

**THE PATH TO THE PINCER: MAPPING THE DEVELOPMENT
OF THE INFANT GOAL-DIRECTED GRASP VIA NOVEL
NEURAL AND KINEMATIC METHODS**

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ABSTRACT

The emergence of prehension, the ability to reach out and grasp an object, marks the start of a shift in infant development by allowing the refined exploration of objects by hand. The onset of purposeful reaching in infancy begins a developmental cascade involving cognitive, motoric, social-emotional, and communicative abilities. Currently, there is a gap in the literature surrounding the development of preshaping, which is the skill of adapting the fingers during approach to grasp an object in a fluid motion. Preshaping can be studied by examining the emergence of the pincer grasp, where only the thumb and index finger are used and these digits are oriented to the object during the reach. We combine novel methodology in video data collection, kinematic analysis, and an electroencephalography (EEG) paradigm to map the development of preshaping from 6 to 14 months of age. Video data were collected biweekly at home by caregivers via a cell phone app. These data underwent kinematic analysis through a machine learning algorithm (HaMeR) to quantify finger movements. EEG data was collected at 14 months old from a tactile oddball paradigm. We found that infants are beginning to preshape their hand gradually from six months old, likely reflecting the integration of vision and touch. The EEG data suggested that by 14 months old, infants show functional groupings of fingers that are similar to that of an adult. Behaviorally coded grasping strategies, but not the change in the degree of preshaping as derived from kinematic data, predicted whether infants display two neural categories of their hand. These subtleties of the interplay between behavioral and neural development can inform our understanding of the relations between the body and brain and can potentially inform identification of motor differences and delays in childhood.

To the little girl who loved science class but never knew how far she could go; we did it.

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CHAPTER 1

INTRODUCTION

A hallmark of infancy is the rapid development of motor abilities, such as reaching and grasping, sitting, crawling, standing, and walking. These skills are developed based on individual sensory experiences situated inside unique contexts (Hadders-Algra, 2018). The focus of the current study is on manual development, specifically the development of the goal-directed grasp. Prehension, the ability to reach out and grasp an object in a single hand (Karl et al., 2018), marks the start of a new developmental period when the infant starts learning and practicing how to explore objects by hand. Studying the trajectory of grasp development and its related neural changes helps to understand this critical period of development at the tipping point of a significant cognitive, motor, social-emotional, and communicative developmental cascade.

In the literature on infant motor development, there has been little emphasis on the development of the goal-oriented infant grasp. As the hand has 21 joints, there are many degrees of freedom within movement that cause problems surrounding both technical and conceptual aspects of research into the emergence of grasping (Jeannerod, 2009). As fundamental as prehension is, developing methodologies needed to study it are time consuming, complicated, and often cannot translate to other contexts (Zhou & Smith, 2022). As a result, the current infant grasp development literature is characterized by small sample sizes, often between just four and 15 individuals (e.g. Thelen et al., 1996; Carvalho et al., 2007) and uses a wide range of methodologies across different age

ranges and involving various kinds of stimuli and objects. In short, the current literature does not offer a thorough view of the nuanced longitudinal development of the goal-oriented infant grasp.

The reach-to-grasp movement is a complex, visually guided process that takes years to fully mature. As the Dual Visuomotor Channel Theory of Jeannerod (1999) explains, the reach and the grasp are two separate movements that involve interacting pathways in the occipital and parietofrontal cortices (Karl & Whishaw, 2014; Whishaw & Karl, 2014). The reach transports and orients the hand to the target while the grasp opens and closes the hand around the target. In order to have a smooth reach-to-grasp motion, as in typically developing adults, the reach and the grasp must be synchronized. This synchronization occurs between the somatosensory metrics of the hand and the intrinsic metrics of the target object (Whishaw & Karl, 2014). In a proficient reach-to-grasp movement, the moving fingers will adjust to the estimated size of a target object during the reach in order to efficiently grasp the object; this skill is called *preshaping* (Corbetta & Santello, 2018; Whishaw & Karl, 2014). Preshaping is a calibration moment between the somatosensory and visual systems and can be thought of as a sign of coordination between these systems. This calibration requires both systems to mature enough to work together (Whishaw & Karl, 2014).

The Developmental Trajectory of Grasping

The trajectory leading to purposeful reach-to-grasp movements starts with basic reflexes, progresses to spontaneous arm and hand movements, called *hand babbling*, then to grasps stemming from accidental object contact, to eventually pairing object contact with vision, and ultimately ends with goal-oriented reach-to-grasp movements that

involve preshaping (Corbetta & Santello, 2018; Wishaw & Karl, 2014). This maturation process can be situated inside of the Neuronal Group Selection Theory (NGST), which is a framework that states that motor development is inherently a non-linear process with multiple phases of transition but is also dependent on factors stemming from both the child and that child's unique environment, including genetics and epigenetics (Hadders-Algra, 2018).

The NGST describes motor development in terms of two phases—primary and secondary variability (Hadders-Algra, 2018). Primary variability for motor development includes early spontaneous movements that build the infants' personal movement repertoire, including all the sensory information about both their own body and the world. In primary variability, infants cannot adapt their movements based on the situation. The secondary variability phase uses all the information gathered in primary variability to select the motor behavior that best fits the specific situation. Secondary variability is based on trial-and-error and functional adaptation. The primary-to-secondary transition occurs around 3-4 months old for motor control. There are individual differences on this transition timing based on child factors including genetics and epigenetics. Trial-and-error practice in reaching and grasping is also enhanced due to improvements in vision (Hadders-Algra, 2018).

