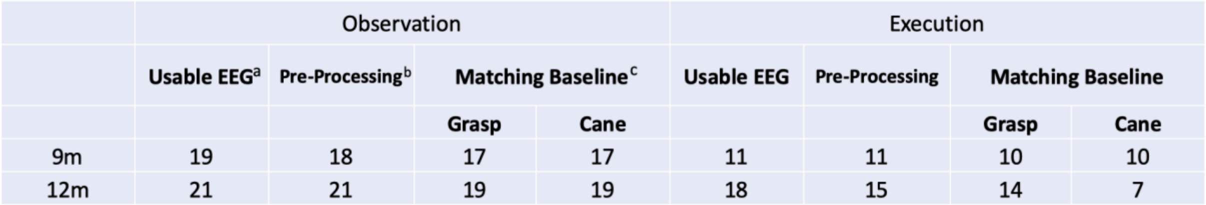
First, video-coded markers were imported onto the EEG dataset and data were downsampled to 500Hz. The subsequent processing steps are identical to those applied in Debnath et al., (2019) and Meyer et al., (2022). The outer ring of electrodes on the 128-channel net have often poor connections in pediatric data (see Debnath et al., 2020 for more detail) and were therefore removed a priori (E17, E38, E43, E44, E48, E49, E113, E114, E119, E120, E121, E125, E126, E127, E128, E56, E63, E68, E73, E81, E88, E94, E99, E107) with 104 channels remaining for analysis. The continuous data were filtered at 0.3 Hz highpass and 50 Hz lowpass using FIR filter provided within the FIRfilt plugin of EEGLAB (Widmann et al., 2015). Then, using FASTER (Nolan et al., 2010) plugin of EEGLAB bad channels were detected and removed. In order to filter out non-neural artifacts including blinks, saccades, or EMG, we applied a hybrid approach of using a copied dataset, applying a 1 Hz high-pass filter and segmenting data into 1-second epochs, removing excessive EMG, and then running ICA on the copied dataset as suggested by Debnath et al. (2020). Then ICA weights were applied to the original dataset. A semi-automatic process using ADJUST EEGLAB plugin (Mognon et al., 2011) identified ICA components and the components were also manually reviewed. Next, time-windows of interest (baseline and observation trial segments) that were contaminated by the infant grasping, not looking, crying or the parent interfering were excluded from further analysis based on video coding. The remaining data were segmented into baseline segments and experimental segments. A voltage threshold rejection (±150 μV) was applied on six frontal channels (E1, E8, E14, E21, E25, E34) to identify and remove additional eye artifacts. For all other channels, we interpolated data for artifacted channels in each epoch. Epochs with more than 10% of interpolated channels were rejected. After preprocessing, 3 participants were excluded in the observation condition from further time-frequency and connectivity analysis because they had an insufficient number of artifact free trials (<3 in each condition). For the execution condition, 12 participants for grasp and 19 participants in the cane-use condition were excluded from further time-frequency and connectivity analysis because they had an insufficient number of artifact free trials (<3 in each condition, following minimum trial requirement of infant mu rhythm studies, Marshall et al., 2011; Debnath et al., 2019). (See Table 4 for a detailed breakdown of inclusion of participants for EEG analysis). For the observation session, there were a mean of 8.3 artifact free grasp trials (range 3–17) and a mean of 7.5 artifact free cane-use trials (range 3–19) in the final 9-month-old dataset, and a mean of 9 artifact free grasp trials (range 4–19) and a mean of 10.4 artifact free cane-use trials (range 4–19) in the 12-month-old dataset. For the execution session, there were a mean of 4.3 artifact free grasp trials (range 3–5) and a mean of 3.7 artifact free cane-use trials (range 3–5) in the 9-month-old dataset, and a mean of 3.1 artifact free trials (range 3–5) in the grasp condition and a mean of 3.3 artifact free cane-use trials (range 3–5) in the 12-month-old dataset. Preprocessed epoch data were then converted into current source density (CSD) using the CSD toolbox (Kayser & Tenke, 2015), and event-related spectral perturbation (ERSP) was calculated on CSD transformed data to estimate the baseline-corrected spectral power (in dB) between 3- to 30Hz for all channels and trials. (The derived EEG data in BIDS format and Matlab analysis scripts are available on the Open Science Framework: https://osf.io/f9da5/).

Time-frequency analysis. Time-frequency decomposition was computed using the EEGLAB newtimef function. To assess infants' neural motor activity during action observation and execution consistent with previous research (Debnath et al., 2019; Marshall et al, 2011; Meyer et al., 2022), our analyses focused on mu power, by measuring baseline-corrected spectral power in the 6-9Hz alpha frequency band in channels overlaying sensorimotor (Central) regions (C3 = E29, E30, E35, E36, E37, E41, E42; C4 = E87, E93, E103, E104, E105, E110, E111;

Figure 8). We did not include the midline channel (Cz) because the activity in Cz is found to be associated with and modulated by leg movements in infants (van Elk et al., 2008; de Klerk et al., 2016) while C3 and C4 are found to be associated with hand and arm movements in infancy (Saby et al., 2013). Mu power during action observation was calculated for the following time windows: anticipatory (-1000ms to 0ms) time window during which E1 is still and no movement is happening, and movement (0ms to 1000ms) during which E1 starts to produce the action (grasp condition: 0 to 500ms entails E1's reach to the toy, and 500 to 1000ms entails the E1's grasp completion of bringing the toy closer to her; cane-use condition: 0 to 1000ms entails E1's cane pulling action). Mu power during action observation was calculated relative to the experimenter present with the object but without movement. Mu power during execution was calculated for infants' action onset (-500ms to 0ms and 0ms to 1000ms) relative to the experimenter present without presence of objects. In addition, power over frontal, parietal, and occipital regions was analyzed as well (see Figure 8).

Table 4

Overview of participants included.



	Observation				Execution			
	Usable EEG[a]	**Pre-Processing**[b]	**Matching Baseline**[c]		**Usable EEG**	**Pre-Processing**	**Matching Baseline**	
			Grasp	**Cane**			**Grasp**	**Cane**
9m	19	18	17	17	11	11	10	10
12m	21	21	19	19	18	15	14	7

a. Usable EEG: Number of participants with enough trials for EEG analysis

b. Pre-Processing: Number of participants with enough trials after pre-processing EEG

c. Matching Baseline: Number of participants who have enough trials after matching baseline and experimental trial so that each experimental trial is preceded by a baseline

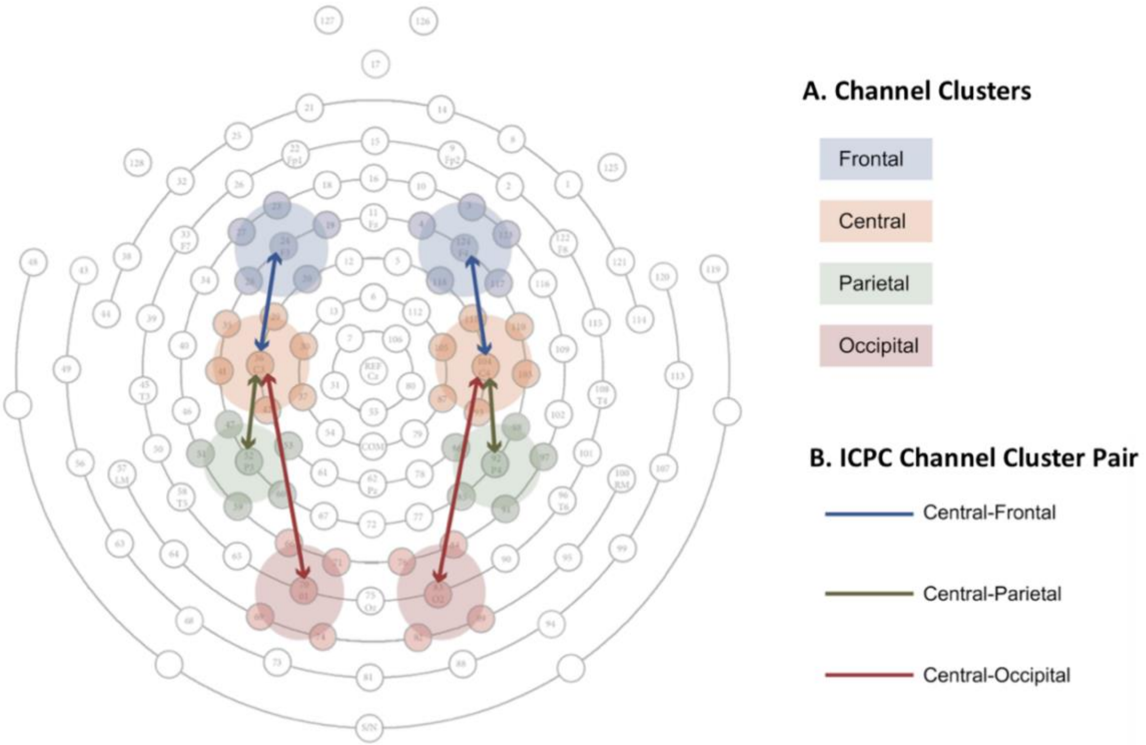


Figure 8. A. Electrode channel clusters, from top to bottom, for Frontal (Blue circle), Central (orange circle), Parietal (green circle), and Occipital (red circle) scalp locations. B. Arrows indicating ICPC channel cluster pair between regions. Blue arrow: Central-Frontal, Green arrow: Central-Parietal, Red arrow: Central-Occipital.

Statistical comparison across time and frequencies. We performed point-wise analyses of spectral power modulation in all electrodes for each time window against a null hypothesis of no change in baseline-corrected power (represented by zero) during the event of interest. We computed one sample non-parametric permutation tests with FDR correction for multiple comparisons against zero for each time point using the “std_stat” function of the EEGLAB toolbox for visualization.

Inter-channel phase coherence. We measured coherence between brain regions by calculating inter-channel phase coherence (ICPC), which estimates the consistency of phase angle difference between two clusters of channels over time and frequency (Cohen, 2014). Phase angles were first calculated from two clusters of electrodes (see below) and then subtracted.

ICPC value (range: 0 to 1) closer to 1 is interpreted as more synchrony between two channel clusters, supporting the idea that when brain regions are functionally coupled, the timing of their oscillatory processes becomes synchronized (Cohen, 2014). As in Debnath and colleagues (2019), we calculated central-based ICPC between channel clusters over central areas and the three other brain areas in both the left (C3– F3, C3– P3, C3– O1) and right (C4– F4, C4– P4, C4– O2) hemispheres (See Figure 8). We also calculated occipital-based ICPC between occipital and the three other brain regions in both hemispheres (left: O1– F3, O1– C3, O1– P3; right: O2– F4, O2– C4, O2– P4). We computed ICPC in both observation of grasping and cane-use conditions at 6–9 Hz frequency during movement time window (0ms to 500ms time-locked to movement onset).

Results

Mu suppression during action execution

To examine whether in this sample of infants the 6-9Hz range covers neural processing of actions, we first assessed neural activity during action execution. In the grasp condition, we analyzed 24 participants (9m- 10, 12m- 14) and in the cane-use condition, we analyzed 17 participants (9m- 10, 12m- 7). We collapsed over age for this analysis to increase power. Time-frequency intervals with power relative to baseline during execution in each condition are displayed in Figure 9A. All activity shown is significantly different from zero at the $p < .05$ level with FDR correction for multiple comparisons. The point-wise analysis revealed that there was significant 6-9Hz mu power suppression in the electrode clusters overlying the motor cortex (Figure 9A, Central) both when approaching the toy/cane to touch it (-500ms to 0ms) and continuing throughout the movement period (0ms to 1000ms), where 0ms is time-locked to first touch of toy/cane (also supported by topographic distribution, Figure 9B). Thus, suppression of power in the 6-9Hz frequency range captures action processing in this sample and can therefore serve as an index of neural motor activation in the observation phase.

Mu and occipital alpha during observation of action

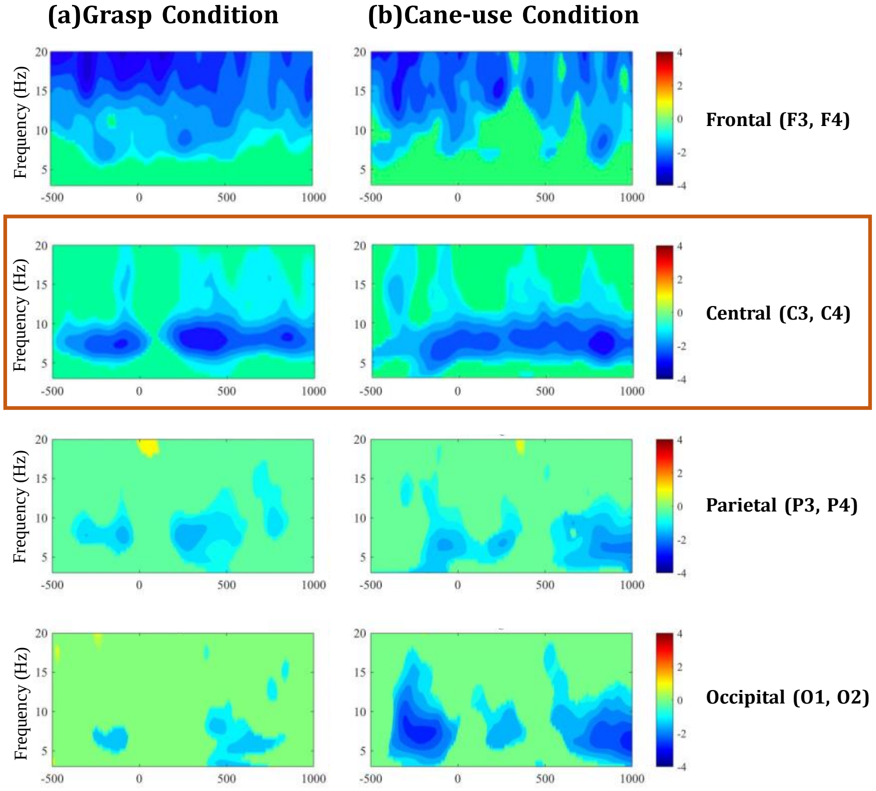
We analyzed 36 (9m- 17, 12m- 19) participants' neural activity during action observation. Figure 10 displays results of comparing alpha power in 6-9Hz frequency range relative to baseline over frontal, central, parietal, and occipital electrode clusters in each condition during the observation phase collapsed over age. All activity shown is significantly different from zero at the $p < .05$ level with FDR correction for multiple comparison.

The point-wise analysis revealed that there was significant mu suppression in the electrode clusters overlying the motor cortex (C3, C4) both prior to the start of the E1's movement (-1000ms to 0ms) and continuing through the movement period for both grasp and cane-use conditions for both age groups (0ms to 500ms) (Figure 10, Central). Significant suppression over the occipital region was evident around the onset of the E1's movement in the grasp condition (0ms to 1000ms), but in the cane-use condition, occipital alpha was significantly suppressed from around 500ms post-movement observation (Figure 10, Occipital). (Verification that mu power and occipital alpha, measured using the baseline in our current study, are reflecting independent neural activity and likely come from different sources is reported in Appendix B).

Mu/occipital alpha suppression and motoric familiarity

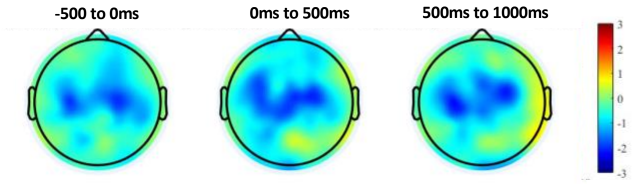
To address our main question of whether motor familiarity influences mu power and occipital alpha, we performed a 4-way mixed ANOVA with condition (grasp, cane-use) and time (anticipatory: -1000ms to 0ms; movement: 0ms to 1000ms) and hemisphere (left, right) as within-subjects variables, and age (9m, 12m) as between-subject variable for each region.

A. Time-frequency plot


(a)Grasp Condition (b)Cane-use Condition

B. Topographic maps of mu (6-9Hz) band

(a)Grasp Condition



(b)Cane-use Condition

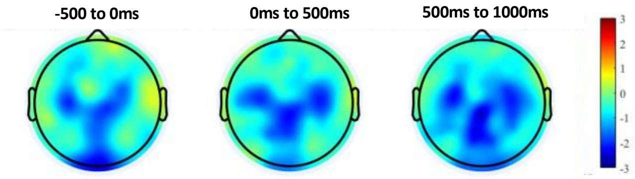


Figure 9. A. Statistically significant time-frequency plot during execution for (a) grasp condition and (b) cane-use condition of spectral power relative to baseline. The color towards blue indicate significant suppression of power. Green in images depicts non-significant ($p > .05$) activity. Power (decibels, dB) is shown by the color bar. B. Topographical maps of mu (6-9Hz) band in 500ms interval during execution for (a) grasp condition and (b) cane-use condition.

We included two time windows due to visual differences across time in the time-frequency plot (Figure 10, central and occipital). For the model with central region, we found a significant main effect of condition (*F*(1,34) = 5.0, *p* = .03) and a significant main effect of time (*F*(1,34) = 1.69, *p* < .001). Follow-up analyses were performed to determine the effects of condition and time. Pairwise t-test between time windows (anticipatory and movement) revealed a significant difference on mu power (*t*(35)= -3.9, *p* < .001), with more mu power suppression observed during the anticipatory period (*M* = -.91 dB, *SE* = .17) than during movement (*M* = -.51 dB, *SE* = .18). Pairwise t-test between condition revealed that there was more overall mu power during observation of grasp action (*M* = -.90 dB, *SE* = .16) than for cane-use action (*M* = -.52 dB, *SE* = .2), (*t*(35)= -2.3, *p* = .03, Cohen's *d* = 0.29; Figure 11).

For the model with occipital region, we found a significant main effect of time (*F*(1,34) = 25.2, *p* < .001), a significant interaction of time and age (*F*(1,34) = 9.3, *p* = .05), and a significant three-way interaction of time, age, and hemisphere (*F*(1,34) = 4.42, *p* < .001). Follow-up pairwise t-test between time windows revealed a significant difference on occipital alpha (*t*(35)= 4.67, *p* < .001), with more occipital alpha suppression observed during the movement (*M* = -1.02 dB, *SE* = .17) than anticipatory period (*M* = -.37 dB, *SE* = .20). The interaction effect of age and time resulted from stronger occipital alpha during movement in 12-month-olds (*M*= -1.35 dB, *SE* = .23) than during anticipatory period in 12-month-olds (*M*= -.35 dB, *SE* = .19), (*t*(35)= 5.88, *p* < .001). No other pair was significant after Bonferroni correction. A follow-up Bonferroni post-hoc t-test on the 3-way interaction was conducted and showed that there was significant difference between anticipatory left (*M*= -.39 dB, *SE* = .34) and movement left (*M*= -1.34 dB, *SE* = .27) in 12-month-olds (*t*(18)=5.36, *p* <.001) and significant difference between anticipatory right (*M* = -.30 dB, *SE* = .29) and movement left in 12-month-olds (*t*(18)=5.69, *p* <.001).

Importantly, in contrast to mu power, occipital alpha power was not modulated by condition.

Together, we found that mu suppression was evident for observation of both familiar and unfamiliar action. This is in line with previous work on infant mu rhythm during observation of grasp action (Debnath et al., 2019; Hwang et al., 2021; Meyer et al., 2022; Southgate et al., 2009), and for novel action (Southgate & Begus, 2013; Virji-Babul et al., 2012). Importantly, greater mu suppression was exhibited during observation of grasp than cane-use action. This provides evidence that infants' mu suppression is modulated by motoric familiarity.