One developmentally important type of grasp is the pincer grasp, which is characterized by using only the thumb and index finger of one hand (Karl et al., 2012). The pincer grasp is used daily for a variety of activities including eating and playing. The pincer grasp is also referred to as a precision grasp or grip. Focusing on the development leading to the pincer grasp, there are two phases of developmental change, but both

phases are housed in the secondary variability phase of NGST. In the first phase, infants explore calibrating speed using haptic feedback from objects, where infants first swipe at objects, and through trial-and-error and adaptation, eventually control the speed of their hand enough to grasp successfully (Corbetta & Santello, 2018). In the second phase, infants build on their proprioceptive and motor knowledge by beginning to preshape and integrating the physical properties of objects into their movement plans to grasp them (Corbetta & Santello, 2018).

Infants progress through these developmental phases on the way to purposeful pincer grasps, but there is no clear consensus on the timing of the phases. For example, Corbetta and Santello (2018) report the first phase employing haptic feedback begins around three to five months of age, while other researchers indicate the start as four to nine months (McCarty et al., 2001; Zhou & Smith, 2022). The second phase is when preshaping emerges; infants start to adjust their hand position and posture during the reach, in anticipation of grasping. Corbetta and Santello (2018) report that preshaping begins around seven to eight months of age, while others indicate this development starts between 6 and 12 months (Hadders-Algra, 2018; Halverson, 1931; Touwen, 1976) or between 9 and 12 months of age (Whishaw & Karl, 2014) and is not yet at the adult level at 24 months of age (Karl & Whishaw, 2014). Notably, researchers agree that a usable pincer grasp is fully developed by 24 months of age while sitting supported (Hadders-Algra, 2018; Karl & Whishaw, 2014; Corbetta & Santello, 2018), even if the full reach-to-grasp movement is not at an adult-likeness until late adolescence (Hadders-Algra, 2018).

The development of preshaping offers a window into grasp development and the interconnections between the somatosensory and visual systems. Preshaping is most clearly represented by the pincer grasp, which is used by older infants to pick up smaller objects. Grasping early in development includes multiple fingers, while proficient pincer grasping involves the use of only the thumb and index finger. The emergence of the pincer involves changes in finger use, with the middle, ring, and little finger beginning to tuck into the palm during the reach, leaving just the thumb and index finger to contact the object. Increasing proficiency in prehension therefore involves changing patterns of relations between the fingers in terms of which fingers work together to carry out grasping actions.

Literature on the changes in finger usage during grasping and grasp development are sparse, and measures focused on individual fingers are rare. Karl and Whishaw (2014) show data related to differential usage of fingers in grasping, but only through one figure where the initial contact point during prehension was illustrated. During a task that required infants to reach out and grasp a rod positioned vertically in front of them, the authors found that, in a cross-sectional sample, between 12 and 24 months the involvement of the middle finger in the grasp decreased from some usage to not being used at all (see Figure 1).

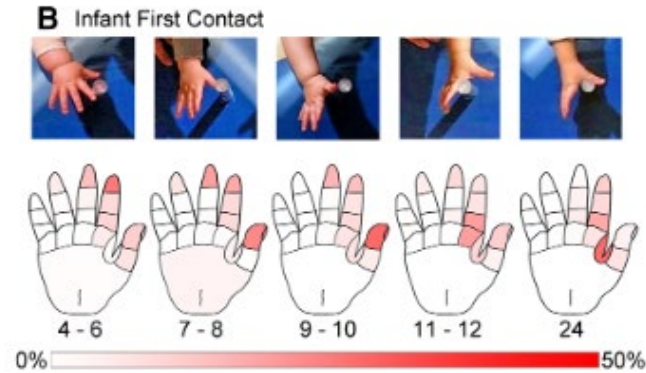


Figure 1. First contact point frequencies. Adapted from Karl and Whishaw (2014)

Studying Prehension: Behavioral Methods and Findings

Kinematic analysis and behavioral coding are two classic methodologies to study motor development (Karl & Whishaw, 2014; Zhou & Smith, 2022). For kinematic analyses, recording video data of body movements using either physical or digital markers placed onto specific areas of the body allows precise movement tracking of the motions performed (Nowak & Hermsdörfer, 2009). This usually involves an in-lab procedure that requires an optoelectronic system involving multiple cameras and perspectives to capture the precise characteristics of the movement (Nowak & Hermsdörfer, 2009) or a system of multiple 2D cameras paired with a reconstruction of the third dimension using an algorithm (Rönnqvist & Domellöf, 2006). For behavioral coding, human coders assign global categories to grasps from video-recorded data by visual inspection. Within the grasping literature, behavioral coding typically refers to holistic coding of grasping strategy used, with different strategies being defined by the

positioning and involvement of the different fingers during the reach and grasp (Karl & Whishaw, 2014).

Traditional options for studying reaching and grasping involves placing markers on the fingers and hand and tracking movement via optoelectronic methods. Grasping studies using optoelectronic devices usually use four or more cameras to capture the entire hand with up to three markers on the back of the palm or wrist (von Hofsten, 1991). There have been few investigations using markers placed near the fingertips such as on the fingernail in five-year-olds and adults (Zoia et al., 2006). There has been some work on individual fingers in children and adults, but this is mainly restricted to either the individual finger movement path (Cruz & Kamper, 2006) or the distance between the tips of the thumb and index finger, usually referred to as the maximum grip aperture (MGA) or just aperture (Jeannerod, 2009; Karl et al., 2019; Zoia et al., 2006). Another method of capturing kinematic data in adults involves using a specialized glove that captures movement patterns and joint angles. However, these gloves, including the CyberGlove, include 18 sensors on different joints of the hand, but do not include the fingertips and are not sized for children (CyberGlove Systems LLC). There is also interest in methodologies that enable markerless tracking of finger movements with only two cameras in the laboratory (Mulla et al., 2025) or with a single camera in any environment with advanced machine learning algorithms (Pavlakos, 2023).

Few longitudinal projects have investigated grasp development in infancy, and most have applied kinematic analysis in relatively small samples, with a focus on the reach. For example, Thelen and colleagues (1996) studied four infants every one to two weeks for the first year and found that improvement in the grasp path was variable

throughout development and that the individual path of the reach was less straight when the infant reached at a higher speed, providing evidence of the highly individualized nature of grasp development. Carvalho and colleagues (2007) studied four infants and found that between four and six months, infants reached more frequently, and the individual path of the reach became straighter at six months old. von Hofsten and colleagues performed multiple studies of the infant grasp and ultimately found that as infants age, they have fewer movement units (i.e., periods of acceleration followed by deceleration) per reach-to-grasp action (1979; 1991). These studies had varying assessment timepoints (e.g., monthly from four to six months old, every other month from five to nine months old, and bimonthly from four to eight months old) and small sample sizes, ranging from 4 to 15 participants. Inconsistencies across studies in terms of which kinematic variables were assessed, the specific tasks and objects used, and lack of replication mean there currently are no standard kinematic measures of the reach-to-grasp movement in infants (Zhou & Smith, 2022).

Behavioral coding of grasping strategies, or how the hand approaches objects before the objects are grasped, have been successfully studied in adults (Hall et al., 2014) and infants ranging from 4 to 24 months old (Karl & Whishaw, 2014). Karl and colleagues identified five grasping strategies that are used by infants and adults in different contexts: *preshape*, *touch and release*, *capture*, *adjust*, and *manipulate* (See Table 1; Karl et al., 2012; Karl & Whishaw, 2014). These strategies are separated into two overall types of grasps, either visual or haptic, whereas a visual grasp integrates vision with haptics and a haptic grasp uses touch only.

Table 1. Prior definitions of individual grasping strategies. Adapted from Karl et al., 2012 and Karl and Whishaw, 2014.

Grasping Strategy	Type of Grasp	Definition
Preshape	Visual	Fingers are partially or fully towards the palm (generally the middle, ring, and little fingers) and grasp ended without any adjustments during or after contact
Touch and Release	Haptic	Finger(s) touches the object, fully releases, then touches the object again to grasp
Capture	Haptic	An open hand with a wide aperture between thumb and index contacts the object, and the rest of the hand is outstretched then closed around the object
Adjust	Haptic	A grasp that includes an adjustment while the object is not fully released
Manipulate	Haptic	The object is moved by at least one digit before being grasped

In a cross-sectional study of infants and adults, Karl and Whishaw (2014) analyzed behaviorally derived grasping strategies alongside kinematic measures during a task to grasp a vertical rod positioned in front of the infant, parallel to their midline. Behavioral coding of 4- to 9-month-old infants indicated primarily a *touch and release* strategy in this age range but the frequency of this strategy decreased with age. Infants aged 9-12 and 24 months used a *capture* strategy the most often. For the *capture* strategy, the frequency increased over time from around 25% in 4- to 6-month-olds to 56% from 9- to 12-month-olds (see Figure 2). At 24-month-old infants, the *capture* strategy was used in 75% of grasps. The 24-month-old infants used *preshape* in the remaining 25% of their grasps, which is significantly more than all younger age groups (4-12 months old). Infants under one year rarely used a *preshape* strategy, suggesting that the integration between vision and haptics may begin to emerge at this age.

Karl and Whishaw (2014) also investigated the interaction between vision and haptics in grasping development in adults reaching while wearing occluding goggles to inhibit viewing the target object. As expected, adults used a *preshape* strategy (72% of the time) when they could see the rod but did not use a *preshape* strategy when their vision was occluded. Interestingly, then, grasping strategy usage in visually occluded adults was indiscernible from that of infants under nine months. The total movement time at 24 months was the same as adults in the vision condition. MGA at first contact with the object seemed to have a quadratic effect where the youngest infants (4-6 months) and the visually occluded adults had no differences in MGA after correcting for hand size. Infants from 9 to 12 months and at 24 months of age had significantly wider MGAs compared to visually occluded adults. Overall, Karl and Whishaw's (2014) findings align with the theoretical ideas of NGST as prehension development is nonlinear and a substantial portion of developmental change happens between 12 and 24 months old.

Somatotopy: Topographic Organization and Categorical Perception

The somatosensory and motor systems in the brain work together to enable effective and efficient manipulation of objects. As the somatosensory and motor systems work in tandem so often, the systems are generally considered together (Ejaz et al., 2015; Bouchard et al., 2013). Both systems have somatotopic organization within the brain, where different regions of the somatosensory and motor cortices in the brain represent a body map of specific regions of the body. This organization is captured by the somatosensory (and motor) homunculus (see Figure 3). Body parts are categorized within this structure, but the boundaries between different body parts may be plastic and depend

on different contexts (Tamè & Longo, 2023). Currently, there is little understanding about how body maps are developed in infancy (Marshall & Meltzoff, 2015).