Mu/alpha suppression and behavioral competence

13 9-month-olds and 17 12m-month-olds had sufficient grasp behavioral execution trials, and 10 9-month-olds and 11 12m-month-olds had sufficient cane pulling behavioral execution trials. The mean grasp latency was 846ms (*SD* = 400) for 9-month-olds and 775ms (*SD* = 280) for 12-month-olds. The mean cane pulling latency was 2158ms (*SD* = 760) for 9-month-olds and 1749ms (*SD* = 978) for 12-month-olds. We found no differences between the two age groups for grasp ($p > 0.5$) and cane pulling ($p > 0.3$, Figure 12) latencies.

To investigate whether mu suppression is associated with behavioral efficiency with an action, we submitted the competence measure (latency to grasp, latency to pull) as our dependent variable and mu power during observation of action (0ms to 1000ms) and age (9m; 12m) as independent variables for each condition in separate regression models. In the grasp condition, the model with age and mu power revealed a marginally significant model, $R^2 = .26$, $F(3, 24) = 2.74$, $p < .06$, and a significant interaction of mu power and age group, ($\beta = -322.6$, SE = 117.5, $p = .01$), and a significant main effect of mu power ($\beta = 248$, SE = 96.3, $p = .02$) on latency to grasp (Figure 13). Follow-up analyses were performed to determine where the interaction effect originated. We found a positive correlation between mu power and grasp latency in 9-month-old group ($r = -.59$, $p < .04$), with faster grasping latency associated with more suppression in mu power. We found no evidence of such relation in the 12-month-old group ($r = -.31$, $p > .2$), possibly due to less variability in the 12-month-old grasping latency to detect meaningful relation. In the cane-use condition, we did not find evidence for a relation of mu power and age on infants' cane pulling latency measure ($p > .1$).

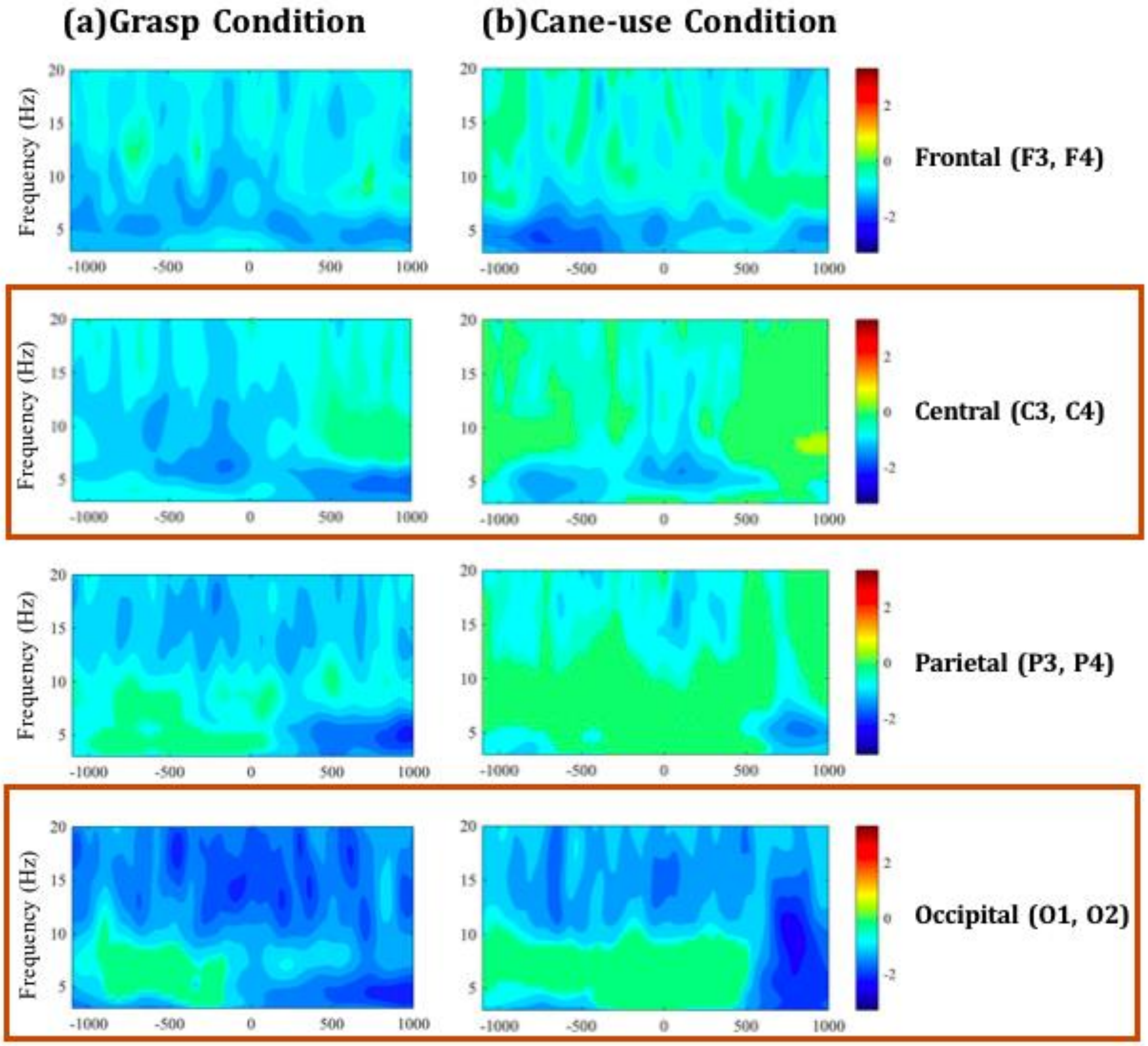


Figure 10. Statistically significant time-frequency plot of spectral power relative to baseline during observation phase for (a) grasp condition, (b) cane-use condition, across age. The color towards blue indicate significant suppression of power relative to baseline. Green in images depicts non-significant (p > .05) activity. Power (decibels, dB) is shown by the color bar.

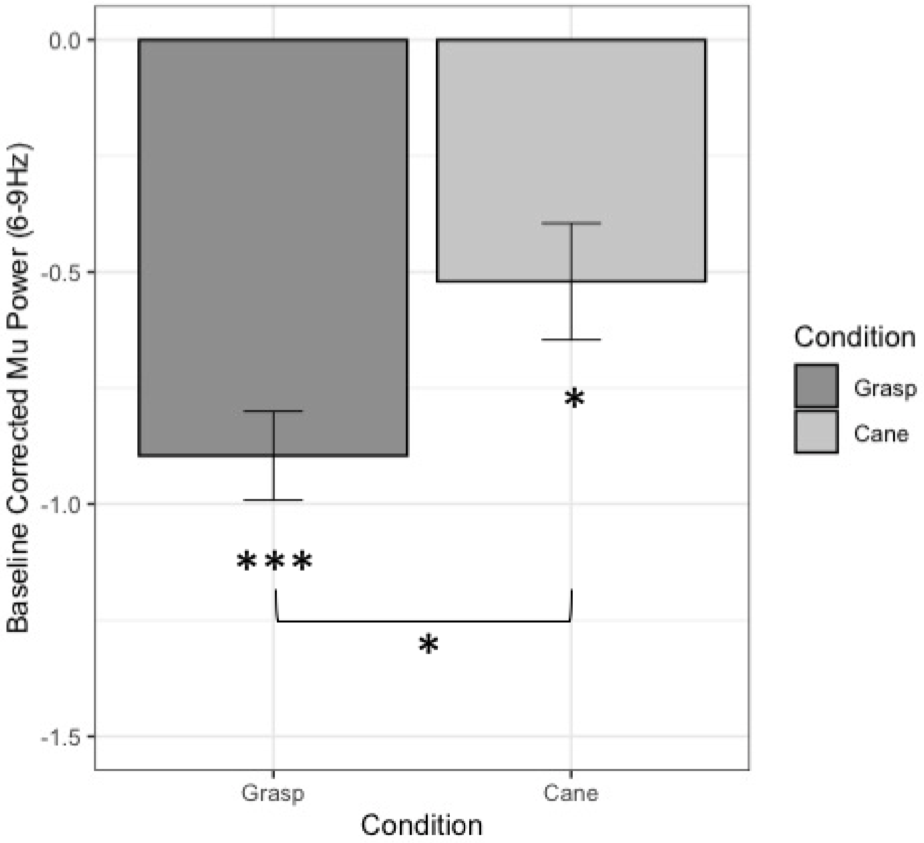


Figure 11. Baseline-corrected power of the alpha frequency band (6-9Hz) over Central (C3, C4) sites as a function of condition (Grasp / Cane-use). Error bar indicates ± 1 SE. *p < .05, ***p < .001.

We also conducted the same analysis with occipital alpha and found no evidence of a relation between occipital alpha and behavioral competence (grasp latency: p > 0.8; cane pulling latency: p > 0.5; correlation between occipital alpha and behavioral competence: $B_{01} = 4.1$, $B_{01} = 3.0$, respectively). These findings suggest that motor experience with a familiar action is uniquely associated with infants' mu suppression during action observation, as has been found in prior studies (Cannon et al., 2016; Gerson, Bekkering et al., 2015; Paulus et al., 2012; van Elk et al., 2008). No such correlation was evident for the novel tool-use action.

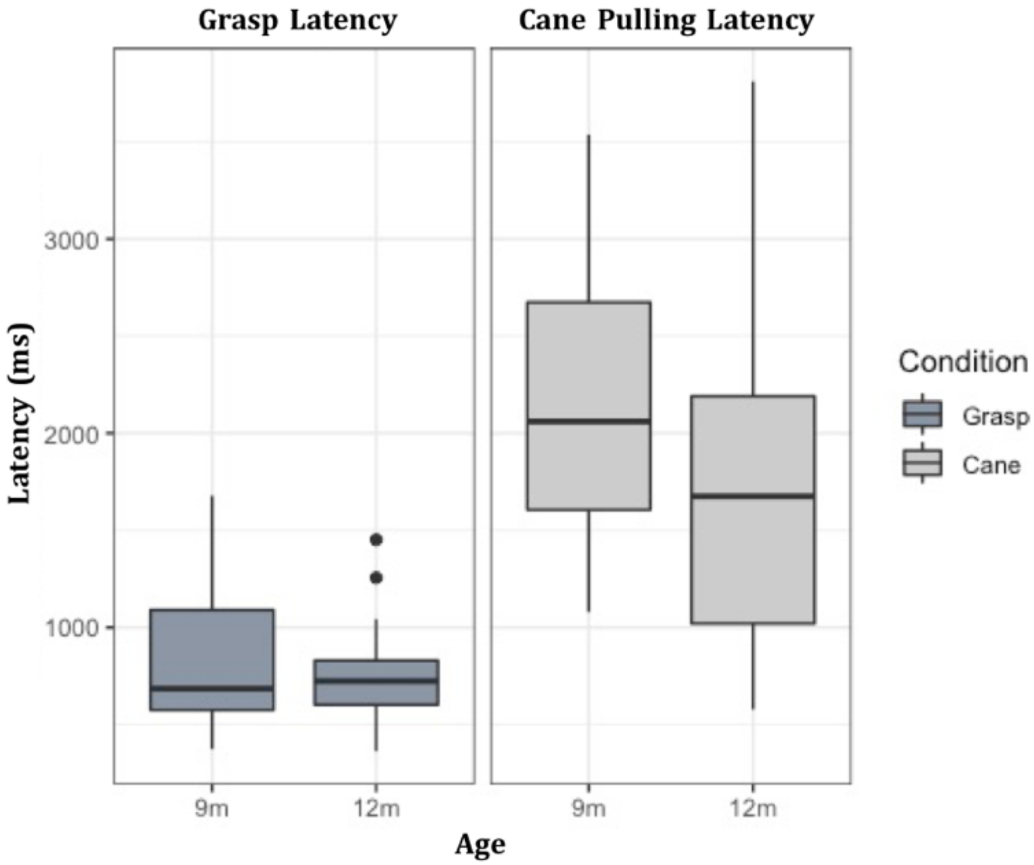


Figure 12. Bar-plot of infant' behavioral competence. Left: Infants' grasping latency, Right: Infants' cane pulling latency, in milliseconds.

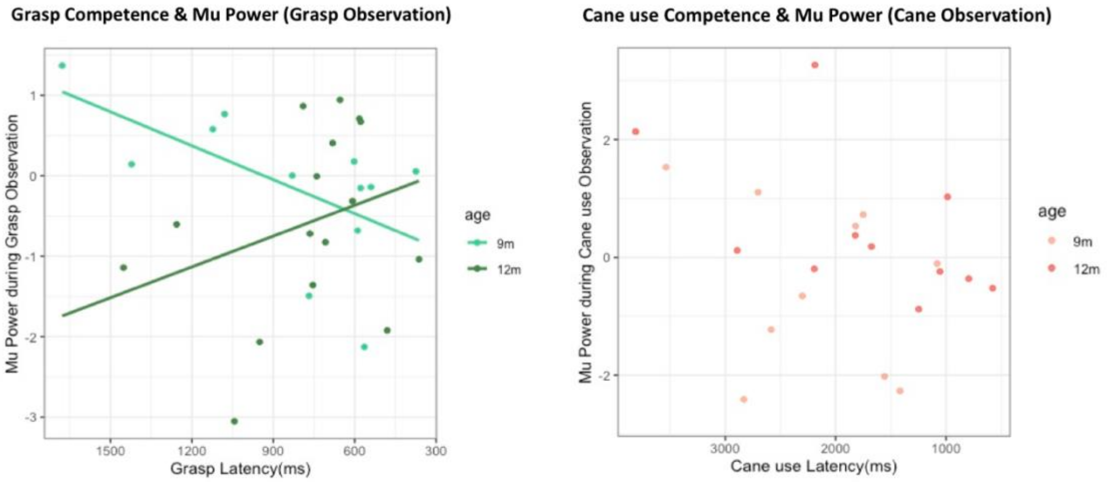


Figure 13. Scatter plot of Mu Power (6-9Hz) overlying central area during observation of grasping action and infants' grasp latency (in milliseconds)(Left), and cane-use action and infants' cane pulling latency (Right). X-axis scale is reversed, indicating faster latency towards right side of the axis. (Note: Left: only the regression line for 9m is significant; the line for 12m is not significant)

Inter-channel phase coherence(ICPC)

Central-based ICPC

To explore functional connectivity of motor and visual processes, we compared ICPC at 6–9 Hz frequency for electrode pairs between central-occipital to that of central-frontal and central-parietal. We analyzed 36 (9m- 17, 12m- 19) infants' ICPC. Our goal in exploring ICPC was two-fold. First, we tested whether we replicate the findings by Debnath et al. (2019) for the grasp condition. Second, we wanted to explore the pattern of ICPC for a novel cane-use action. We analyzed the ICPC in a 3-way mixed ANOVA with age (9m, 12m) as a between-subject factor and hemisphere (right, left) and electrode-pair (central-frontal, central-parietal, central-occipital) as within-subject factors independently for each condition (grasp, cane-use).

For ICPC in the grasp condition, the analysis revealed a significant main effect of electrode-pair ($F(2, 68) = 5.12$, $p < .05$), and a significant interaction effect of hemisphere and age ($F(1,68) = 4.3$, $p < .05$; partial eta squared = 0.14). Follow up pair-wise comparisons after Bonferroni correction revealed that $ICPC_{CO}$ ($M = .39$, $SE = .08$) was significantly higher than $ICPC_{CF}$ ($M = .36$, $SE = .08$; $t(35)= 2.56$, $p = .01$) and $ICPC_{CP}$ ($M = .36$, $SE = .07$; $t(35)= 2.62$, $p = .02$) (Figure 14(a)). For the interaction effect of hemisphere and age, no pairs were significant after Bonferroni correction; however, the interaction effect seemed to be originated from differences in 12-month-olds. Descriptively, there was higher connectivity in the left ($M = .37$, $SE = .01$) than right hemisphere ($M = .35$, $SE = .01$) in the 12-month-olds across pairs. In the cane-use condition, we did not find evidence for a difference between electrode-pair connectivity (Figure 14(b)). Thus, we replicate the findings in Debnath et al., (2019) for the grasp condition and confirm that motor and visual areas are functionally connected during observation of familiar, grasping action. We find no evidence for a difference of connectivity among regions during observation of a novel, tool-use action.

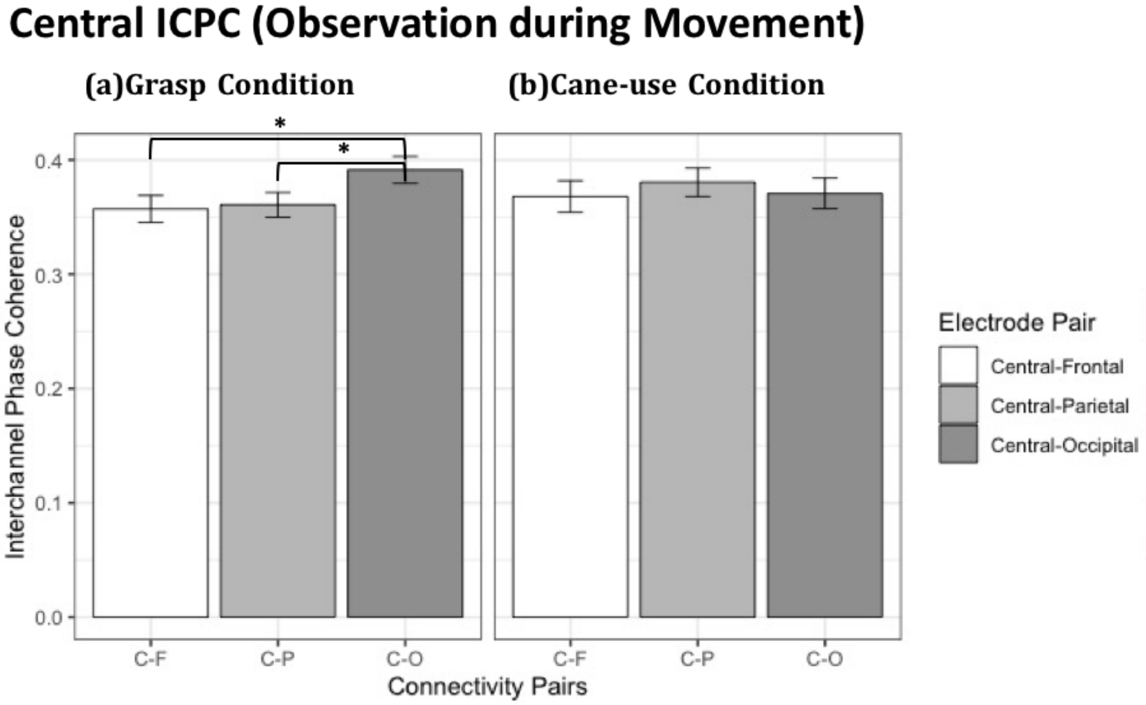


*Figure 14. Average of central-based ICPC during observation of (a) grasp and (b) cane-use action. Error bar indicates ± 1 SE. *p < .05.*

Occipital-based ICPC

For a full replication of Debnath et al., (2019), we also measured ICPC between occipital and three brain regions (frontal, central, and parietal) in both hemispheres (left: O1– F3, O1– C3, O1– P3; right: O2– F4, O2– C4, O2– P4) for a full replication of Debnath et al., 2019. We computed ICPC during movement time periods (0ms to 500ms time-locked to movement onset) in both observation of grasping and cane-use action at 6–9 Hz frequency for the cluster of electrodes pairs in both the left and right hemispheres, and then were averaged across trials. We then analyzed the occipital-ICPC in a 3-way mixed ANOVA with age (9m, 12m) as a between-subjects factor, and within-subjects factors hemisphere (right, left) and electrode-pair (occipital-frontal, occipital-parietal, occipital-central) independently for each condition (grasp, cane-use).