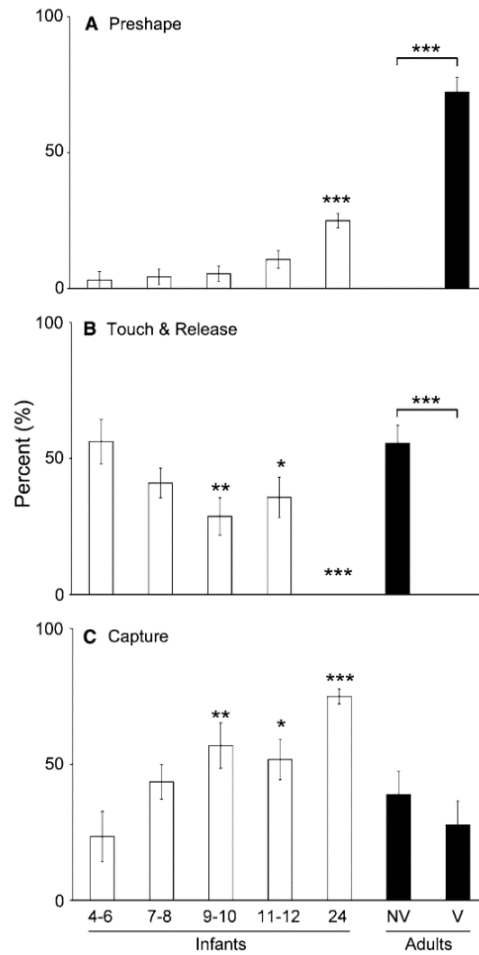


Figure 2. Grasping strategy usage from Karl & Whishaw (2014).

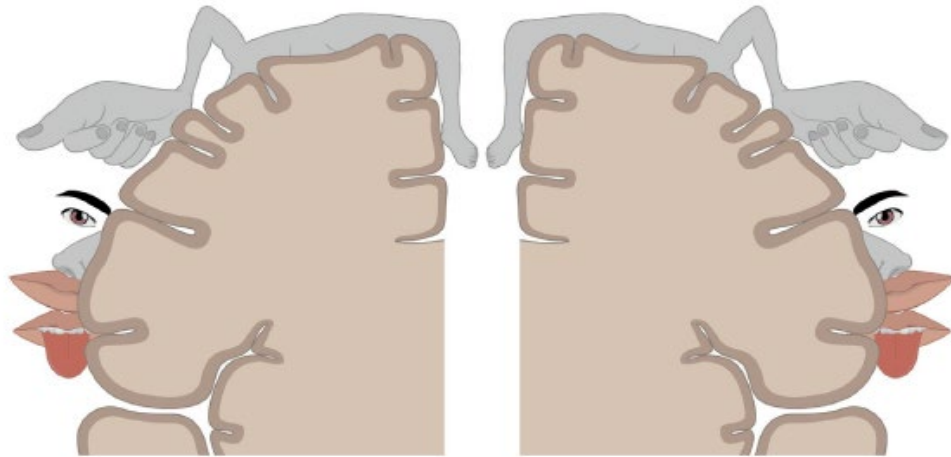


Figure 3. Primary somatosensory cortex with the homunculus. Adapted from Tamè and Longo (2023).

Categorization within the body map influences cognition via categorical perception (CP) (Damper & Harnad, 2000). Through behavioral testing of perceptual differences between two locations on the body, CP is indicated by an overestimation of the distance between two locations when they fall over a body part boundary (Tamè & Longo, 2023). For example, the distance between the forearm and hand crossing the wrist boundary will be overestimated compared to two points on the forearm in adults (de Vignemont et al., 2009) and in children (Knight et al., 2016). There is also anatomical evidence of boundary regions, although mostly in animal models. Both monkeys and rodents have regions with comparatively low myelination, called septal regions, separating representations of each finger (for monkeys) (Jain, 1998) and each whisker (for rodents) (Woolsey & van der Loos, 1970). There is evidence for septal regions in humans that separate the representations of the hand and face (Flechsigs, 1920). The location of the septal regions aligns with regions of functional connectivity, indicating

that these categorical boundaries may not be due to only anatomical location, but also functional use (Tamè & Longo, 2023).

Categorical Perception & Neuroscience

Given that grasping maturation during infancy involves changing relations between the fingers and in the body map of the hand, it is instructive to consider what measures might provide a window into these relations between the fingers and the body map. Building on prior work, we suggest that aspects of the relations between the fingers in infancy can be investigated using an event-related potential (ERP) component called the somatosensory mismatch negativity (sMMN). ERP components are derived from an electroencephalography (EEG) task where there is a repeated event or stimulus. The sMMN is elicited during a tactile oddball paradigm; it provides a window into the relations between body parts and allows for inference surrounding categorical boundaries in the body map (Horger et al., 2024; Shen et al., 2020; Shen, Smyk et al., 2018a; Shen, Smyk et al., 2018b; Shen, Weiss et al., 2018). In an sMMN oddball design, a train of tactile stimuli is presented to one location (the standard location), with occasional stimuli presented to a different (deviant) location. The brain's response to stimulation of deviant locations in relation to the response to the standard stimuli can provide insight into the relations between body parts (e.g., different fingers). A categorical boundary is inferred from the difference in the magnitude of the sMMN responses, where a larger response is indicative of a boundary being crossed. It is important to note that this sMMN measure is a continuous variable, instead of a strictly categorical one (e.g. dichotomous decision about distance perception), therefore, we can only infer a perceptual categorical boundary.

Initial work on the sMMN from our laboratory used a standard location on the proximal forearm near the wrist with deviant locations on the hand and the distal forearm (towards the elbow), such that the standard location was equidistant from the two deviant locations. This wrist paradigm was studied with adults (Shen, Smyk, et al., 2018a) and infants (Shen et al., 2020). In both infants and adults, the sMMN response to the deviant location of the hand was larger than the response to the deviant on the proximal forearm (see Figure 2). This finding is consistent with behavioral work with adults and older children suggesting that the wrist is a categorical boundary in tactile perception (Knight et al., 2014; 2016; de Vignemont et al., 2009) and it suggests the utility of the sMMN for examining the relations between body parts in infancy.

In a related study, Shen, Smyk, et al. (2018a) employed an sMMN oddball paradigm with infants that involved tactile stimulation to three fingers: the thumb, middle finger, and little finger. In that study, the adult sMMN response to the thumb (deviant location) was larger than the response to the little finger (other deviant location), even though both locations were equidistant from the middle finger (standard location) in anatomical terms (see Figure 4). These results suggested that there is a categorical boundary within the body map in the brain of the hand, with a separation between the thumb and little finger (Shen, Smyk, et al., 2018a). Shen et al. (2018a) speculated that this category boundary could be based on finger usage, with the thumb and index finger in one category as they are typically used together, and the other digits (middle, ring, and little finger) in another category. There is further neuroimaging evidence on the importance of function in the body map of the hand, Mastria and colleagues (2023) examined finger representations in the brain of adults and found that the perceived

structure of the hand was related to finger representations more than actual hand anatomy or finger kinematics. Overall, there seems to be an interplay between anatomy and function within the body map of the hand, however, the interplay during the developmental progression of body map maturation is unknown.

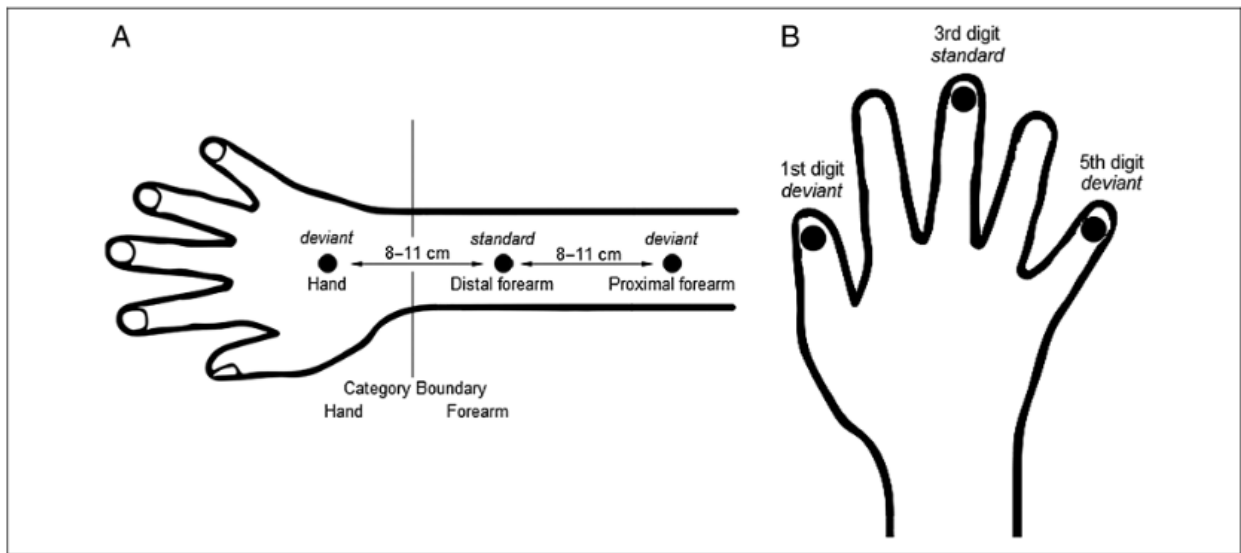


Figure 4. Placement of tactile stimulators. Oddball paradigms with adult participants in Shen, Smyk, et al., 2018a.

Studying Prehension: Relating Brain and Behavior

Investigating kinematic measures and brain signals together offers another approach to study prehension. The majority of the literature that combines kinematic and EEG methodologies together focuses on recording neural signals during prehension (e.g., Sburlea & Muller-Putz, 2018; Noviello et al., 2024). Understanding the temporal organization that unfolds during reaching and grasping could directly inform the

development and refinement of neuroprosthetics and brain-computer interfaces (Sburlea & Muller-Putz, 2018; Yang et al., 2015). To our knowledge, there are currently no studies using ERPs and kinematics in children or infants, simultaneously or not, and no focus on addressing fingers beyond the thumb and index finger.

In the current study, we chose to focus on infant brain responses to tactile stimulation to examine aspects of the relations between different fingers. This builds on our prior work on EEG and MEG responses to stimulation of various parts of the infant body (Meltzoff et al., 2019) but leverages the utility of the sMMN for examining the relation between different body parts. As noted above, the sMMN is an ERP component that is elicited using a tactile oddball paradigm and can be used to investigate the boundaries within the neural body map (Horger et al., 2024; Shen et al., 2020; Shen, Symk et al., 2018a; Shen, Symk et al., 2018b; Shen, Weiss et al., 2018). The sMMN is reported within 90 and 200ms after stimulus onset for adults (Shen, Smyk, et al., 2018a; Shen, Smyk, et al., 2018b) and between 60 to 180ms for infants (Shen et al., 2020; Shen, Weiss, et al., 2018). The sMMN is the tactile equivalent of the more established auditory MMN component, which is elicited from an auditory oddball paradigm (Duncan et al., 2009, Garrido et al., 2009; Tsolaki et al., 2015). The auditory MMN response occurs around 100 to 250ms for adults and around 250 to 400ms for infants after stimulus onset and is derived from a comparison of ERP responses to standard and deviant sounds (Duncan et al., 2009; Kuhl & Rivera-Gaxiola, 2008).