For occipital-ICPC in the grasp condition, the analysis showed a main effect of electrode-pair ($F(2, 68) = 9.1$, $p < .001$). No other main effects nor interactions were significant. Follow up pair-wise comparisons after Bonferroni correction revealed that ICPC$_{OC}$ ($M = 0.39$, $SE = 0.08$) was significantly higher than ICPC$_{OF}$ ($M = 0.33$, $SE = 0.09$, p < .001) and ICPC$_{OP}$ ($M = 0.34$, $SE = 0.09$, $p = .013$) (Figure 15(a)). In the cane-use condition, we did not find evidence for a difference between electrode-pair connectivity (Figure 15(b)). Thus, together with findings on central-based ICPC, we replicate the findings in Debnath et al., (2019) for the grasp condition and confirm that 1) observed mu power is distinct from visual alpha and 2) motor and visual areas are functionally connected during observation of familiar, grasping action. We find no evidence for a difference of connectivity among regions during observation of a novel, tool-use action.

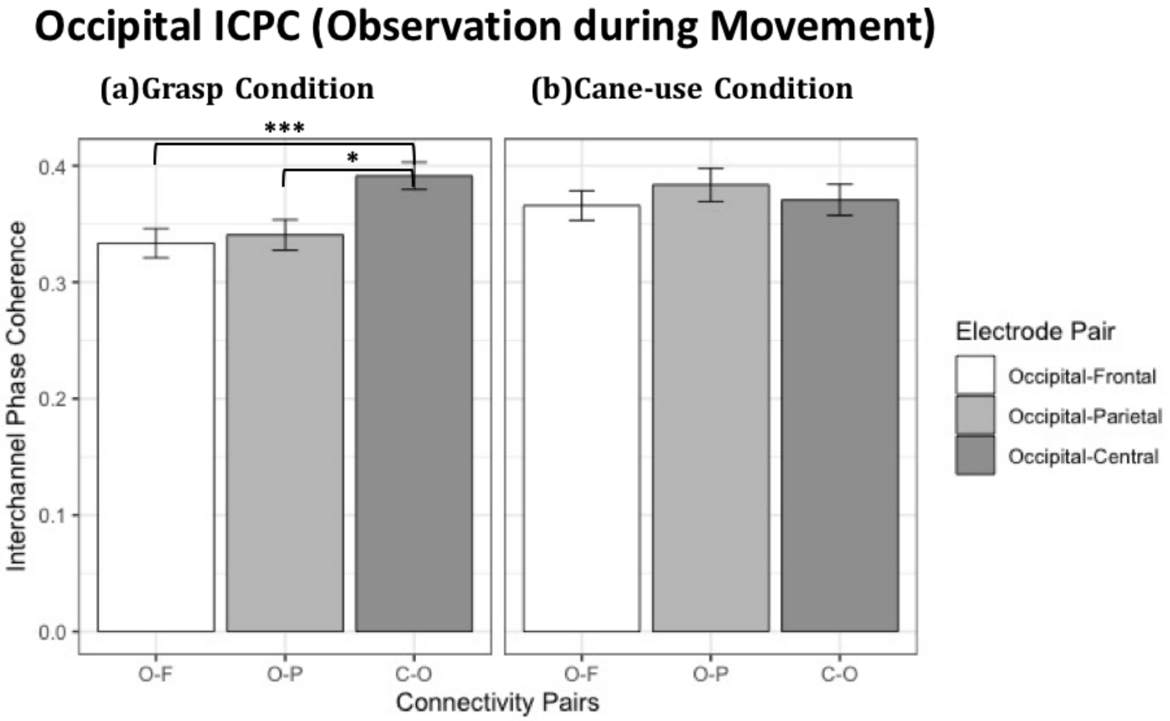


Figure 15. Average of occipital-based ICPC during observation of (a)grasp and (b)cane-use action. Error bar indicates ± 1 SE. *p < .05, ***p < .001.

Discussion

In this EEG study, we used a tight controlled within-subjects design to systematically compare 9-and 12-month-old infants' distinct motor and visual processes to motorically familiar and unfamiliar actions using alpha power in the 6–9 Hz frequency range. More specifically, we investigated whether there are differences in central and occipital alpha during observation of motorically familiar versus unfamiliar actions. We extended our analyses by exploring associations of behavioral competence and mu power, and by investigating functional connectivity in the 6–9 Hz frequency range.

We pursued several methodological approaches, including using baselines that carefully matched the visual aspects of the experimental window, to more clearly assess distinct action-specific motor process and visual attentional processes in response to familiar versus novel actions. We found that both mu suppression and occipital alpha suppression were evident during observations of both motorically familiar and unfamiliar actions, though they were distinct in the pattern they exhibited. Mu suppression was present during action anticipation (before movements occurred) and throughout the movement period, while occipital alpha was present during the onset of movement and not during action anticipation. This suggests that mu suppression is independent of an attentional response to the visual aspects of the stimulus. More importantly, mu suppression was stronger for familiar than for novel actions, whereas the level of occipital alpha suppression did not vary as a function of motor familiarity. While this replicates Southgate & Begus (2013) and Virji-Babul et al. (2012) by showing that mu suppression is evident during observation of familiar and novel action, these findings also differ from previous ones in that mu suppression is sensitive to motoric familiarity. Virji-Babul et al. (2012) did not report occipital alpha power and thus it is unclear to what extent alpha effects were driven by motor or visual areas. In addition to not finding a difference between central and occipital alpha as a function of motor familiarity, Southgate & Begus (2013) found an increase in occipital alpha from baseline. This might reflect potential visual effects related to the demand of the task beyond motor processes that may have affected their findings, but this possibility remains unexplored.

Consistent with prior research relating expertise in action and neural motor activity during observation of familiar action in adults and infants (Calvo-Merino et al., 2006; Cannon et al., 2016; Cannon et al., 2014; Cross et al., 2006; Orgs et al., 2008), we found that mu suppression was specifically associated with infants' own competence in actions. We found a correlation between 9-month-old infants' grasp latency and the level of mu power during observation of grasping actions. For occipital alpha no such relation was evident. It should be noted that the lack of evidence for an association between mu power and grasp competence in the 12-month-old group is not necessarily an indication of no relation, but could be due to little variability within the 12-month-old grasp competence. Indeed, as infants gain more experience with an action, they produce more stable and accurate movements (Thelen et al., 1996; von Hofsten, 2004). Thus, we provide supporting evidence that motor competence is associated with mu power for familiar action, that is not found with occipital alpha.

Also, we found no evidence for such relation between mu suppression during observation of novel actions and infants' competence in novel actions. While, in general the interpretation on the lack of evidence for a relation should be interpreted with extreme caution, it is in this case not surprising and was expected given that the novel action is outside of the infants' motor repertoire at this age. It is an open question whether we would observe a change in this relation as infants gain experience and learn to produce means-end actions. Future work should directly address this possibility.

Together, while our results regarding mu power show that mu suppression is exhibited for both familiar and novel actions, we also observe a unique pattern for motoric familiarity in the way that is reflected in mu suppression. The level mu suppression is modulated by motoric familiarity, and mu suppression during observation of familiar action specifically correlates with infants' own actions. Nevertheless, it is difficult to reconcile the puzzle on the underlying neural correlates of perception of motorically familiar action by relying on mu power alone.

Exploring functional connectivity between networks, rather than isolated regional neural markers, may be a better indicator regarding the underlying mechanism during perception of motorically familiar action. Critically, many infant EEG studies report activation of mu and occipital alpha during observation of actions (Cannon et al., 2016; Yoo et al., 2015; Filippi et al., 2016; de Klerk et al., 2016); however, only few have directly explored whether activity from central and occipital alpha are functionally related during action observation (Debnath et al., 2019). When we extend our analyses beyond mu power to the functional connectivity of motor and visual processes, we find a clearer role of motor familiarity on neural processes of action perception. During observation of familiar grasping actions, central-occipital phase coherence in the 6-9Hz frequency range was higher than phase coherence between areas with shorter distance like central-parietal and central-frontal electrode pairs across age. In other words, central and occipital areas were functionally more connected compared to their connections with other brain regions. Debnath et al. (2019) suggested that higher phase synchronization between central and occipital regions indicates that while activity in motor and visual regions reflect distinct processes, they are functionally linked. We did not find evidence for such a specific connectivity pattern during observation of the novel tool-use action. Thus, we introduce the possibility that neural correlates of perceiving motorically familiar versus unfamiliar action may be reflected in integrated activity of a neural network.

Understanding the dynamic of interconnected networks in the brain can provide insights on functional capabilities infancy (Gao et al., 2017). As such, the application of functional connectivity in this study sheds light on the potential possibility of inter-relation between motor experience and motor-visual connectivity. That is, the functional connectivity between motor and visual regions during observation of familiar grasping action may be a product of active experience in grasping and observing one’s grasp. Infants start grasping for objects at 3-4 months and become proficient in grasping around 8-to 9-months of age (von Hofsten & Fazel-Zandy, 1984). Actions such as grasping, allow observation of direct physical changes. For instance, when one produces a grasping action, the effect of grasping is clearly visible in that the object moves closer and looks bigger (Woodward, 2005). Therefore, accumulated experiences with producing grasps and observing their effects could have built on stronger connections between motor and visual regions, thereby functionally playing a role in perception of others’ grasps. In fact, Pineda (2005) hypothesized that coupling between different sources of activity could be responsible for the relation between perception and action, and researchers already have emphasized the potential functional significance of motor-visual coactivation (Fox et al., 2016), specifically in the developmental population (Bowman et al., 2017). This also aligns well with the theory on bidirectional action-effect associations which stresses the link between motor system activation and visual processing during action perception (Paulus, 2012). More work is needed, yet our findings highlight the potential significance of exploring the dynamics of interconnected networks in the infant brain, which may better illuminate the underlying processes of action perception.

Future directions

An open question is whether and to what extent new motor experience with a novel action modulates neural activity in infancy. At the behavioral level, extensive literature has demonstrated that active experience on a novel action alters infants' processing of others' actions (Gerson, Mahajan, Sommerville et al., 2015; Gerson & Woodward, 2014a; Libertus & Needham, 2010; Sommerville et al., 2008; Sommerville et al., 2005). For instance, Sommerville et al. (2008) trained 10-month-old infants on using a cane to retrieve an out-of-reach toy. They found that having this active experience changed infants' goal understanding of another person's cane-use action. EEG studies have found consistent results on the role of active experience when processing others actions as well (Bakker et al., 2016; Gerson, Bekkering, & Hunnius, 2015; Paulus et al., 2012). Our study contributes to the literature by showing that active experience with a familiar action is associated with stronger mu suppression and with neural communication between motor and visual areas during observation. However, with the current analysis, we cannot draw any conclusions about whether mu power or functional connectivity is *modulated* by learning a novel skill. It will be important to corroborate whether active experience or training of novel action subsequently generates stronger mu power to trained action and whether training induces changes in functional connectivity between motor and visual processes.

Another crucial direction would be to build upon our understanding of the dynamic communication between regions during action perception in infancy. Our study expanded on the approach to explore connectivity between regions, and it revealed critical implications on action perception. However, it is restricted to regional connectivity and does not consider interactions across large scale neural networks. Computational approaches and methodological innovation in this regard would be important to depict a comprehensive picture of connections across the whole brain during action perception, and further elucidate how the network of communication between areas changes as a function of experience.

Lastly, in order to accurately depict whether and how active motoric experience affects generating efficient connectivity routes during action perception, research has yet to gain understanding on how motor skill acquisition changes neural processing, in particular structural and functional connectivity patterns. Surprisingly little is known and documented about the links between changes in early motor development and neural processes associated with production of action. Only a few studies document changes in EEG power or coherence associated with changes in motor skill in infancy (*resting-state EEG*- Bell & Fox, 1996; Corbetta et al., 2014; Xiao et al., 2018; *during action execution*- Nishiyori et al., 2016; 2021). This is a critical gap in the literature that necessitates attention for better understanding of the relation and coordination between infants' motor control and changes in neural activity. Importantly, if changes in power or coherence coincide with changes in motor experience or ability, a holistic interpretation can be made regarding the role of motor experience on neural reorganization and the mechanism involved with the interplay between action perception and execution (Gonzalez et al., 2016).

Conclusion

Together, our findings provide fundamental evidence on the neural correlates and novel insights about motor-visual processes during infants' action perception of familiar and novel actions. Specifically, observation of familiar actions exhibited stronger motor-related response distinct from general visual processes, and was associated with specific functional connectivity between motor and visual areas compared to connections with other brain regions. This paves the way for future research to make use of methodological approaches to parse motor-specific neural activity while also to consider neural processing in a dynamic network. This further broadens the scope of infant EEG mu rhythm procedures and its interpretations.

Chapter 4: Exploring the relation between intervention experience and functional connectivity

Behavioral studies have provided evidence that infants' action perception is connected to and affected by their own experience producing the observed actions (Ambrosini et al., 2013; Filippi & Woodward, 2016; Gerson, Mahajan, Sommerville et al., 2015; Gerson & Woodward, 2014a, 2014b; Kanakogi & Itakura, 2011; Loucks & Sommerville, 2012; Sommerville et al., 2008; Sommerville & Woodward, 2005). For instance, as infants gain experience in reaching, they differentially generate anticipatory saccades to others' action end-points (Ambrosini et al., 2013; Kanakogi & Itakura, 2011) and respond selectively to others' goals. Providing infants with novel experience of actions that are outside of their current motor repertoire also influences infants' action perception (Gerson, Mahajan, Sommerville et al., 2015; Gerson & Woodward, 2014a, 2014b; Skerry et al., 2013; Sommerville et al., 2008; Sommerville et al., 2005). Although at 3 months, infants cannot readily grasp objects nor do they attend differentially to changes in action goal structure, they can experience apprehending objects while wearing velcro-covered ‘‘sticky mittens’’ (Sommerville et al., 2005). Following a short in lab training session with the "sticky mittens", this experience enabled infants in the training condition, compared to those in the control condition, to respond systematically to others' goal-directed actions (Gerson & Woodward, 2014; Skerry et al., 2013; Sommerville et al., 2005). In essence, infants' action perception is connected to and affected by their own action experience, and changes in own motor experiences influence the way infants process others' actions. While the association between production and interpretation of action is robustly found in behavioral studies, less is known about the underlying neural mechanisms that are involved in the link between active experience and action perception.

Neural mirroring has been suggested as a mechanism that links action experience and action perception (Di Pellegrino et al., 1992; Gallese et al., 1996; Marshall & Meltzoff, 2014; Pineda, 2005). Neural mirroring is the overlapping pattern of brain activity that occurs during the execution of an action and the observation of that same action when someone else produces it. As a potential index of neural mirroring, a growing number of studies has examined the mu rhythm within electroencephalogram (EEG), which reflects oscillations in the alpha frequency band (adults 8-13Hz, infants 6-9Hz) recorded over the sensorimotor cortex (Cannon et al., 2014; Cuevas et al., 2014; Fox et al., 2016; Marshall & Meltzoff, 2014; Muthukumaraswamy et al., 2004). Power in the mu rhythm is found to be suppressed (also called mu suppression) during both action execution and action observation, and cortical source localization studies provide supportive evidence that the mu rhythm is associated with activity in the sensorimotor cortex in adults and infants (Hari et al., 1997; Thorpe et al., 2016; Toro et al., 1994). Given that mu suppression occurs not only during action execution but also during action observation (Fox et al., 2016; Marshall et al., 2011), numerous studies have investigated the neural correlates of action perception in infants focusing on mu suppression and found evidence of mu suppression during action observation in infancy (Filippi et al., 2016; Marshall et al., 2011; Meyer et al., 2022; Nystrom, 2008; Nystrom et al., 2011; Southgate et al., 2010; Southgate et al., 2009).

Moreover, recent findings suggest that the magnitude of mu suppression during infants' action observation relates to their proficiency in producing the action (Cannon et al., 2016; Chung et al., 2022; Gerson, Bekkering, & Hunnius, 2015; Paulus et al., 2012; Upshaw et al., 2016; van Elk et al., 2008). Specifically, mu suppression is evident during the observation of a motorically familiar action, more so than for actions the infant has not engaged in (Chung et al., 2022). Variability in infants' motor competence is associated with the level of mu suppression during observation of action (Cannon et al., 2016; Upshaw et al., 2016; van Elk et al., 2008). Furthermore, in a training experiment, infants who learned to engage in a new action generated mu suppression in response to hearing the sounds associated with that action, but not when infants only had observational experience (Paulus et al., 2012; Gerson, Bekkering, & Hunnius, 2015). Together, these findings begin to shed light on the neurocognitive mechanisms involved in the development of action perception. Even so, measuring region-specific neural activity provides a limited window into how functional neural networks are connected during action perception. Cognitive functions are likely to be associated with inter-regional communication among multiple networks (Xie et al., 2019; Xie & Nelson, 2021), and thus the action-perception link may be more complex than previously studied, involving multiple neural networks that are functionally related during action perception (Bonini, 2017; Bowman et al., 2017).

A growing body of neuroscientific findings and theoretical proposals highlight integrative processes that may be an inherent part of action perception, namely motor and visual attention processes (Hommel et al., 2001; Kilner et al., 2007; Paulus, 2012; Pineda, 2005; Urgen & Saygin, 2020). Particularly, researchers refer to the action observation network (AON) involving a distinct set of brain regions including parietal, premotor regions, and occipitotemporal networks, which is associated with action understanding as well as visuomotor learning (Buccino et al., 2001; Nelissen et al., 2011; Urgen & Orban, 2021). Relatedly, theoretical accounts of action representation focus on the functional relations between sensorimotor regions and visual/auditory attentional processes (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Kilner, Friston, & Frith, 2007; Paulus, 2012; Pineda, 2005). For example, researchers in support of the predictive processing perspective argue that action understanding results from reciprocal (hierarchical) communication between the visual cortex and the motor cortex (Kilner et al.,

2007) as a means to process information in the environment and generate appropriate responses and minimize prediction errors (Clark, 2013; Friston, 2005). The system generates predictions to compare them with the sensory input, and then uses this information to update the priors and, ultimately, to minimize prediction errors. In infancy, a similar process could be in place, forming and refining representations generated from their own actions to make predictions about others' actions (Keysers & Perrett, 2004; Köster et al., 2020). In sum, functional communication between motor and visual processes could be central in the process of encoding and understanding others' actions. Nevertheless, the evidence concerning the underlying mechanism of coordination between networks in infancy is scarce.

Recent findings on functional connectivity in the infant alpha frequency range (6-9Hz) in EEG between visual and motor areas during observation of actions within infants' motor repertoire provide supporting evidence that active experience may be associated with neural motor-visual coordination. Debnath et al. (2019) examined alpha (6–9 Hz) frequency band oscillations during observation of grasping action and found that visual and motor areas were more connected than other control circuits that were closer in spatial distance (e.g., central-frontal, central-parietal). Chung et al., (2022) replicated the result for grasping actions and also showed, in a controlled within-subjects design, that infants did not show similar connectivity patterns when they observed a motorically unfamiliar tool use action. These findings serve as evidence of an emerging pattern of connectivity during observation of familiar actions in infancy. Following on this finding, Colomer and colleagues (under review) investigated the relative specialization of motor-visual connectivity and found that it was modulated by infants' action expertise. That is, infants more competent in grasping objects showed higher levels of motor-visual coupling during action anticipation (Colomer et al., under review). In brief, observing familiar actions elicits functional connectivity between visual and motor processes in infants; this connectivity scales with infants’ motor development, suggesting that as infants gain proficiency in a new motor skill, visual and motor processes become functionally organized during the observation of actions.

During the first year of life, infants experience dynamic changes in newly emerging action capacities. Around 9-to 12-months, as infants become efficient and proficient in their reaching and grasping actions (von Hofsten, 2004; von Hofsten & Rönnqvist, 1988), this also marks the onset when infants begin to produce pointing (Bates et al., 1975; Leung & Rheingold, 1981). Behavioral findings have indicated that as infants gain experience in producing their own pointing, they also understand that others’ pointing gestures are directed towards a referent (Brune & Woodward, 2007; Woodward & Guajardo, 2002) and are able to respond appropriately to others’ pointing (Behne et al., 2012; Liszkowski & Tomasello, 2011). Critically, although intentional action (i.e. grasping) and communicative action (i.e. pointing) are behaviorally similar in their form of presentation, pointing is a type of gesture that conveys information (e.g., to share attention to an object or an event) (Novack & Goldin-Meadow, 2017). Thus, exploring 10- to 12-month-olds provides a special window of opportunity to investigate changes in functional networks as infants are learning a novel communicative action, namely pointing, compared to actions that they have had prolonged experience with, namely grasping.

Despite the wealth of behavioral studies that focus on infants' emerging production (Bates et al., 1975; Butterworth & Morissette, 1996; Leung & Rheingold, 1981; Liszkowski et al., 2007) and comprehension of pointing (Carpenter et al., 1998; Daum et al., 2013; Melinder et al., 2015; Sodian & Thoermer, 2004), little is known about the neural underpinnings of this communicative action. Evidence from functional imaging studies in adults shows that the regions of the action observation network (premotor cortex, superior and inferior parietal cortices, and lateral temporal cortex) are involved in perception of gestures (Yang et al., 2015), and others have found activity in the superior temporal sulcus, occipital areas, and inferior temporal gyrus during observation of gestures (Dick & Broce, 2016; Dick et al., 2009). However, these studies have examined iconic or metaphoric gestures and not pointing per se. The few studies that have specifically observed the mu rhythm during observation of pointing in adults (Avanzini et al., 2012; Quandt et al., 2012) report significant mu suppression during observation of pointing (but see Pomiechowska & Csibra, 2017). To date, there are only a couple of infant EEG studies that address neural activity during observation of pointing (St.John et al., 2016; Salo et al., under review). While St John et al. (2016) report mu suppression during observation of pointing; it is unclear whether their results were calculated with respect to a baseline. Salo (2018) collected information about 10-to-12 month old infants' prior experience in production of pointing, and conducted a training study to assess whether increasing infants' exposure to pointing would support activation of the motor system as measured via enhancement of mu suppression during observation of pointing gestures, and in turn would facilitate language skills. Overall, increasing infants' exposure to pointing through a brief parent intervention was associated with an increase in infants' mu suppression during observation of pointing. This is a result that is similar to what has been found for grasping action, and it raises questions about functional connectivity during observation of pointing in development, and the role of experience in modulating specific functional connections.

Present Study

In the current study, we asked whether motor-visual connectivity is evident during infants' perception of a communicative action, pointing, and whether this connectivity varies as a function of infants' experience with pointing. In order to address functional connectivity during infants' perception of pointing, and whether functional connectivity varies as a function of infants' experience with pointing, we re-analyzed the EEG data collected by Salo (2018), making use of the methodological approach used in Debnath et al., 2019, Chung et al., 2022, and Colomer et al., (under review). Salo (2018) collected infants' EEG activity during observation of pointing gestures and grasping actions.

Research Questions

The research questions and analytic plan were pre-registered (https://osf.io/6sxv7/). The specific research questions were as follows:

Connectivity modulated by motor familiarity. Our first question was to ask whether infants recruit the same functional neural networks when they observe an action that they have long experience with, such as grasping (around 6 months of experience), as compared to when they observe an action they are just learning, such as pointing.

1. Do 10-to 12-month-old infants exhibit higher central-occipital connectivity than control cluster pairs during observation of grasping action (of which they have had prolonged experience with)?
2. Do 10-to 12-month-old infants exhibit higher central-occipital connectivity than control cluster pairs during observation of pointing (of which they are beginning to acquire)?

Connectivity modulated by experience. Next, since the specialization of motor-visual connections is found to be related to motor expertise in grasping (Colomer et al., under review), it is possible that variation in infants' experience with pointing would affect the specialization of motor-visual connections during pointing observation. Thus, we wanted to directly explore whether experience with pointing relates to the specific recruitment of motor and visual areas during pointing observation.

3. Do infants who are reported to be pointers (by parents) exhibit higher specific central-occipital connectivity relative to whole-brain as compared to non-pointers?
4. Do infants who received the training intervention exhibit higher specific central-occipital connectivity relative to whole-brain as compared to control group?

By addressing these questions, we aim to elucidate whether experience could be the driver of strengthening communication between motor and visual processes, thereby potentially playing an integral role in facilitating changes in the way infants perceive others' communicative action. Motor and visual processes could be coordinated during the perception of an action just as infants begin to produce the action. More specifically, it could be that even a short amount of experience in pointing is associated with higher levels of functional connectivity between motor and visual processes during observation of pointing. Alternatively, changes in functional connectivity during action perception based on a relatively short period of experience (e.g., in this case, 1 month) may not be specific to a particular network, but more broadly distributed across the whole-brain network. The infant brain may need prolonged experience with an action to reliably select specific-network activations that allow a more efficient processing of the upcoming stimuli.

Methods

Participants

81 full-term infants aged 10 to 12 months (*M* = 10 months 23 days, Range: 10m 1d-12m 24d; 39 females, 42 males) participated in this study. Of that, 72 (*M* = 11 months 29 days, Range: 11m 1day -14m 15days; 34 females, 38 males) returned for the Time 2. For Salo (2018) sample size was based on effect sizes for detecting group differences in previous training studies

with infant pointing (Matthews et al., 2012) and adult mu rhythm (e.g.,, Cannon et al., 2014). Participants represented a relatively diverse racial background (62% Caucasian, 15% Hispanic, 11% African-American, 4% Asian, 19% mixed-racial, and 4% did not report race). One infant (female) was diagnosed with a developmental delay during the course of the study and was subsequently removed from the analysis, yielding a final sample of 81 infants who provided behavioral only or behavioral and EEG data at either Time 1 or Time 2. Inclusion criteria for participation in the study was based on parent report and as follows: (a) the child was between 10 and 12 months of age at the time of their first visit, (b) the child was not born pre-term, and (c) the child did not have hearing loss or a known condition that might affect cognitive development. The age range of 10- to 12 months was chosen because this is when pointing gestures begin to emerge, on average (Bates, Camaioni, & Volterra, 1975). This study was approved by the University Institutional Review Board.

Procedures

Participants took part in two visits to the lab, approximately one month apart (Mean time between visits = 34.54 days; range: 27-67). The procedures for the two lab visits (Time 1 and Time 2) were identical. Parents completed several questionnaires reporting on their family demographic information and at Time 1 only parents also reported on whether their child had yet begun pointing, and if so, the age at which their child began to produce points. Infants participated in an EEG task designed to measure neural activity during observation of pointing gestures and grasping actions. At the end of Time 1, families were randomly assigned to either the training intervention group to receive the Pointing to Success training (Rowe & Leech, 2019) or to the control group to receive no training. The follow-up Time 2 lab visit ended after the EEG task.

EEG action perception task

EEG was recorded from scalp electrodes using a 128-channel HydroCel Geodesic Sensor Net and sampled at 500 Hz using EGI software (Net Station v4.5.4; Electrical Geodesics, Inc., Eugene, OR). Impedance values for all EEG channels were kept below 100 kΩ. Infants sat on a parent's lap in front of a black wooden puppet stage. At the start of the task and of every trial, a curtain was raised to reveal the presenter and/or stimuli. Each trial was preceded by a 3-second baseline period during which a multi-colored swinging pendulum was present on stage (Figure 16). During observation of point trials the curtain was raised to reveal a presenter sitting across from the infant with a toy centered on the stage. The presenter first got the infant's attention by saying "Hi, Baby!", and then looked to and simultaneously pointed to the toy. The trial ended when the curtain was lowered. The procedure for the observation of grasp trials was the same except the presenter grasped, rather than pointed to, the toy. Infants were presented with a maximum of 30 trials, or up to 15 of each trial type presented in a random order. Infants completed a mean of 17.21 trials (*SD* = 7.01, Range: 3-40) at Time 1, and a mean of 17.72 trials (*SD* = 5.93, Range: 0-30) at Time 2.

Pointing to Success Training

Parents in the training group received the Pointing to Success intervention (Rowe & Leech, 2019), a brief educational video, supplemented by conversation and modeling with an experimenter, to explain the importance of pointing and encourage parents to point more often with their child. Parents were then asked to practice pointing with their child for 15 minutes each day over the following month and were given a set of toys to aid in this practice. Families were contacted via email (or phone if they preferred) once weekly to remind them to continue with the pointing practice. The Pointing to Success intervention (Rowe & Leech, 2019) is documented to observe an increase in both parents' and infants' pointing. Therefore, since Salo et al (under review) did not directly manipulate infants' pointing production, it is a working assumption that infants in the training group have gained an increase in their pointing production. Parents in the control condition were given the same set of toys to bring home but were not given any information regarding pointing. During the period of time between the initial and follow-up lab visits, parents in the control condition were only contacted once to remind them about their upcoming visit.

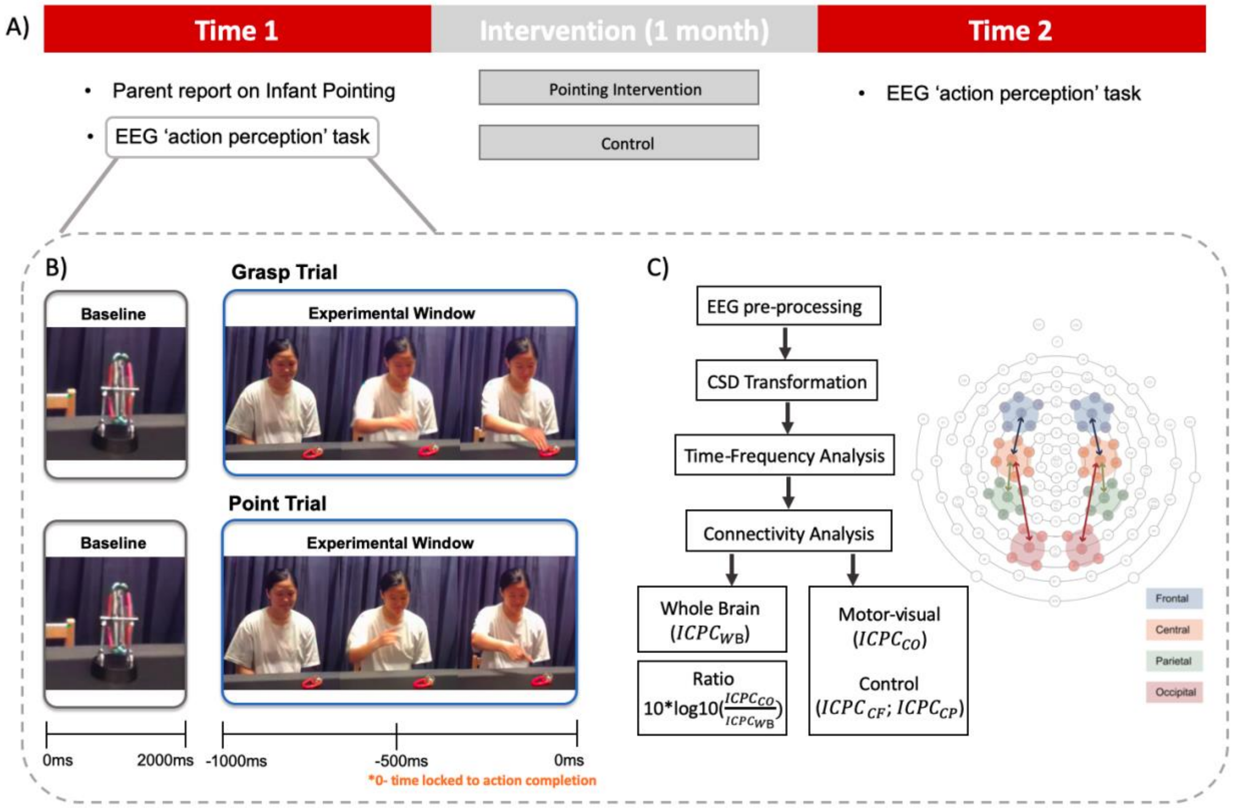


Figure 16. A) Schematic of the experimental paradigm. B) Schematic time-line of observation trials in which 0 represents the movement completion (top: grasp condition; bottom: point condition). C) Steps to calculate connectivity values in each network of interest (motor-visual network ($ISPC_{CO}$) and control networks ($ICPC_{CF}$; $ICPC_{CP}$); whole-brain ($ICPC_{WB}$)). Scalp plot on the right depicts the ROIs of interest, including frontal, central, parietal, and occipital areas.

Pointing Status at Time 1

At Time 1, parents filled out a short survey asking if and when their infant had started pointing. This parent report of child pointing was used as an index of infants' pointing ability. Of 41 infants who had provided useable EEG data for Pointing observation at Time 1, 28 were reported to be pointers and 13 to be non-pointers. Of the 28 infants reported as those who started pointing, the average onset of pointing was 9.71 months (*SD*=1.16, Range: 7-11.5).

Data Analysis

Video-coding analysis

Videos of the EEG task were coded to identify and synchronize live events with the continuous EEG recording. Two independent coders viewed each video off-line, frame-by-frame, to identify the frame in which the presenter completed the point or the grasp. Video was recorded at a frame rate of 30Hz, allowing for coding accuracy within approximately 33ms. Inter-rater agreement, within 100ms (approximately 3 frames), was achieved on 98% of the point trials and 99% of the grasp trials. Trials on which the infant made any reaching or grasping actions, gestures, or gross motor movements, or on which the caregiver interfered through movement, gesture, or speaking were removed from analysis.

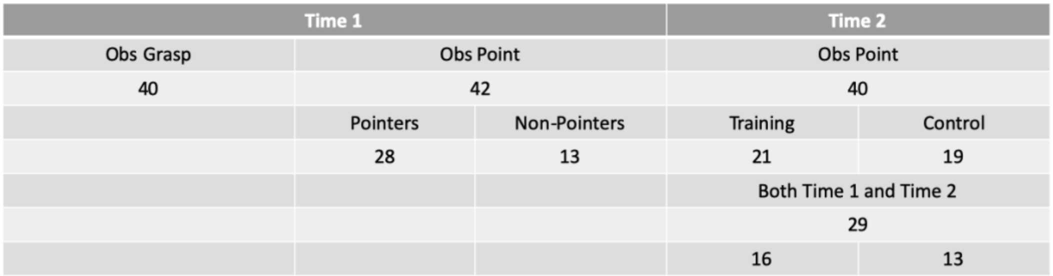
EEG data processing

The EEG data preprocessing procedure followed the Maryland analysis of developmental EEG (MADE) pipeline developed by researchers at University of Maryland (Debnath et al., 2020). Recordings were converted and exported to a Matlab-compatible format (The Mathworks, Natick, MA) using Net Station software. EEG data (pre)processing was conducted using EEGLAB (v14.0.0) toolbox (Delorme & Makeig, 2004). Continuous EEG was filtered (0.5 Hz highpass and 50 Hz lowpass) and then decomposed through ICA to identify artifactual components through both automatic and manual identification processes. After removal of the artifactual components, the data were segmented into 2-second epochs surrounding the events of interest. The segmentation window for both observe trials was - 1500ms prior to the completion of the grasp or point through 500ms after the completion of the grasp or point. For the baseline correction, the first 2-second window of the 3-second baseline event (pendulum presentation) was used. To remove eye movement artifacts, a voltage threshold rejection (±250µV) was applied in the six frontal channels (electrodes 1, 8, 14, 21, 25, 34). The same voltage threshold was applied to all other channels, and any rejected channels in each epoch were interpolated by artifact free data of the surrounding channels within that epoch. If more than 10% of channels within an epoch were interpolated, that epoch was rejected. After artifact rejection, missing channels were interpolated using spherical interpolation as implemented in EEGLAB. Data was then converted into current source density (CSD) using the CSD toolbox (Kayser & Tenke, 2015). All further processing and analyses were performed on the CSD transformed data.

Several infants' data were excluded prior to processing due to technical issues (Time 1 N=11; Time 2 N=3), or due to not having enough trials to process, often because the infant fussed out prior to the task starting (Time 1 N=5; Time 2 N=2), leaving data from 65 infants to be processed at Time 1, and 67 at Time 2. After preprocessing, participants were excluded, within each condition, if they had fewer than 3 artifact free trials. This minimum requirement is based on previous infant EEG mu rhythm studies (Debnath et al., 2019; Marshall et al., 2011). At Time 1, infants provided a mean of 3.91 grasp trials (Range: 0-10) and a mean of 4.03 useable point trials (Range: 0-11); 24 participants were excluded in the grasp condition and 23 participants were excluded in the point condition. At Time 2 infants provided a mean of 3.64 useable grasp trials (Range: 0-10) and a mean of 3.70 useable point trials (Range: 0-8); 25 participants were excluded in the grasp condition and 27 participants were excluded in the point condition. Due to data loss in the EEG processing steps, sample sizes vary depending on the condition and time point being considered. (See Table 5 for a breakdown on information of participant inclusion).

Table 5

Breakdown on information of participant inclusion for EEG analysis.



Time 1			Time 2	
Obs Grasp	Obs Point		Obs Point	
40	42		40	
	Pointers	Non-Pointers	Training	Control
	28	13	21	19
			Both Time 1 and Time 2	
			29	
			16	13

Connectivity Analysis

Inter-channel phase coherence analysis. We measured inter-channel phase coherence (ICPC), which estimates the consistency of phase angle difference between two clusters of channels over time or trials in a given frequency (Cohen, 2014). Phase angles were first calculated from two clusters of electrodes and then subtracted. ICPC value (range: 0 to 1) closer to 1 is interpreted as more synchrony between two clusters, based on the idea that when neural networks are functionally coupled, the timing of their oscillatory processes become synchronized in phase (Cohen, 2014).

Two approaches were used to explore connectivity between central (motor) and occipital (visual) areas during action observation. One approach measured connectivity in the central-occipital network relative to adjacent networks to compare patterns of connectivity when observing grasping and pointing. The other approach measured motor-visual connections relative to the global level of connectivity in the whole-brain network to uncover the effects of experience on the specialization of motor-visual connections.