The sMMN has been utilized to study categorical boundaries in both adults (Horger et al., 2024; Shen, Smyk, et al., 2018a; Shen, Smyk, et al., 2018b) and infants (Shen et al., 2020; Shen, Weiss, et al., 2018). For example, Shen, Smyk, and colleagues

(2018a) used the sMMN to probe the relations between the middle finger and the thumb, the index finger and the little finger of the dominant hand in right-handed adults (see Figure 4). The middle finger was the standard location for the tactile stimulation, which received 80% of the stimulation, while the thumb and the little fingers were the deviant locations for the same tactile stimulation, which received 10% each. As noted above, the change in stimulation levels from standard to deviant is what results in the sMMN response. The authors found that the sMMN response was larger to thumb stimulation than to the little finger stimulation. Given that the middle finger was the standard stimulus, this indicates that the thumb and little finger are not in the same category in the neural body representation. This may be due to the function of the individual fingers such as in the pincer grasp (Shen, Smyk, et al., 2018a). These findings were recently replicated in another adult sample (Horger et al., 2024).

These findings provide evidence that the sMMN response can be used to investigate neural aspects of the relations between body parts, which in turn is related to the study of body representations and body maps. However, there is a gap in knowledge around how these representations and maps develop (Meltzoff & Marshall, 2020). Employing the sMMN response in relation to stimulation of infant fingers has not yet been done and could potentially provide useful information on the developing relations between the digits in relation to the development of the grasp, including changes in finger involvement as infants become more proficient at grasping. Elucidating the relation between the sMMN as a brain measure of the relation between fingers, and the behavioral development of grasping behavior could provide further insights into the nuances of prehension development in infancy.

Current Study

Little is known about the fine-grained development of the infant reach-to-grasp movement and the relation between the development of prehension and neural measures of the relations between fingers. As outlined above, there are missing pieces across the various methodologies used and ages studied, with no prior research examining the neural representation of the infant hand in relation to the development of finger usage in grasping. We aim to fill these gaps in the literature by investigating reach-to-grasp video data longitudinally from a relatively large sample of infants (at least in relation to prior studies), as well as examining the relation between physical prehension skills and the neural representation of the infant hand as indexed by the sMMN response.

The present study aims to investigate the development of grasping proficiency by combining two unique methods—longitudinal at-home biweekly video collection of prehension from 6 to 13 months old and a novel EEG paradigm to understand neural aspects of the relations between the fingers of the infant hand at 14 months of age. The aim is to further the understanding of infant grasp development and link longitudinal development of grasping behavior to neural measures related to representations of the body (in this case, the relations between fingers). We aim to add to existing literature by applying novel methods including at-home video collection by caregivers and kinematic data automatically derived from videos via a machine-learning algorithm, and through relating these behavioral data to the measures of the infant neural body representation of the hand. In all, we aim to provide a well-rounded picture of grasp development, including both behavioral and neural measures.

Given the gaps and methodological constraints in the extant literature, this novel study has the potential to provide a view of the developmental nuances of grasp development by considering two types of behavioral data longitudinally (kinematic and behavioral coding) together with an EEG measure (the sMMN, collected at the end of the study) to paint a picture of how infants develop the ability to efficiently reach and grasp. The specific aims are as follows:

Aim 1: The first aim is to investigate the fine-grained development of grasping from 6 to 13 months of age, and it includes two sub-aims:

Aim 1a): We will employ behavioral coding to study how the use of grasping strategies changes over time. Our hypothesis is that younger infants will use the *touch and release* strategy most often, then with increasing age, infants will start to use the *capture* strategy more often, based on results from Karl and Whishaw (2014). Although this prior work also suggests that the emergence of hand preshaping is gradual, we expect to see increases in the frequency visual strategy usage over the age range of the longitudinal video collection (6 to 13.5 months).

Aim 1b): We will also develop a kinematic variable called grasp proficiency that indexes the degree of preshaping. Specifically, grasp proficiency will be the sum of the linear distances in 3-D space between the tip of the little and middle fingers and their respective knuckles (the metacarpophalangeal joints) (see Figure 5 for a visual representation). The inclusion of the distance between the knuckles and the middle and little fingertips comes from the fact that preshaping for a pincer grasp involves tucking of these fingers (and the ring finger) leaving the thumb and index finger ready to contact the

object and grasp it. Therefore, we expect preshaping to be associated with decreasing distances in 3-D space between the knuckles and the tip of the middle and little fingers, as these fingers become tucked. When infants are younger and are less proficient at grasping, they will have a less preshaped grasp when contacting the object. Therefore, grasp proficiency will start out low, with distances between the thumb and index and between the knuckles and little and middle fingers being initially larger (reflecting the full extension of the fingers) but becoming increasingly smaller as the infant begins to preshape and tuck their (non-index) fingers during the reach, ahead of grasping the object. We hypothesize that grasp proficiency will grow over time, showing smaller distances, with the overall rate of change and starting value showing individual differences.

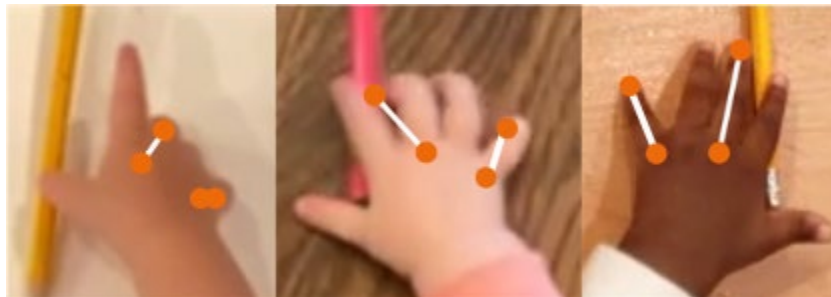


Figure 5. Examples of different values of grasp proficiency. Calculated as the sum of the distances between the middle finger and the middle knuckle and the little finger and the little knuckle at first contact. Shorter distances indicate higher proficiency.

Aim 2: The second aim is to relate the neural correlates of the relations between infant fingers at 14 months old to the longitudinal development of grasp proficiency from 6 to 13.5 months old. This aim has two sub-aims:

Aim 2a): Identify the sMMN and examine differences between the two deviant conditions (thumb and little finger). The first step towards this aim is to identify and score the sMMN ERP component using a temporal principal component analysis (tPCA). After the tPCA, we will determine the influence of multiple factors, including electrode region, hemisphere, and oddball deviant condition, on the raw sMMN amplitude. We hypothesize that the sMMN is present in the data and the amplitude is enhanced (more negative) for the thumb deviant condition compared to the little finger deviant condition.

Aim 2b): We also will determine the overall relationship between the longitudinal growth of grasp proficiency and grasping strategy usage in predicting the sMMN amplitude. Specifically, we will use two variables derived from the grasp strategy data. The first one is the overall proportion of timepoints where the infants used a visual type of grasp (*emerging or full preshape* strategies) and the second one is a dichotomous variable of whether a visual type of grasp (*emerging or full preshape* strategies) was utilized during the last timepoint at 13.5 months old. Missing data at this timepoint (n = 4) was coded as ‘no visual grasp.’ We hypothesize that there will be main effects of the grasp proficiency growth trajectory and the proportion of times a visual type of grasp was used, where a steeper negative trajectory and a higher proportion will be related to sMMN amplitude. We hypothesize that there are interactions between the grasp proficiency growth trajectory, the proportion of times a visual type of grasp was used, and whether a visual type of grasp was used at 13.5 months old interacting with

the EEG task condition. We expect a steeper negative trajectory of grasp proficiency growth to be related to an enhanced (more negative) sMMN amplitude for the thumb difference condition. A greater proportion of times a visual type of grasp was used will also be related to an enhanced sMMN amplitude for the thumb difference condition. Evidence of a visual type of grasp at 13.5 months old will be related to an enhanced sMMN amplitude for the thumb difference condition. These interactions will provide insight into which behavioral aspects of grasping are related to the neural sMMN amplitudes.

CHAPTER 2

METHODS

Participants

We recruited 110 families with 6-month-old infants to participate in a two-part study. The first part is longitudinal at-home data collection from 6 to 13 months old, with data collection points every two weeks, and the second part is an in-person lab visit at 14 months old. Recruitment was mainly through mass postcard mailings using birth record information of parents with infants younger than 6 months of age. Birth records were obtained through a partnership with the Pennsylvania Department of Health. Secondary recruitment methods included social media advertisements, distributing postcards and flyers to local businesses, and by word-of-mouth. Eligibility criteria included a gestational age of between 37 and 43 weeks and no significant health issues or developmental conditions.

The first 20 participants in the longitudinal video collection were pilot participants, which included a slightly different protocol for recording videos than was used in the remainder of the study. For this reason, pilot participants are not included in the following analyses. Aside from the pilot participants, six participant families completed the consenting and video training process but decided to not proceed with participation in the study. 14 participant families started but did not complete the study. This left an overall sample size of 70 participant families who contributed longitudinal videos and attended the 14-month lab visit. Out of the 70 participants who contributed at-home videos, 65 participants had enough biweekly videos to be included in the

longitudinal analysis (the criterion being that a family needed video data from at least 10 out of the 16 possible biweekly age points). Of these 65 participants, 43 had usable EEG data according to our data quality thresholds (see below). These 43 participants comprise the sample for this dissertation project (see Figure 6). See Table 2 for the participant demographics of this sample.

Table 2. Participant demographics.

N = 43		Child Sex	
Age at first usable video		63%	Female
M = 6.62 months SD = .53		37%	Male
Maternal Education		Yearly Family Income	
25%	Associate or Bachelor's Degree	5%	<\$50,000
40%	Master's Degree	7%	\$50,000-\$74,999
14%	Doctoral Degree	16%	\$75,000-\$99,999
16%	Professional Degree	12%	\$100,000-\$124,999
		60%	>\$125,000
Race		Ethnicity	
79%	White	81%	No Hispanic, Latino/a/x, or Spanish Origins
5%	Asian	3%	Cuban
5%	Asian and White	3%	Mexican, Mexican American, or Chicano/a/x
5%	Black or African American and White	8%	Another origin
5%	Black or African American		
2%	White and Arab American		