Central-occipital network relative to adjacent networks. Comparing pairs of ICPC analyses that differ in terms of spatial distance has proven useful in identifying an emerging pattern of functional interregional brain activity between central and occipital regions during action perception. Debnath and colleagues (2019) explored and compared across pairs of electrodes that differ in distance: central-occipital (ICPC$_{CO}$), central-frontal (ICPC$_{CF}$), and central-parietal (ICPC$_{CP}$) (See Figure 16). This comparison is based on the idea that, if there is spurious connectivity due to volume conduction, electrodes that are close to each other should have stronger connectivity values (Cohen, 2014). Debnath et al., (2019) found higher connectivity in ICPC$_{CO}$ than in the other pairs with smaller inter-regional distance, suggesting that central and occipital areas are functionally connected during action perception. Chung et al., (2022) replicated this pattern for grasping actions, but not during observation of an unfamiliar tool use actions. To explore emerging patterns of motor-visual connectivity during perception of action modulated by familiarity, we calculated ICPC over trials between channel clusters over ICPC$_{CO}$, ICPC$_{CF}$, and ICPC$_{CP}$ in both the left (C3– F3, C3– P3, C3– O1) and right (C4– F4, C4– P4, C4– O2) hemispheres (See Table 6). As in Debnath et al. (2019) and Chung et al. (2022). This approach was used to address questions 1 and 2.

Table 6

Electrodes included in Frontal, Parietal, Central and Occipital ROIs.

	Left Hemisphere	**Right Hemisphere**
Frontal	'E19', 'E20', 'E23', 'E24', 'E27', 'E28'	'E3', 'E4', 'E117', 'E118', 'E123', 'E124'
Parietal	'E47', 'E51', 'E52', 'E53', 'E59', 'E60'	'E85', 'E86', 'E91', 'E92', 'E97', 'E98'
Central	'E29', 'E30', 'E35', 'E36', 'E37', 'E41', 'E42'	'E87', 'E93', 'E103', 'E104', 'E105', 'E110', 'E111'
Occipital	'E66', 'E69', 'E70', 'E71', 'E74'	'E76', 'E82', 'E83', 'E84', 'E89'

Specialization of central-occipital network. Normalizing central-occipital connectivity has proven useful in identifying specialized networks of action perception in the developing brain and individual differences based on action experience. Global, unspecific connections at the whole-brain level have been found to be associated with age or maturation (Boersma et al., 2011; Miskovic et al., 2015; Xie et al., 2019), and motoric competence (Colomer et al., under review) within the alpha frequency range. Therefore, without normalization, it would be difficult to assess whether changes in specific networks are due to experience or due to global changes in the brain. Particularly, Colomer et al. (under review) used global whole-brain connectivity ($ICPC_{WB}$) to normalize connectivity estimates between specific regions as index of how strong the level of central-occipital connectivity was relative to the global connectivity of the whole-brain network. Critically, the specialization of central-occipital connectivity was found to be modulated by motor experience (Colomer et al., under review). In line with this, we normalized the connectivity of the motor-visual network relative to the global levels of whole-brain connectivity. Specifically, we calculated ICPC between each pair of electrodes, which resulted in a 104 x 104 adjacency matrix per participant, condition, trial, frequency step and time step. Adjacency matrices were then averaged across condition, frequencies, and trials and organized in 15 clusters of electrodes (Table 7) to obtain a more robust estimate of connectivity between regions (Xie et al., 2017). Finally, a $ICPC_{WB}$ was calculated per time step, participant, and condition as an average connectivity of all cluster pairs. Next, we normalized $ICPC_{CO}$ relative to $ICPC_{WB}$ of the corresponding participant. Normalization was calculated as the ratio of connectivity between visual and motor areas relative whole-brain: $10*\log10(ICPC_{CO} / ICPC_{WB})$. A value of 0 would indicate identical level of connectivity between the cluster pair and $ICPC_{WB}$. Values > 0 would indicate more connectivity in the central-occipital cluster pair, whereas values

< 0 would indicate less connectivity as compared to ICPC_{WB}. This approach was used to address questions 3 and 4.

Table 7

Electrodes in each of the ROIs used to calculate whole-brain connectivity.

ROI	**Electrodes**
Frontal Pole	'E1', 'E8', 'E9', 'E14', 'E15', 'E21', 'E22', 'E25', 'E32'
Central Frontal	'E4', 'E5', 'E10','E11', 'E12','E16', 'E18','E19
Left Frontal	'E20','E23','E24', 'E26','E27', 'E28', 'E33', 'E34'
Right Frontal	'E2', 'E3', 'E116','E117', 'E118','E122', 'E123', 'E124'
Left Temporal	'E39', 'E40', 'E45', 'E46', 'E47', 'E50', 'E51', 'E57', 'E58'
Right Temporal	'E96', 'E97', 'E98', 'E100', 'E101', 'E102', 'E108', 'E109', 'E115'
Central Z	'E6', 'E7', 'E13', 'E31', 'E80', 'E106', 'E112'
Left Central	'E29', 'E30', 'E35', 'E36', 'E37', 'E41', 'E42'
Right Central	'E87','E93', 'E103', 'E104', 'E105', 'E110', 'E111'
Central Parietal	'E54', 'E55', 'E61', 'E62', 'E78', 'E79'
Left Parietal	'E52', 'E53', 'E59', 'E60', 'E65'
Right Parietal	'E85','E86', 'E90', 'E91', 'E92'
Central Occipital	'E67','E72','E75','E77'
Left Occipital	'E66', 'E69', 'E70', 'E71', 'E74'
Right Occipital	'E76', 'E82', 'E83', 'E84', 'E89'

Analysis Plan

Connectivity modulated by motor familiarity

Our first goal was to identify functional network pattern during observation of a familiar grasping action. Our second goal was to explore the functional network pattern for an action that infants have less experience with, namely pointing. We computed ICPC (-1000ms to 0ms time-locked to action completion) in both observation of grasping and pointing action in 6–9 Hz frequency for the cluster of electrodes pairs ICPC_{CO}, ICPC_{CF}, and ICPC_{CP} in both the left and right hemispheres, and average across trials. Then, we conducted a 2-way mixed ANOVA with within-subjects factors hemisphere (right, left) and electrode-pair (central-frontal, central-parietal, central-occipital) for grasping (*N*=40) and pointing (*N*=42) independently at Time 1.

Connectivity modulated by experience

Our third goal was to explore whether prior experience in pointing modulated relative specialization of central-occipital connectivity. Our fourth goal was to explore whether the pointing intervention modulated relative specialization of central-occipital connectivity. We computed ICPC$_{\mathrm{CO}}$ (-1000ms to 0ms time-locked to action completion) during observation of pointing and normalized ICPC$_{\mathrm{CO}}$ by individual level of ICPC$_{\mathrm{WB}}$. To answer our question of whether prior experience in pointing modulates specific connectivity, we conducted a 2-way mixed ANOVA with between-subjects factor status (pointers (N=28), non-pointers (N=13)) and within-subjects factors hemisphere (right, left) on ICPC$_{\mathrm{CO}}$ relative to ICPC$_{\mathrm{WB}}$ at Time 1. To answer our question of whether directly intervening on infants' pointing experience modulates specific coupling of central-occipital coherence during the observation of pointing, we conducted a 2-way mixed ANOVA with training status as between-subjects factors (training (*N*=21), control (*N*=19)) and within-subjects factors hemisphere (right, left) on ICPC$_{\mathrm{CO}}$ relative to ICPC$_{\mathrm{WB}}$ at Time 2.

Results

Main Analyses

Connectivity modulated by motor familiarity

Do 10-to 12-month-old infants exhibit higher central-occipital connectivity than control cluster pairs during observation of grasping action? The analysis revealed a main effect of electrode-pair ($F(2, 80) = 3.2$, $p = .04$). With sphericity correction, we found a marginally significant effect of electrode-pair (*p* = .054). Follow-up one-tailed pair-wise comparisons revealed that ICPC$_{CO}$ (*M*= .45, *SE* = .01) was significantly higher than both ICPC$_{CP}$ (*M* = .42, *SE* = .01; *t*(40) = 2.478, *p* <.001) and ICPC$_{CF}$ (*M*=.42, *SE*=.01; *t*(40) = 1.8, *p* =.037) (Figure 17(a)). Thus, although marginally significant, this data pattern conceptually replicates the findings in Debnath et al., (2019) and Chung et al.,(2022) for the grasp condition and confirm that motor and visual areas are functionally connected during observation of familiar, grasping action.

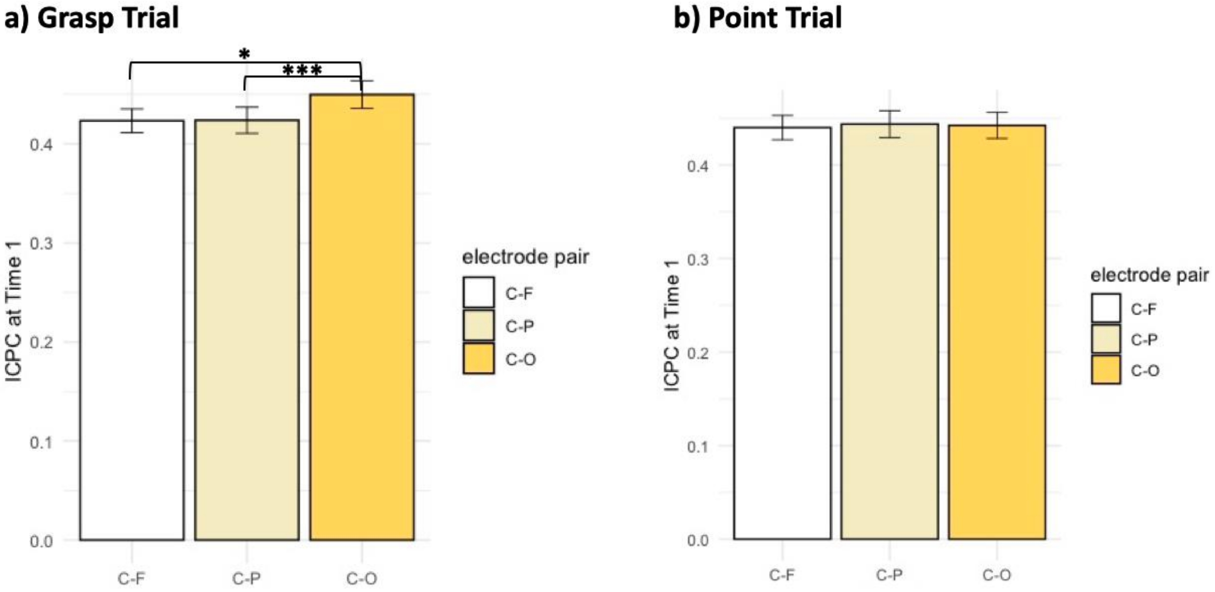


Figure 17. Average of ICPC between channels pairs over frontal, central, parietal and occipital areas in 6–9 Hz frequency band during observation of (a) grasp and (b) point action. Error bar indicates ± 1 SE. ***p < .001, *p<.05.

Do 10-to 12-month-old infants exhibit higher central-occipital connectivity than control cluster pairs during observation of pointing? In the point condition, we did not find evidence for a difference between electrode-pair connectivity(*F*(2, 82) = 1.85, *p* = .164; Figure 17(b)).

Connectivity modulated by experience

Do infants who are reported to be pointers exhibit higher specific central-occipital connectivity as compared to non-pointers? Regression model (*p* >.741) revealed no significant effect of pointing status (*p* >.288), hemisphere (*p* >.567), nor pointing status and hemisphere interaction (*p* >.572). We found no evidence for a difference between pointers and non-pointers on normalized ICPC$_{CO}$ (pointers: *M*= 0.14, *SE*= 0.07; non-pointers: *M*= 0.28, *SE*= .2; *t*(39) = -.69, *p* > .495; see Figure 18).

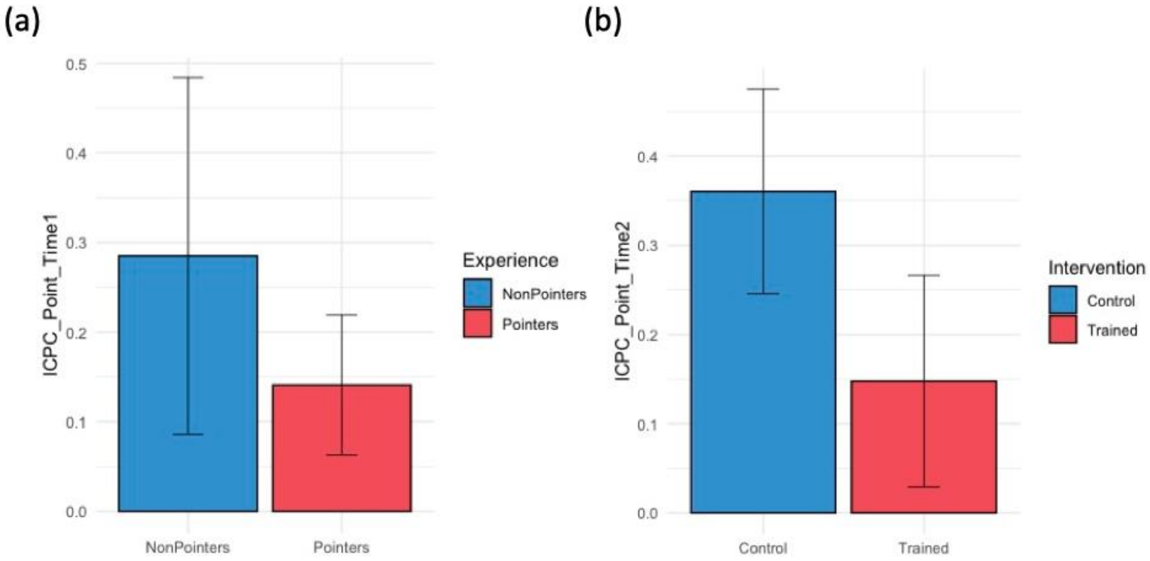


Figure 18. Mean ICPC$_{CO}$ normalized by ICPC$_{WB}$ in 6–9 Hz frequency band during observation of pointing modulated by (a) pointing status and (b) PtS intervention. Error bar indicates ± 1 SE.

Do infants who received the training intervention exhibit higher specific central-occipital connectivity as compared to control group? Regression model (*p* > .509) revealed no significant effect of intervention status (*p* >. 266), hemisphere (*p* > .879), nor intervention status and hemisphere interaction (*p* > .927). There was no evidence for a difference between trained and control group on normalized ICPC$_{CO}$ (trained: *M*= 0.15, *SE*= 0.12; control: *M*= 0.36, *SE*= .11; *t*(38) = -1.43, *p* > .133; see Figure 18).

Descriptive analysis on normalized central-occipital connectivity

Although there was no statistical evidence that indicated a difference in normalized central-occipital connectivity modulated by experience in pointing, those infants who were less experienced in pointing descriptively seemed to exhibit higher $ICPC_{CO}$, indicated by descriptive statistics (Time 1: pointers- *M*= 0.14 (*SE*= .02), non-pointers- *M* = 0.28 (*SE* = .07); Time 2: trained- *M*= 0.15 (*SE*=.12), control- *M*= 0.36 (*SE*= .11). As normalization was calculated as the ratio of connectivity between visual and motor areas relative whole-brain using the formula: $10*\log10(ICPC_{CO} / ICPC_{WB})$, the value of normalized connectivity could be affected by either a difference in the raw $ICPC_{CO}$, in raw $ICPC_{WB}$, or a combination of differences of $ICPC_{CO}$ and of $ICPC_{WB}$ between groups. Therefore, to explore what accounted for descriptive differences in the normalized central-occipital connectivity, we compared raw $ICPC_{CO}$ and whole-brain connectivity levels between groups at each time point.

Results for the level of $ICPC_{CO}$ were comparable between those who were pointers versus non-pointers (pointers: *M*= 0.44, *SE*= 0.01; non-pointers: *M*= 0.44, *SE*= .03) at Time 1, and those who received training versus who were in the control condition (trained: *M*= 0.46, *SE*= 0.02; control: *M*= 0.46, *SE*= .02) at Time 2. If anything, it seemed as if those who were reported as pointers at Time 1 and those in the training intervention at Time 2 (pointers: *M* = 0.42, *SE* = 0.01; trained: *M* = 0.44, *SE*= .02) exhibited higher levels of overall $ICPC_{WB}$ compared to non-pointers and those in the control group (non-pointers: *M* = 0.41, *SE* = 0.02; control: *M* = 0.42, *SE*= .02), respectively (see Figure 19). Although speculative, this suggests that the results of the normalized $ICPC_{CO}$ could be accounted for by a larger contribution of higher levels of global whole-brain activity in the ones who had more pointing experience. Experience with pointing may induced an increase in overall $ICPC_{WB}$. However, it is difficult to confirm this hypothesis with data acquired from distinct time points, as data from Time 1 and Time 2 may include data from different set of participants.

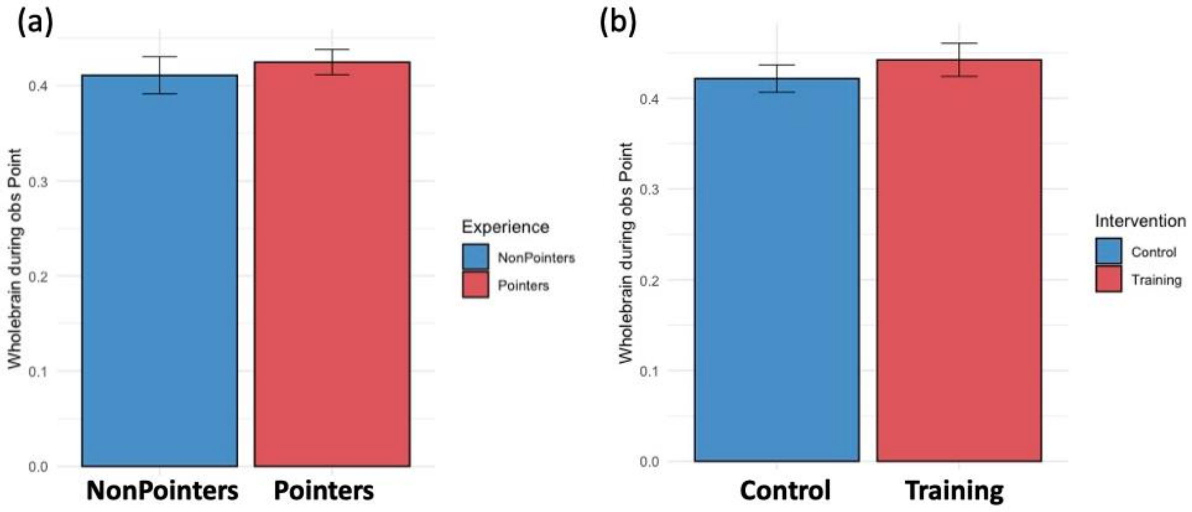


Figure 19. *$ICPC_{WB}$ in 6–9 Hz frequency band during observation of pointing modulated by (a) pointing status and (b) PtS intervention. Error bar indicates ± 1 SE.*

Exploratory Analysis

In order to more accurately describe and detect the role of pointing experience on global connectivity at the whole-brain level, we explored the participants who provided data for both time points (Time 1 and Time 2). This approach provided a total of 29 infants, 16 in the training condition and 13 in the control condition.

First, we compared $ICPC_{WB}$ between time points for each condition during observation of pointing. We conducted a 2-way ANOVA with training status as between-subjects factors (training, control) and within-subjects factors Time (Time 1, Time 2) on $ICPC_{WB}$ during observation of pointing. This model resulted in a significant interaction between training status and time ($F(1, 27) = 9.25$, $p = .005$). Increase in $ICPC_{WB}$ from time 1 to time 2 in the training condition was supported by a pair-wise t-test ($t(15) = -2.3$ $p = .035$). Decrease in $ICPC_{WB}$ from time 1 to time 2 in the control condition was marginally significant (*t*(12) = 2.0 *p* = .068). The results provide evidence that there is an overall increase on the level of ICPC_{WB} from Time 1 (*M*= .38, *SE*= .01) to Time 2 (*M*= .43, *SE*= .02) for the training condition; while there is a trend of a decrease in the control condition (Time 1: *M*= .45, *SE*= .02; Time 2: *M*= .40, *SE*= .02) (Figure 20). We also conducted the same analysis with ICPC_{WB} for each condition and time during observation of grasping (Training: 16, Control: 12) and found no evidence of a relation of time and training status (*p* > .2). Additionally, pairwise between Time 1 and Time 2 for training (*t*(15) = 0.22, *p* > .831) and control (*t*(11)= -1.44, *p* > .177) revealed no evidence for a difference in global connectivity during observation of grasp. This provides evidence that the intervention experience with pointing specifically led to changes in connectivity during observation of the trained action.

Next, we plotted adjacency matrices of difference between Time 1 and Time 2 for each condition to evaluate whether there were selective increases in connectivity across particular pairs of electrodes (Figure 21). The adjacency matrices contribute to the finding that there is an overall increase in ICPC_{WB} between electrode pairs in the training condition, but a decrease in the control condition. Importantly, we did not find any evidence for a difference in any specific pair of electrodes but rather a general increase overall across the brain.

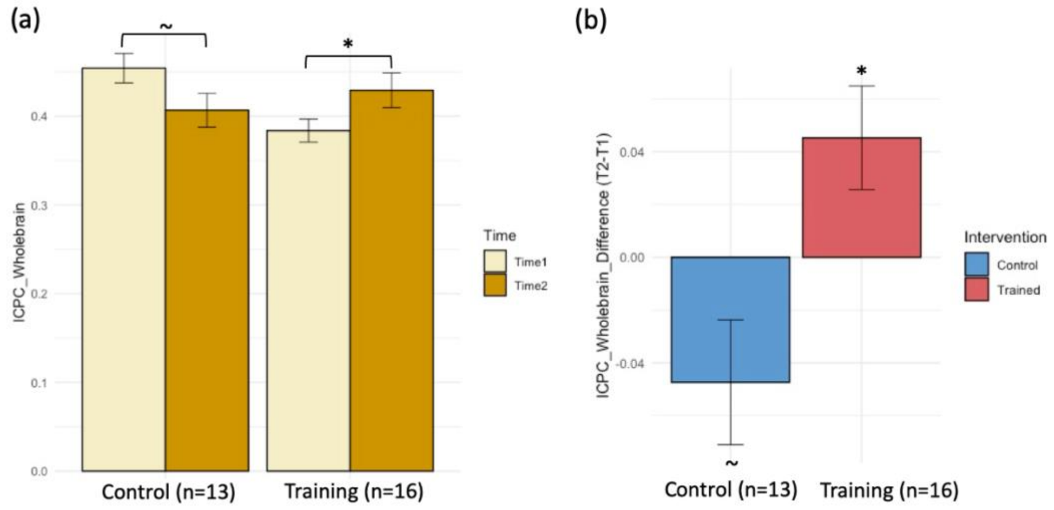


Figure 20. (a) ICPC$_{WB}$ in 6–9 Hz frequency band during observation of pointing at Time 1 and Time 2 (b) Difference of ICPC$_{WB}$ between Time 1 and Time 2. Error bar indicates ± 1 SE.

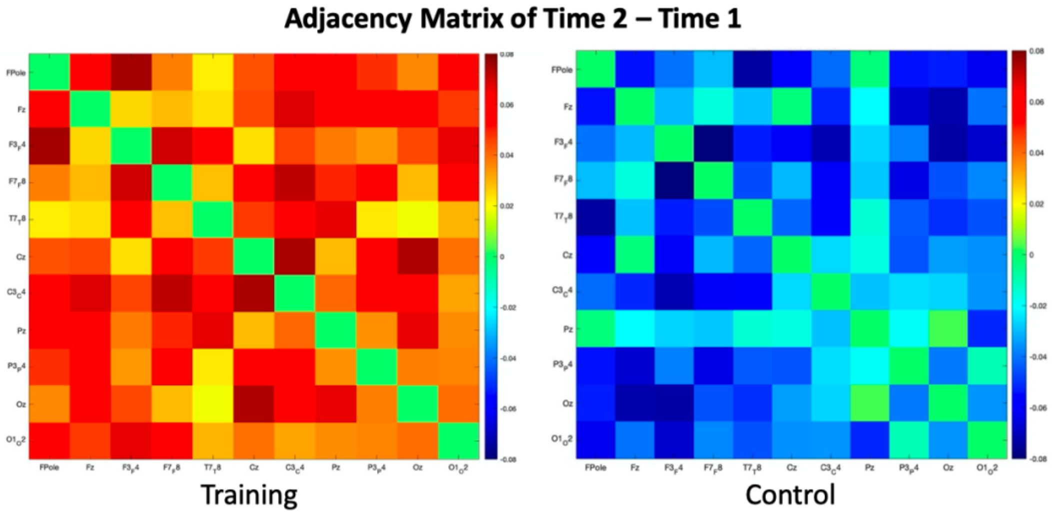


Figure 21. Adjacency Matrix of ICPC difference between Time 1 and 2 across 11 pairs of electrode pairs. ICPC is shown by the color bar (The color towards red indicates higher coherence).

Discussion

In this EEG study, we investigated infants' functional connectivity between neural networks in the alpha (6–9 Hz) frequency range recruited during observation of others' actions as a function of experience. More specifically, we explored whether infants exhibited functional connectivity between motor and visual areas during observation of actions with which they have more experience (i.e. grasping) and during observation of actions with which they have relatively less experience, pointing actions, which also are communicative actions that differ in purpose from grasping actions. Furthermore, we explored whether individual differences in infants' own experience and providing more experience in the action that infants have less experience with (i.e. pointing actions) exerts changes in the level of functional connectivity between motor and visual areas.

First, consistent with prior research, we found that infants' central-occipital phase coherence in the alpha frequency range was higher than phase coherence between areas with shorter distance like central-parietal and central-frontal electrode pairs during observation of familiar grasping actions (Debnath et al., 2019; Chung et al., 2022). In other words, motor (central) and visual (occipital) areas were functionally more connected compared to their connections with other brain regions. However, we did not find evidence for a stronger central-occipital connectivity pattern during observation of pointing. As in Chung et al., (2022), this could be reflective of differential coordination of neural networks during action processing of motorically familiar relative to less familiar action. That is, infants start grasping around 4- to 6-months but pointing production does not emerge until 9- to 10-months of age. Presumably, infants in this study have had at least 6- to 7-months of experience with grasping compared to around 1- or 2-months of experience, if any, with pointing at the time of data collection. The absence of specificity in motor-visual coupling during observation of pointing could be resulting from differences in the amount of motor experience infants have had with grasping versus pointing. It is an open question whether we would observe motor-visual coordination during observation of pointing in older infants who have had extended period with experience in pointing.

Our finding of higher motor-visual coordination during observation of grasping in the current study, along with Debnath et al., (2019) and Chung et al., (2022) gives support to the hypothesis that the neural activity underlying processing and encoding of others' actions may involve an integration of functional connectivity between motor and visual processes. Prior studies have also provided evidence that the strength and specificity of motor-visual coupling could be modulated by infants' action experience (Colomer et al., under review) and the social context (Meyer et al., 2022). This is consistent with a growing literature emphasizing connections among motor and visual networks when processing and encoding action (Pineda, 2005; Kilner, Friston, & Frith, 2007; Paulus, 2012). Kilner and colleagues (2007) propose that action understanding could be supported by reciprocal communication between the visual cortex and the motor cortex and modulated by prior knowledge of the observer, reflecting the brain's attempt to minimize errors between what is observed and what is expected. Relatedly, the ideomotor theory argues that active experience and repeated occurrences of action guides infants' processing of others' action by activating their neural motor representation, and thereby guiding attention to the relevant information (Paulus, 2012). Over the approximately 6 months of experience with grasping, infants would have accrued many opportunities to observe and experience changes in their coordination of grasping and its effects on objects. With prolonged experience and practice, infants produce more stable and accurate movements (Thelen et al., 1993). Thus, prolonged experience could be strengthening efficient connections of relevant areas involved in action processing.

We had hypothesized that experimentally manipulating infants' pointing experience, namely providing them with the Pointing to Success intervention (Rowe & Leech, 2019), would lead to increased motor-visual connectivity during observation of pointing. However, in the current data we did not find evidence of a relation between pointing experience and the level of connectivity of motor-visual networks. We provide two possible explanations for this unexpected result on the lack of relation between pointing experience and motor-visual connectivity .

First, the lack of evidence for a relation between pointing experience and motor-visual connectivity could be due to a limitation of the infants' pointing production measure. The Pointing to Success intervention has been shown to increase infants' pointing production (Rowe & Leech, 2019), and therefore we assumed similar effects in this study as well. However, no direct measure of pointing competence was collected after the training period. Thus, although we were able to detect potential effects of training, we were not able to explore directly whether competence in pointing production was associated with changes in connectivity. Thus, the intervention could have led to interesting variability in infants' pointing experience; however, we may have been limited in our ability to capture and associate pointing production with functional connectivity.

Second, the lack of effects of pointing experience on motor-visual coupling could be due to inherent differences between grasping and pointing. Grasping and pointing share similarities as they are both physical hand movements, though we need to acknowledge the difference in the intention behind grasping actions and pointing. The intention of an action such as grasping is to interact with and make changes on the physical world. However, gestures such as pointing do not have a direct effect on an object like grasping does (Novack & Goldin-Meadow, 2017) but rather is driven by a communicative intent. Gestures are representational actions and the goal is to convey and communicate information (Goldin-Meadow, 2017). Therefore, pointing in and of itself is meaningless as an action unless it is understood as containing information based on communicative intent (e.g.,, get me that out-of-reach object) (Daum et al., 2013). In this sense, the neural regions that become more connected through experience of grasping and pointing may overlap, but will likely also differ.

Functional imaging studies in adults provide evidence that regions involved in action observation, such as the premotor cortex, inferior parietal cortices (IPC), and posterior superior temporal sulcus (STSp), are involved in perception of gestures (Dick & Broce, 2016; Dick et al., 2009; Holle et al., 2008; Straube et al., 2011). At the same time, regions involved in conceptual processing—namely the inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG), underlie processing of semantic and linguistic information in iconic gesture perception (see Yang et al., 2015; Dick & Broce, 2016 for review). Preliminary evidence for this is also found in children (Dick et al., 2012; Wakefield et al., 2013). Wakefield et al., (2013) show age-related differences in processing of gestures such that the frontal and motor regions were not consistently recruited in young children (5-to 10 years) in contrast to adults during observation of co-speech iconic gestures. The authors argue that less experience in producing gestures may be why children do not show consistent activity in the motor cortex, and suggest that activity in the motor cortex may increase with greater experience producing gestures. In contrast to the results in the motor cortex, the pMTG, related to semantic representation of gesture, was activated in both children and adults during perception of co-speech gesture. Notably, the finding that pMTG was recruited during co-speech gesture even in young children and that this activation increased with age, serves as evidence that networks that are involved with processing semantics may be importantly involved in processing gestures. Therefore, motor and visual regions may be functionally connected during observation of others' grasping action, but for pointing, temporal areas like pMTG may play an important role. Utilizing methods that allow better spatial localization such as fMRI or fNIRS will be needed to better understand the regions that are activated during processing of pointing, which will inform us about the dynamic networks involved with perception of pointing.

Although we did not find evidence for an effect of experience on specific connections, we found tentative evidence from exploratory analysis that infants who participated in the training demonstrated enhanced overall connectivity across the brain compared to infants who were not assigned to the training intervention. This effect of training appeared to be specific to the observation of the trained, pointing action. There was no effect of PtS training on whole-brain connectivity during observation of grasping. The relation between training experience and increase in global connections across the brain during observation of pointing suggest that the PtS training experience exerted changes in the level of whole-brain connections, and longer experience with pointing may be required to build on specific and efficient functional connections between motor and visual areas.

The literature in motor development shows that infants explore a wide range of varied movement patterns until they repeatedly produce more effective patterns that work and decrease patterns that do not work (Corbetta et al., 2018; Thelen & Corbetta, 1994). This is complemented by the theory of neuronal group selection (TNGS) which proposes that early in skill acquisition, diverse areas of neurons would be active as movement options are explored. As expertise in skills are acquired, neural activity in parallel would become more focal and efficient (Nishiyori et al., 2016). As such, a similar process might govern the trajectory of perception of action. Introducing a novel experience, like pointing, may be associated with a general increase in connectivity across the brain for processing the new action that infants are beginning to learn. When starting to acquire a new skill, it may be that cross connections throughout the brain emerge with the attempt to encode and process the upcoming unfamiliar stimuli (Friston, 2005). This could involve an integration of long distance connections (associated with planning and control) and local connections (associated with perception and cognitive processes) (Thatcher et al., 1986). Over time, more efficient routes are built and strengthened via experience and expertise as infants accumulate experience in producing a novel action and predicting its effects, as well as observing and processing the same actions produced by others, potentially showing an inverted-‘U’ shaped pattern of global connectivity with development. Our findings regarding a potential increase in global connectivity across the brain for infants who received pointing training may depict the early stages of this learning process. Our findings regarding higher motor-visual connectivity relative to neighboring areas during observation of grasping may reflect later stages of learning during which the brain has specialized and formed efficient paths in processing grasping actions through accumulation of experiences with grasping. Thus, the current study raises the idea that different phases in action learning may be related to differential changes in the neural underpinnings of action perception, modulated by experience.

Findings from prior literature provide conceptual evidence in support of this hypothesis. For instance, research indicates onset of locomotion is associated with overproduction of cortical connections across the scalp (Bell & Fox, 1996; Corbetta et al., 2014; Xiao et al., 2018). Bell & Fox, (1994) found that 8-month-old infants who have just begun to crawl exhibited greater overall connectivity than either pre-locomotor infants or expert crawlers. Similar findings were reported with infants who have started walking (Corbetta et al., 2014). These findings suggest an interplay between the onset of locomotion and changes in cortical organization, leading to abundant connection across the scalp. However, these studies point to changes in the general cortical organization, since the findings are from data collected and analyzed during resting-state or sleep, and not based on activity during an experience-related action observation per se. There are only a handful of studies that have measured task-related functional connectivity during action observation (Amoruso et al., 2017; Rotem-Kohavi et al., 2014). These studies depict a change from ‘disorganization to order’ modulated via experience and expertise. Amoruso et al., (2016) examined whether expertise in tango dance would modulate differences of variability in EEG functional networks during observation of tango dance actions in adults. They found that there was less variability and more robust functional architecture in networks of expert tango dancers compared to beginners when they observed others dance. A similar pattern was found in infants as well. Rotem-Kohavi et al., (2014) investigated functional networks in 4-to 11-month-old infants and found that network activity in response to observing non-experienced motion (i.e., independent walking) was much less structured compared to that of adults; while, there was no evidence of a difference during motorically familiar and experienced motion (i.e., grasping). These findings suggest that novices and beginners may exhibit less structured and inefficient network activity during task-related observation compared to experts, and that networks become structured and organized via experience. However, these studies do not indicate whether expertise in experience leads to changes in specificity of a particular network.

Future Directions

Regarding the link between action experience and action perception, it would be important to expand on and investigate the relation between expertise in pointing and functional connectivity. More specifically, future research is needed to test whether infants’ pointing competence is indeed associated with changes in global levels of whole-brain connectivity with relatively short experience, and changes in functional motor-visual connectivity with longer experience. Relatedly, it is unclear whether patterns of functional connectivity support comprehension of pointing. Behavioral studies converge on evidence that action development is related to changes in perception of others’ actions and responses to others’ actions. However, whether dynamic functional connectivity can be assessed as a neural correlate underlying this change is yet to be examined.

Another important direction for future research is to articulate the process and trajectory of ‘how’ the networks change to be more structured and efficient through experience. How does motor experience and training build on efficient connections and how does that relate to changes in overall connections across the brain? Does it affect connections specifically when processing the “*trained*” action? With technological advances, developmental researchers can also utilize innovative methods that allow comparable interpretation with adult research on functional connectivity. For instance, using EEG or fNIRS and providing ways to visualize and quantitatively articulate network organization, i.e. graph theory or analyses that are analogous, would allow integration and interpretation with prior adult studies on functional connectivity.

Conclusion

In sum, we replicate previous research showing higher motor-visual connectivity during observation of others’ grasping action in infancy, as compared to connectivity between other regions. However, we did not find such region-specific evidence during observation of pointing, though we found preliminary evidence for an increase in overall connectivity across the infant brain. We acknowledge that short-term experience may not exert fast changes and connections across relevant regions on action perception. This study emphasizes the need to investigate and document the process by which active experience affects changes in functional connectivity, and whether experience and expertise generate specific and efficient routes across key brain regions during perception of action. Our study paves the way for future developmental cognitive neuroscience research to investigate functional neural networks and its implications on cognitive development.

CHAPTER 5: GENERAL DISCUSSION

Considerable research suggests that action perception is associated with and shaped by experience in the first year of life (Hunnius & Bekkering, 2014; Woodward, 2013; Woodward, 2009; Woodward & Gerson, 2014). In this dissertation, I investigated the relation between action experience and action perception, considering questions that have been left open by prior research. First, active experience has been measured in two ways– by assessing the development of motor skills and by assessing the effects of short-term training interventions– leaving open questions of how these two aspects of experience may interact in supporting action understanding in infancy. By obtaining a metric of infants' motor development and conducting a training intervention within the same study, I aimed to explore the potential interplay between the types of experience and its role on action understanding. Second, behavioral data from infants show that both variations in motor skills and induced short-term experience are linked to action perception. But they leave open the question concerning the mechanisms that may support the action and perception link. In the second and third studies in this dissertation, I investigated the neural correlates that underlie infants' perception of actions that are within versus outside the repertoire of actions they are able to produce, and the neural correlates that are associated with action training.

Summary of findings

In Study 1, I assessed how in-lab training and infant's motor skills interact in supporting action understanding in infancy. First, I replicated both prior findings that infants' own action competence and action training is associated with infants' analysis of others' actions. Further, the results indicated a compensatory relation between action training and infants' own motor skills by demonstrating that action training improved action understanding, particularly for those infants who started out with lower means-end motor skills. This pattern was specific to means-end skills not accounted for by general metrics of motor development.

In Study 2, I assessed the neural underpinnings reflecting the role of motor experience on action perception. I aimed to better isolate action-specific processes and visual processes to understand their contributions during action perception, and further investigated whether functional connectivity of these processes is modulated via motor development during action perception. I found that while motor and visual processes were evident for both motorically familiar and unfamiliar actions, neural motor activity was stronger for familiar grasping actions that infants had prolonged experience with. When I extended the analyses beyond mu power to the functional connectivity of motor and visual processes, selective motor-visual functional connectivity was found during observation of familiar action, a pattern not observed for novel action. These results revealed a distinctive pattern of neural correlates (i.e. functional motor-visual connectivity) associated with action development suggesting that experience over developmental time matters in the context of action perception.

In Study 3, I asked whether similar patterns of connectivity are evident during infants' perception of a newly trained action. To do so, I explored whether intervention experience with a newly emerging communicative action, i.e. pointing, exerted changes in the level of functional connectivity between motor and visual areas in infancy. I replicated the findings of higher functional motor-visual connectivity during observation of grasping action. However, this pattern was not observed during observation of pointing, and was not modulated by infants' pointing experience. I found preliminary evidence that pointing training enhanced global connectivity across the brain compared to those who were not assigned to the intervention. This suggests that functional connectivity based on intervention experience may initially be broadly distributed across the whole-brain network, and that the infant brain may need prolonged experience to reliably build on specific network activations.

Taken together, the results across the three studies in this dissertation go beyond prior work on the link between active experience and action perception by demonstrating the nature of the relation between infants' own action development and action training in their effects on action perception. Particularly, I found in Study 1 that the effect of action training on action perception was especially prominent in those coming in with less advanced motor skills. Training provided an opportunity for infants with less advanced motor skills to use the cane in a coordinated manner and to direct their attention to goals, which they could not yet glean on their own. Contrary to infants coming in with less motor skills, it is possible that the training task had primed infants with advanced motor skills of what they already accrued over experience. This raises an open question of whether task difficulty modulates the interplay between motor development and training. Future studies should continue to explore whether providing more demanding action training exerts a different pattern of an interplay between infants' motor skills and training on action understanding.

Furthermore, I expanded on the infant EEG mu rhythm procedures frequently used in infant neuroscience to explore connectivity between processes, revealing critical insights on meaningful dynamic connections that are associated with action development (specialized motor-visual connectivity) and action training (increased global connectivity) during action perception. With advanced neuroimaging techniques, studies using fMRI have been able to trace and map changes in neural reorganization in the developing baby brain (see Gao et al., 2017, Zhao et al., 2019 for a review). Importantly, these studies have noted that changes in functional connections across systems have been implicated to be associated with behavior and cognitive abilities (Gao et al., 2017). I acknowledge that further work is needed to fully understand the neural correlates of intervention experience, as the neural activity associated with action training in this study was explored with a different kind of action (i.e. pointing) in comparison to the action associated with prolonged action development (i.e. grasping). Nevertheless, this dissertation sheds light on a novel interpretation that infants' experience builds on functional connections across networks that potentially support their ability to make sense of actions and interactions of others.

Findings from this dissertation also provide insights to a story of how active experience impacts perception of others' actions and the changes in the underlying mechanism governing action perception across the first year of life. It is clear that active motor experience is one of the contributing factors that shapes cognition across the life span. Nevertheless, not much is documented on the developmental shift of neural connections that occur regarding infants' action perception abilities during the transition from being a novice to an expert in an action. Understanding the trajectory of this change is important to depict and delineate a panoramic picture of the link between active experience and action perception.

Findings of Studies 2 and 3 provide a good starting point on this process. In Study 2, I have measured functional connectivity, and competence measured for those who are experts, and have had long-term experience in that action (i.e. grasping). In Study 3, we have measured functional connectivity right at the midst of learning a new action (i.e. pointing). Together, these findings introduce a plausible hypothesis: During the initial stages of functional action development as infants start acquiring a new skill, the brain may not have ways to process novel actions. Thus, it may be that cross connections throughout the brain emerge as infants attempt to make inferences about the unfamiliar stimuli (Friston, 2005). Infants would start to gain experience and expertise in producing the novel action and predicting its effects, as well as observing and processing the same actions produced by others. This active experience could build on more efficient routes (i.e. motor-visual connectivity) for processing and understanding the action.

Similar perspectives have already been suggested for the emergence of functional motor action. Perspectives such as dynamic systems theory (Thelen & Corbetta, 1994), theory of neuronal group selection (TNGS) (Sporns & Edelman, 1993), and developmental systems approach (Gottlieb et al., 2006) all argue that functional behaviors are the product of the interactions among the nervous system, environment, and body dynamics. The ontogeny of new patterns of behavior such as reaching are discovered initially through wide range of exploration, leading to the reproduction and fine-tuning of the attempts that have proven successful (Corbetta et al., 2018). Relatedly, the TNGS posits that the initial stages of action development are associated with highly redundant and excessive synaptic connections, and with experience, neural activity would become more focal, efficient, and topographically specialized (Sporns & Edelman, 1993). These perspectives are supported by both behavioral (Bertenthal & Clifton, 1998; Corbetta et al., 2018; Thelen & Corbetta, 1994; von Hofsten, 1989) and neural empirical evidence (Nishiyori et al., 2016; Xiao et al., 2018; Corbetta et al., 2014; Bell & Fox, 1994) in action development.

The working hypothesis regarding the trajectory of action perception is also conceptually compatible with the well-known process of perceptual narrowing in developmental psychology, a phenomenon in which perceptual mechanisms starts out broad and non-specific, but become fine-tuned as a function of experience that is found in the domain of face (Haan et al., 2002; Kelly et al., 2007; Pascalis et al., 2002), speech (Kuhl et al., 2006; Polka & Werker, 1994; Tees & Werker, 1984; Werker & Tees, 1984), and music (Trainor et al., 2012; Trehub & Hannon, 2006). More work is needed to confirm whether action perception is indeed involved with fine-tuning of functional connections. That is, future work should confirm whether motor-visual connections would eventually emerge with increased amount of sensorimotor experience.

Future Directions

The findings of this dissertation also raise new avenues for future research. First, although the findings of Study 2 are in line with a growing body of evidence developmental neuroscience findings indicating that infants demonstrate more neural motor activity and functional motor-visual connectivity is active during familiar action that infants have experience with (Cannon et al., 2016; Gerson, Bekkering, & Hunnius, 2015; Paulus et al., 2012; van Elk et al., 2008; Yoo et al., 2016; Chung et al., 2022; Debnath et al., 2019), the current set of findings lack direct evidence to validate the hypothesis that the neural responses reflects the analysis or interpretation of the agent's action per se. Without measurements or controls to associate neural activity with participants' social cognition, the functional significance of this activity on action perception is unclear (Filippi et al., 2016). To date, there are two studies that explored the relation between neural motor activation and action understanding (Filippi et al., 2016) and imitation (Köster et al, 2020). For instance, Filippi et al. (2016) measured alpha oscillations in 7-month-old infants while infants participated in the goal imitation paradigm (Hamlin et al., 2008). They found that the strength of mu suppression during observation of grasping actions in 7-month-olds was related to the infants' propensity to imitate the goal of the observed actor by subsequently selecting the same toy that the actor had grasped. This study provides first evidence that neural motor activation may play a role in assessing the other agent's goal. Köster et al., (2020) investigated the relationship between this alpha activity and subsequent imitation of the observed actions in 10- and 20-month-olds. They found that, overall, infants' action observation was associated with an increase in alpha power, rather than a decrease in alpha power, thereby indexing inhibition of the sensorimotor cortex (rather than an increase in sensorimotor activation). Potential methodological explanations for this unexpected finding has been suggested (de Klerk & Kampis, 2021). Nevertheless, studies like these open interesting insights and interpretations on the relation between neural responses and cognition in infancy.

To start, it could be valuable to re-analyze Filippi et al., (2016) and explore whether dynamic functional network activity (e.g., higher level of motor-visual connectivity) is directly associated with subsequent goal responses in Filippi et al., (2016), as found in the level of mu suppression. Moreover, an integration of methods, such as measuring EEG during the goal imitation task in Study 1 would provide a direct way that sheds light on the functional significance of neural activity during action perception modulated by aspects of infants' experience. For instance, it would provide an opportunity to explore whether the relation between specialization in motor-visual connectivity and infants' goal responses is modulated by infants' motor skills (imitation-first condition), and whether the connectivity patterns prior to subsequent goal responses during the goal imitation paradigm differs for those who are trained versus not. Critically, this design would allow a systematic comparison of whether action training is indeed associated with increases in global connections across the brain.

Moreover, prior literature suggests that the motor system undergoes specialization in activity with accumulated experience in action execution (Nishiyori et al., 2016, 2020; Bell & Fox, 1994; Corbetta et al., 2014). A few studies examining resting-state mu rhythm oscillations (utilized as a biomarker of motor-related function) with infants documented functional changes across the mu rhythm in relation to emerging functional motor skills (Xiao et al., 2016, 2018). In a recent study, Xiao et al., (2018) found an increase in resting-state mu power with age and that functional fronto-parietal connectivity was positively related to emergence of reaching skills. Even so, it is currently unknown how these execution-related neural shifts are implicated in perception-action link (Gonzales et al., 2016). In order to fully understand the mechanism of how action development interacts with changes in action perception, longitudinal studies that directly measure changes in participants' motor competence, its effects on brain reorganization, and how these changes relate to action perception are critically needed.

Conclusion

In conclusion, the research in this dissertation sheds new light on the interplay between action development and action training on action perception during early development, and provides evidence on the underlying neural mechanisms that are associated with this link. This work further broadens the scope of infant EEG mu rhythm procedures and its interpretations on the neural correlates of action perception by shedding light on dynamic functional network activity during action perception associated with action development and action training. This dissertation paves the way for future developmental cognitive neuroscience research to investigate changes in functional neural networks that occur with experience and its implications on action perception.

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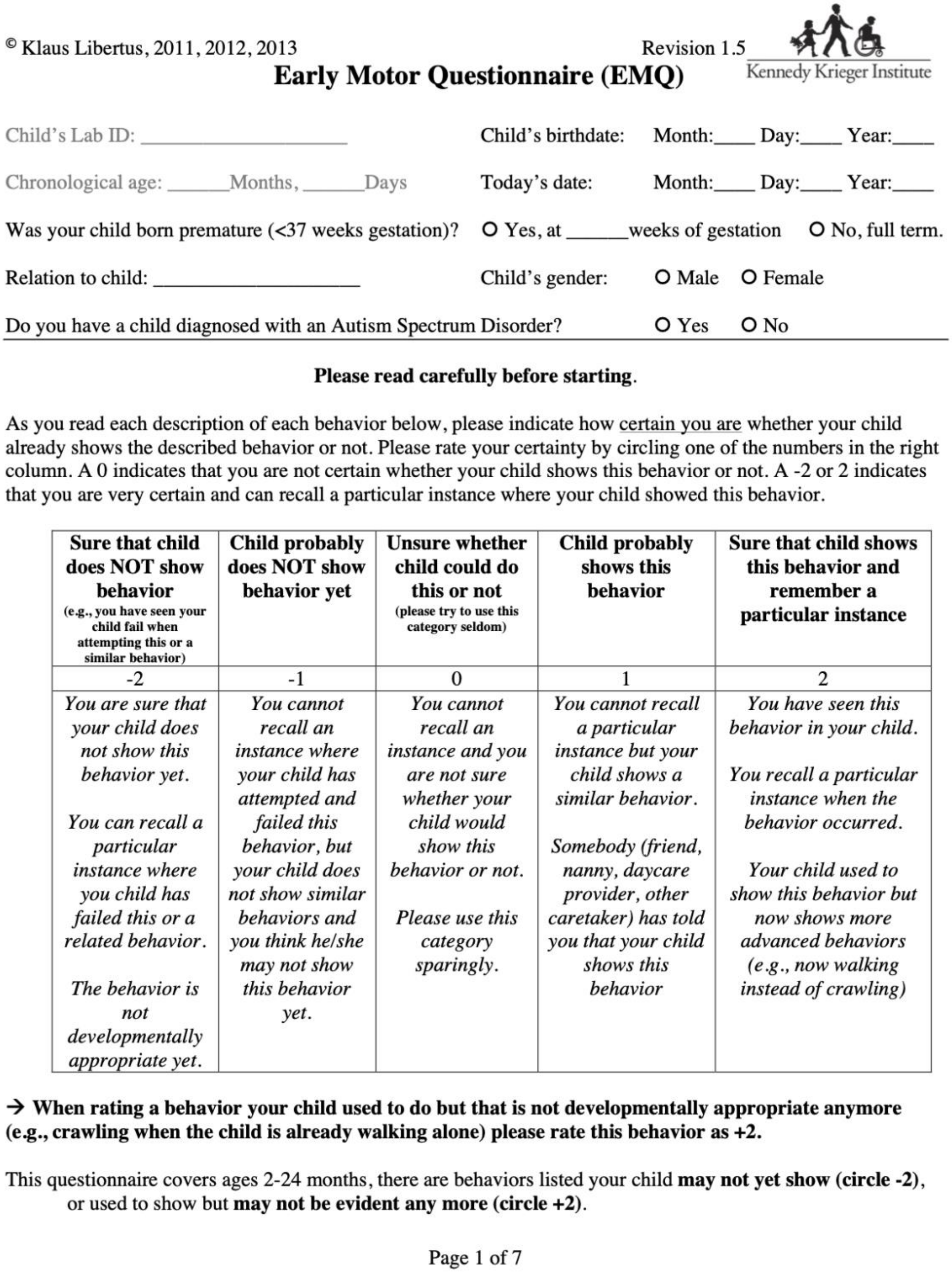
APPENDIX A: Early Motor Questionnaire



Revision 1.5

Kennedy Krieger Institute

Early Motor Questionnaire (EMQ)

Child's Lab ID: ____________________ Child's birthdate: Month:____ Day:____ Year:____

Chronological age: ______Months, ______Days Today's date: Month:____ Day:____ Year:____

Was your child born premature (<37 weeks gestation)? ○ Yes, at ______weeks of gestation ○ No, full term.

Relation to child: ____________________ Child's gender: ○ Male ○ Female

Do you have a child diagnosed with an Autism Spectrum Disorder? ○ Yes ○ No

Please read carefully before starting.

As you read each description of each behavior below, please indicate how certain you are whether your child already shows the described behavior or not. Please rate your certainty by circling one of the numbers in the right column. A 0 indicates that you are not certain whether your child shows this behavior or not. A -2 or 2 indicates that you are very certain and can recall a particular instance where your child showed this behavior.

Sure that child does NOT show behavior (e.g., you have seen your child fail when attempting this or a similar behavior)	**Child probably does NOT show behavior yet**	**Unsure whether child could do this or not** (please try to use this category seldom)	**Child probably shows this behavior**	**Sure that child shows this behavior and remember a particular instance**
-2	-1	0	1	2
You are sure that your child does not show this behavior yet. *You can recall a particular instance where you child has failed this or a related behavior.* *The behavior is not developmentally appropriate yet.*	*You cannot recall an instance where your child has attempted and failed this behavior, but your child does not show similar behaviors and you think he/she may not show this behavior yet.*	*You cannot recall an instance and you are not sure whether your child would show this behavior or not.* *Please use this category sparingly.*	*You cannot recall a particular instance but your child shows a similar behavior.* *Somebody (friend, nanny, daycare provider, other caretaker) has told you that your child shows this behavior*	*You have seen this behavior in your child.* *You recall a particular instance when the behavior occurred.* *Your child used to show this behavior but now shows more advanced behaviors (e.g., now walking instead of crawling)*

→ When rating a behavior your child used to do but that is not developmentally appropriate anymore (e.g., crawling when the child is already walking alone) please rate this behavior as +2.

This questionnaire covers ages 2-24 months, there are behaviors listed your child **may not yet show (circle -2)**, or used to show but **may not be evident any more (circle +2)**.

Sure that child does NOT show behavior (e.g., you have seen your child fail when attempting this or a similar behavior)	**Child probably does NOT show behavior yet**	**Unsure whether child could do this or not** (please try to use this category seldom)	**Child probably shows this behavior**	**Sure that child shows this behavior and remember a particular instance**
-2	-1	0	1	2

Section 1: Gross motor skills

(49 items)

In the following please think about your child's gross motor skills and motor control. These skills relate to how easily your child is able to control his or her own movements, orient, obtain toys, or move around the room.

→ Skills are organized by posture and increase in difficulty within each posture.

When held up against your shoulder, your child will

01) snuggle in and rest at your body immediately?	-2	-1	0	1	2
02) hold head steady without support when looking around?	-2	-1	0	1	2
03) hold head steady while you bounce up and down	-2	-1	0	1	2
04) hold head steady while you walk or bend down	-2	-1	0	1	2

When lying on his/her tummy, your child will

05) lift head slightly up from the ground and turn head to one side	-2	-1	0	1	2
06) lift head fully off the ground by pushing on his/her forearms	-2	-1	0	1	2
07) roll over to be on his/her back	-2	-1	0	1	2

When lying on his/her back, your child will

08) move arms and legs vigorously (kicking and reaching movements)	-2	-1	0	1	2
09) hold on to your hands and pull herself/himself up to a sit without help	-2	-1	0	1	2
10) roll over to be on tummy	-2	-1	0	1	2
11) roll over to one side and push up into a crawling position	-2	-1	0	1	2
12) get up into a standing position by rolling to a side without help or aids	-2	-1	0	1	2
13) stand up without rolling to a side by sitting up and then moving forward	-2	-1	0	1	2

When sitting on your lap with back support provided by you, your child will

14) hold his/her head up and steady when looking around the room	-2	-1	0	1	2

When placed into a crawling position resting on hands and knees, your child will

15) shift weight to one arm and extend the other to reach, wave, or point	-2	-1	0	1	2
16) lift up bottom and remain in this position for a short time?	-2	-1	0	1	2
17) crawl forward for a few steps (3-5)?	-2	-1	0	1	2

When placed into a sitting position on the floor, your child is able to

18) sit independently without support (hands lifted up)	-2	-1	0	1	2
19) use hands and legs to scoot forward on his/her bottom?	-2	-1	0	1	2
20) maintain a stable sitting position while turning head and torso to look around?	-2	-1	0	1	2
21) hold on to some furniture and pull into a standing position	-2	-1	0	1	2
22) shift into a crawling position and try to crawl forward	-2	-1	0	1	2

Sure that child does NOT show behavior (e.g., you have seen your child fail when attempting this or a similar behavior)	**Child probably does NOT show behavior yet**	**Unsure whether child could do this or not** (please try to use this category seldom)	**Child probably shows this behavior**	**Sure that child shows this behavior and remember a particular instance**
-2	-1	0	1	2

When placed into a standing position, your child will

23) bounce up and down slightly while holding on to you with both hands	-2	-1	0	1	2
24) take a few (wobbly) steps while holding on to you with one hand	-2	-1	0	1	2
25) stand alone for a few seconds without help	-2	-1	0	1	2
26) walk 4 or 5 steps independently with arms raised	-2	-1	0	1	2
27) is able to stand and toss a ball at the same time without loosing balance and falling over	-2	-1	0	1	2
28) squat down to pick up a toy from the ground	-2	-1	0	1	2

When placed in front of a flight of stairs, your child is able to

29) creep up the stairs independently?	-2	-1	0	1	2
30) walk up stairs (4-5 steps) with both hands held by a caregiver?	-2	-1	0	1	2
31) walk up stairs (4-5 steps) with one hand held by a caregiver?	-2	-1	0	1	2
32) walk up stairs alone while holding onto a wall or railing?	-2	-1	0	1	2
33) walk up stairs without aid? (4 or more steps)	-2	-1	0	1	2
34) creep down the stairs independently (feet first)?	-2	-1	0	1	2
35) walk down stairs without aid or help?	-2	-1	0	1	2

When moving around freely, your child will

36) run short distances around the room	-2	-1	0	1	2
37) run around the room making turns and stops without falling	-2	-1	0	1	2
38) kick a ball or small toy forward with one of his/her feet	-2	-1	0	1	2
39) stand on one foot when holding your hand (e.g., during dancing)	-2	-1	0	1	2
40) demonstrate walking on toes for a short time	-2	-1	0	1	2
41) jump in place with both feet up in the air (e.g., during dancing)	-2	-1	0	1	2
42) hop in place while balancing on one foot	-2	-1	0	1	2
43) jump down from boxes, small steps, or similar without falling	-2	-1	0	1	2

When walking down a hallway or small room, your child will

44) walk in a straight line for a few (4-5) steps with arms up	-2	-1	0	1	2
45) walk in a straight path without bumping into the walls using arms to balance	-2	-1	0	1	2
46) walk in a straight line with arms lowered and swinging freely	-2	-1	0	1	2

During free play or pretend play, you notice your child is able to

47) walk backwards for several (5 or more) steps?	-2	-1	0	1	2
48) jump forward over small obstacles such as a curb or box?	-2	-1	0	1	2
49) purposefully do a somersault?	-2	-1	0	1	2

Sure that child does NOT show behavior (e.g., you have seen your child fail when attempting this or a similar behavior)	**Child probably does NOT show behavior yet**	**Unsure whether child could do this or not** (please try to use this category seldom)	**Child probably shows this behavior**	**Sure that child shows this behavior and remember a particular instance**
-2	-1	0	1	2

Section 2: Fine motor skills

(48 items)

In the following please think about your child's fine motor skills such as reaching, grasping, orienting, and drawing. How easily can your child manipulate small objects and coordinate his/her hands?

→ Skills are organized by posture and increase in difficulty within each posture.

While observing your child lying on his/her back in a crib, baby gym, or on the floor, you notice your child

01) holding his/her hands close to the body in little fists occasionally?	-2	-1	0	1	2
02) tightly holding on to a toy placed into his/her hand?	-2	-1	0	1	2
03) bringing both hands together near the face, chest, or tummy?	-2	-1	0	1	2
04) opening up the fingers of each hand spontaneously?	-2	-1	0	1	2
05) spontaneously bringing one hand up to the mouth?	-2	-1	0	1	2
06) pulling on a string to obtain an object beyond reach?	-2	-1	0	1	2

When sitting on your lap or in a high chair while playing with toys, you notice your child is able to

07) successfully hold on to a small object such as a ring or stick?	-2	-1	0	1	2
08) reach for a toy with one hand by extending the arm and fingers?	-2	-1	0	1	2
09) successfully grasp a toy with one hand following a reach?	-2	-1	0	1	2
10) transfer toys from one hand to the other hand?	-2	-1	0	1	2
11) purposefully bang toys on the table or tray?	-2	-1	0	1	2
12) purposefully drop toys or throw them off the table?	-2	-1	0	1	2
13) manipulate one toy with both hands simultaneously?	-2	-1	0	1	2
14) place beads on a string without help?	-2	-1	0	1	2

When sitting without support on the floor or in a small chair, you notice your child

15) shaking small toys such as a rattle without loosing balance?	-2	-1	0	1	2
16) picking up small objects (e.g., cheerios) using index finger and thumb?	-2	-1	0	1	2
17) holding one toy in each hand and banging them together?	-2	-1	0	1	2
18) taking toys out of a box, bucket, or container?	-2	-1	0	1	2
19) putting toys into a box, bucket, or container?	-2	-1	0	1	2
20) stacking 3 or more blocks vertically?	-2	-1	0	1	2

When playing with a book or magazine, most of the time your child will

21) turn several pages at the same time?	-2	-1	0	1	2
22) turn one page at a time?	-2	-1	0	1	2

Sure that child does NOT show behavior (e.g., you have seen your child fail when attempting this or a similar behavior)	Child probably does NOT show behavior yet	Unsure whether child could do this or not (please try to use this category seldom)	Child probably shows this behavior	Sure that child shows this behavior and remember a particular instance
-2	-1	0	1	2

When drawing on a sheet of paper using a crayon or pen, your child will

23) grip the crayon with a fist?	-2	-1	0	1	2
24) grip the crayon with thumb and index finger (right side down)?	-2	-1	0	1	2
25) make a mark on the paper in any direction?	-2	-1	0	1	2
26) mark vertical lines on the paper?	-2	-1	0	1	2
27) mark horizontal lines on the paper?	-2	-1	0	1	2
28) copy and reproduce simple drawings (e.g., circle) by a caregiver?	-2	-1	0	1	2
29) copy and reproduce multi-stroke drawings (e.g., square)?	-2	-1	0	1	2
30) copy and reproduce complex drawings (e.g., letters, triangle, cross)?	-2	-1	0	1	2
31) draw letters the right way round and proportional in size?	-2	-1	0	1	2

When playing with a sheet of paper, your child can do the following with the paper

32) grasp the paper and pull or wrinkle it?	-2	-1	0	1	2
33) roll the paper in a tube shape?	-2	-1	0	1	2
34) fold the paper three times (any way)?	-2	-1	0	1	2
35) fold the paper in half two times to form a square?	-2	-1	0	1	2

When playing with a shape sorter or piggy bank, you notice your child

36) is able to successfully place circular shapes into the sorter?	-2	-1	0	1	2
37) is able to place complex shapes (e.g., triangle) into the sorter?	-2	-1	0	1	2
38) rotates and successfully inserts small objects (e.g., coins)?	-2	-1	0	1	2

When playing with building blocks, you notice your child will

39) stack block towers of 6 blocks or more?	-2	-1	0	1	2
40) add a block to a tall tower without knocking it over?	-2	-1	0	1	2
41) copy you or other children by building a similar tower?	-2	-1	0	1	2

When playing with activity books or color books, your child occasionally will

42) fill in color areas while staying inside the object's boundaries?	-2	-1	0	1	2
43) connect lines in a maze or draw by numbers game?	-2	-1	0	1	2

When getting dressed or undressed, your child sometimes is able to

44) open shoelaces by pulling?	-2	-1	0	1	2
45) open Velcro latches by pulling?	-2	-1	0	1	2
46) open zippers by pulling?	-2	-1	0	1	2
47) open buttons?	-2	-1	0	1	2
48) close a zipper or buttons by himself/herself?	-2	-1	0	1	2

Sure that child does NOT show behavior (e.g., you have seen your child fail when attempting this or a similar behavior)	**Child probably does NOT show behavior yet**	**Unsure whether child could do this or not** (please try to use this category seldom)	**Child probably shows this behavior**	**Sure that child shows this behavior and remember a particular instance**
-2	-1	0	1	2

Section 3: Visual reception

(31 items)

In the following please think about your child's visual and receptive skills. Can your child make out small details on pictures? Does your child orient to sounds and respond to stimulation easily?

→ Skills are organized by posture and increase in difficulty within each posture.

While lying on his/her back in a crib, baby gym, or on the floor, your child sometimes will

01) fixate on objects that are moved close to your child's eyes?	-2	-1	0	1	2
02) turn the head all the way to one side (90°) to follow your face?	-2	-1	0	1	2
03) notice his/her own hands and look at them for some time?	-2	-1	0	1	2
04) swat at toys hanging from a baby gym or car seat?	-2	-1	0	1	2

While sitting on your lap or fully supported in a high chair or car seat, you have noticed your child

05) follow a person or object by turning his/her head slightly?	-2	-1	0	1	2
06) turn the head from side to side (180°) to follow something interesting?	-2	-1	0	1	2
07) shift eye gaze back and forth between your face and an object?	-2	-1	0	1	2
08) focus on a far away object (e.g., toy across the room)?	-2	-1	0	1	2
09) orient to noises and visually search for the cause of the noise?	-2	-1	0	1	2
10) extend his/her arms towards an object that is close by?	-2	-1	0	1	2
11) pull on a string or cloth to obtain a connected object?	-2	-1	0	1	2

When your child is sitting on the floor on his/her own without support, your child will

12) pull an object to reveal another object that was hidden underneath?	-2	-1	0	1	2
13) find a hidden object when given multiple choices to search?	-2	-1	0	1	2
14) turn cups right side up during play?	-2	-1	0	1	2
15) sometimes use objects functionally and appropriately on him/herself (e.g., comb own hair with comb, eat with spoon)?	-2	-1	0	1	2
16) sometimes use objects functionally and appropriately on others (e.g., comb your hair, feed puppet)?	-2	-1	0	1	2

When playing with your child sitting at a table or in a high chair with tray attached, your child will

17) open and close a book using two hands?	-2	-1	0	1	2
18) touch pictures in a book and vocalize about them?	-2	-1	0	1	2
19) turn cups right side up during play?	-2	-1	0	1	2
20) nest 2 or 3 nesting cups or containers by putting one inside another?	-2	-1	0	1	2
21) nest 4 or more nesting cups or toys correctly?	-2	-1	0	1	2

When playing with a wooden puzzle or form board, you child is able to

22) insert simple, rounded shapes correctly into the puzzle?	-2	-1	0	1	2
23) insert shapes with edges (e.g., triangle) correctly into the puzzle?	-2	-1	0	1	2

Sure that child does NOT show behavior (e.g., you have seen your child fail when attempting this or a similar behavior)	Child probably does NOT show behavior yet	Unsure whether child could do this or not (please try to use this category seldom)	Child probably shows this behavior	Sure that child shows this behavior and remember a particular instance
-2	-1	0	1	2

When being asked to find or show an item, your child is able to

24) find items of pairs (e.g., where is the other shoe, sock, glove)?	-2	-1	0	1	2
25) find identical items (e.g., this is your spoon, where is my spoon)?	-2	-1	0	1	2
26) match pictures in a picture book (e.g., where is the other dog)?	-2	-1	0	1	2
27) match letters (e.g., pointing out same letters)?	-2	-1	0	1	2

When cleaning up after play or sorting during play, your child can when asked to

28) sort toys by category (e.g., blocks in one box, puppets in another)?	-2	-1	0	1	2
29) sort toys by shape, size, or color?	-2	-1	0	1	2

When reading a book or looking at a picture in a newspaper or photo book, your child will

30) point to the same item or person across multiple pictures?	-2	-1	0	1	2
31) look to where you point?	-2	-1	0	1	2

Comments and concerns:

APPENDIX B: Chapter 3 Supplementary Material

Below presents analyses that provide verification on whether the baseline utilized in Study 2 was successful in reducing the influence of visual differences on the level of mu power.

Decision of baseline during action observation

Originally, the still image of E1, without any objects present was planned to serve as baseline in the action observation phase. However, after ample consideration we chose as baseline the first frame when E1 was visible with objects (toy and cane) present, but not moving for 500ms (Figure 6 in Study 2). The reason for this is that this baseline is closer in time and closely matches the visual scenes of the action observation experimental window for each condition, which allows to capture action-specific motor processes (Evidence provided below).

Mu and occipital alpha during observation of action

In order to verify whether the baseline utilized in the current study was successful in reducing the influence of visual differences on the level of mu power, we compared data in 6–9 Hz frequency band from our current study (visually-matched baseline) from data using a baseline that does not take visual differences into account (visually-unmatched baseline) (Figure 22). Specifically, we compared 1) the level of occipital suppression and 2) the relation between mu power suppression and occipital alpha suppression for each baseline type. We computed alpha power in the 6-9Hz frequency range over central and occipital electrode clusters during Anticipatory (-1000ms to 0ms) and Movement Onset (0ms to 1000ms) for each condition (Grasp, Cane-use) using the two types of baselines. For this question, we did not expect age-related differences and thus the data presented is collapsed across age. Descriptive statistics of mu power suppression and occipital alpha for each condition and time using two types of baselines are provided in Table 8.

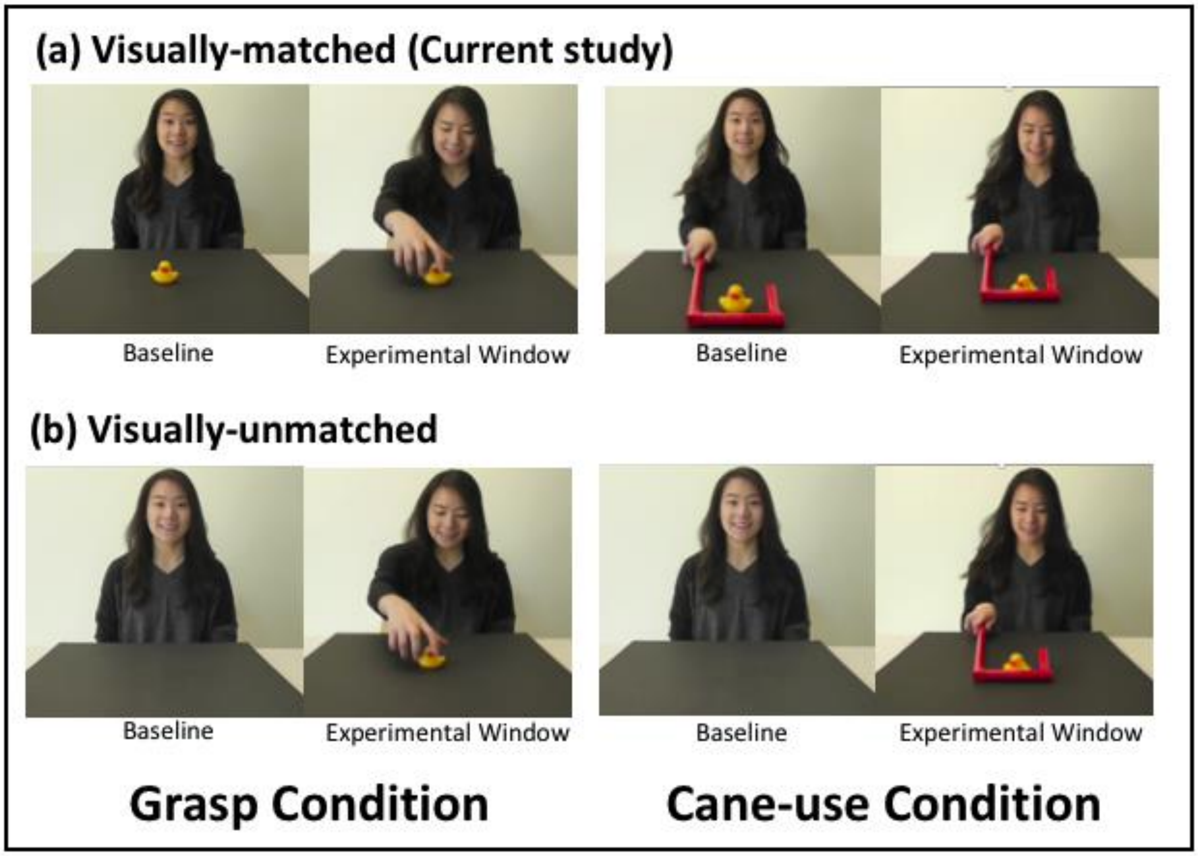
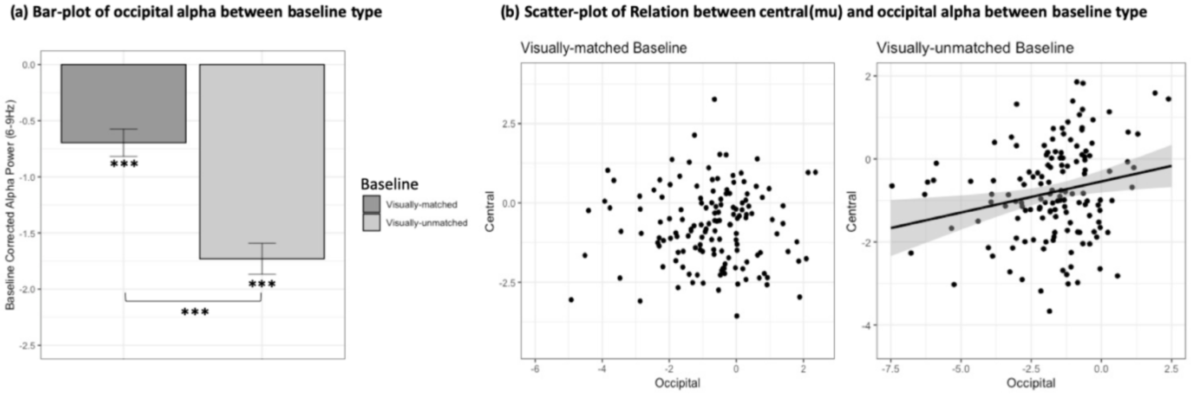


Figure 22. Depiction of (a)visually-matched and (b)visually-unmatched baseline and experimental windows for grasp and cane-use observation trials.

First, we compared the level of occipital alpha suppression between the two baseline types. A 3-way repeated measures ANOVA with condition, time, and baseline type as within-subjects variables for occipital region revealed a significant main effect of baseline type ($F(1,35) = 22.4$, $p < .05$) and time ($F(1,35) = 21.8$, $p < .05$). Follow-up pair-wise t-test against baseline type revealed that the level of occipital alpha suppression was significantly less in the visually-matched (current study) baseline than the visually-unmatched baseline, $t(35) = -7.94$, $p < 0.001$ (Figure 23a, mean difference = -1.03). Follow-up pair-wise t-test against time revealed that the level of occipital alpha suppression was significantly greater during movement onset compared to anticipatory period across baseline type, $t(71) = -6.65$, $p < 0.001$ (mean difference = .65).

To address our question checking whether power measured over central clusters is associated with strength of power measured at occipital clusters, we performed a linear regression with central mu power, time, and condition as independent variables and occipital alpha as the dependent variable. The model with visually-unmatched baseline was significant, R^2 = .14; *F*(7,136)= 3.29, *p* = .007, with a main effect of central alpha (β = .68, *SE* = .25, *p* = .03) and a significant main effect of time (β = -.94, *SE* = .43, *p* = .03). Pearson correlation between central and occipital alpha power revealed was *r* = .24, *p* < .01, with a Bayes factor of BF_{10}= 6.9, indicating evidence of a strong relation (Figure 23.b). The model for visually-matched baseline was not significant, providing no evidence for a relation between mu power and occipital alpha (*p* >.1; Figure 23.b). We also provide a Bayes factor of BF_{01} = 8.7, indicating moderate evidence for no relation (*r* = .04, *p* >.6). Together, these findings suggest that mu power and occipital alpha measured with the visually-matched baseline in our current study are reflecting independent neural activity and likely come from different sources. Thus, we confirm that mu power reflects motor-specific components from the neural signal during action observation in our dataset.


(a) Bar-plot of occipital alpha between baseline type

(b) Scatter-plot of Relation between central(mu) and occipital alpha between baseline type

Visually-matched Baseline

Visually-unmatched Baseline

Figure 23. (a) Bar-plot of occipital alpha in 6–9 Hz frequency band using visually-matched and visually-unmatched baseline (collapsed over condition and time). Error bar indicates ± 1 SE. ***p < .001. (b) Scatter-plot of relation between alpha measured over central and occipital regions in 6–9 Hz frequency band using visually-matched and visually-unmatched baseline (collapsed over condition and time).

Table 8

Descriptive statistics of baseline-corrected power over central and occipital regions in 6–9 Hz frequency band using visually-matched and visually-unmatched baseline.

			Visually-matched Baseline	Visually-unmatched Baseline
Region	Condition	Time	Baseline-corrected power (*SE*)	Baseline-corrected power (*SE*)
Central	Grasp	Anticipatory	-1.11 (.17)	-0.83 (0.18)
		Movement	-.68 (.19)	-.40(.17)
	Cane-use	Anticipatory	-.71 (.2)	-1.22 (.22)
		Movement	-.33(.24)	-.84(.2)
Occipital	Grasp	Anticipatory	-.56 (.25)	-1.56 (.30)
		Movement	-1.13 (.20)	-2.13 (.25)
	Cane-use	Anticipatory	-.18(.25)	-1.25(.27)
		Movement	-.91(.23)	-1.97 (.26)