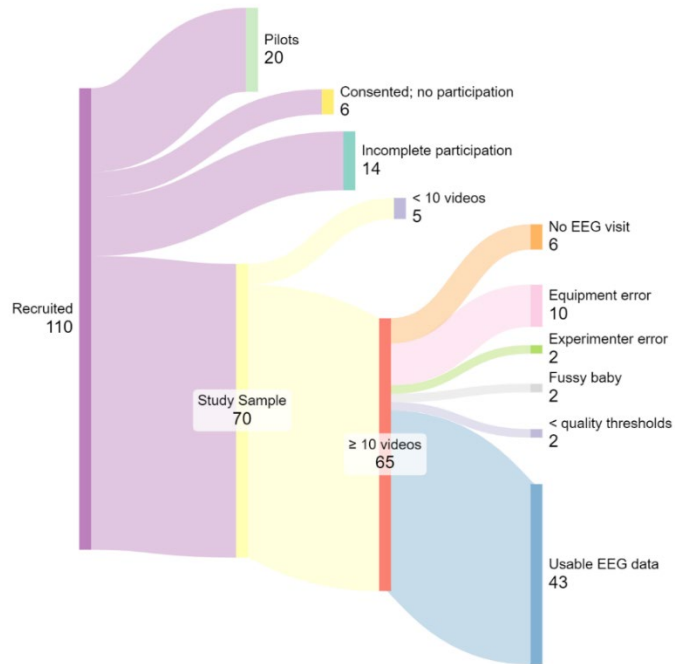


Figure 6. Sample attrition

At-Home Behavioral Observation

Caregivers were trained to use a custom cellphone application called TrHandy to collect videos of their infant grasping every two weeks in a semi-standardized protocol (see Figure 7). A set of videos (2-3) were recorded and submitted every two weeks from when the infant was 6 to 14 months old to have at least one usable video per timepoint. The semi-standardized protocol included the infant sitting in a highchair (either stand alone or attached to a table/counter) and the caregiver holding a barrier in front of the infant to block their view of the tray, then the caregiver placed an unsharpened pencil on the infants' tray in a vertical position at the infant's midline and removed the barrier (see Figure 7). To accurately record interpretable distances in the video, participants were

instructed to include a calibration card of known size within each video (either a magnet that we sent them or a credit-card-sized-card). To reduce 2D-3D distortion, caregivers were instructed to maintain the camera as parallel as possible to the working surface. Caregivers recorded the infant's reach-to-grasp movement with the cell phone application. This process was repeated until the infant successfully grasps the pencil.

After recording a video, the caregiver was prompted to check if the video followed all instructions and whether to send the video or not. Caregivers would repeat this process until they sent at least two videos they felt were valid. Researchers checked these videos for completeness and usability and noted if a video is not usable for the analyses. Caregivers were asked to record a new set of videos if needed. We consider the protocol to be semi-standardized due to variability between participants, including differences in type and style of highchair and barrier used. Each participant was assigned a different animal name that is used to log into the application and was a video identifier.

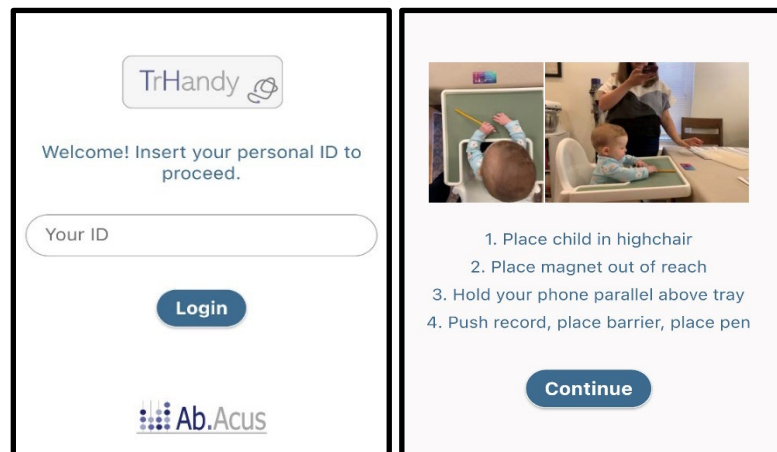


Figure 7. Protocol instructions within TrHandy.

The videos were automatically encrypted through the application and then were sent to a study-specific email address where research assistants then decrypted, performed a quality check, and sorted the videos. Videos were kinematically tracked using HaMeR, a transformer-based approach for **Hand Mesh Recovery** (Pavlakos et al., 2023). HaMeR uses 2D input, either images or videos, to recreate the 3D hand in a variety of contexts. Each image or video frame is fed into the transformer to be mapped using MANO (hand **M**odel with **A**rticulated and **N**on-rigid **d**e**f**o**r**mations) (Romero et al., 2017) to extract pose, shape, and camera parameters. MANO was developed to cope with occlusion and noise in kinematic data and was trained using 1000 high-resolution 3D scans of hands of 31 adult subjects in up to 51 poses (Romero et al., 2017). After the extraction with MANO, a regressor uses those parameters to project the 3D mesh and 3D points onto the image or video frame (see Figure 8 for example HaMeR 3D mesh visual output). Despite variations in skin colors and finger occlusions, HaMeR can recreate the hand with 2-3x improvements in the percentage of correct joint key-points in manually annotated videos in comparison to other hand tracking methods (Pavlakos et al., 2023). This method is more accurate in comparison to similar methods due to the extensive training data set and the deep network architecture (Pavlakos et al., 2023). The training data included 2.7M example images from controlled environments (2,542,200 images; 94%) and naturalistic settings (157,800 images; 6%), and both 2D and 3D data. The naturalistic in-the-wild data include videos and images obtained from Google and Bing image searches (Fang et al., 2023; Jin et al., 2020; Lin et al., 2014), Flickr (Chao, et al., 2015; Chao, et al., 2018; Fang et al., 2023; Jin et al., 2020; Lin et al., 2014), YouTube (explicitly included videos of humans performing tasks of daily living; Simon et al.,

2017), and videos extracted from an online New Zealand Sign Language practice website (Simon et al., 2017). Overall, this training dataset is 4x larger than a dataset commonly used in hand pose estimation, FrankMocap (Rong et al., 2021). In a direct comparison, HaMeR outperformed all other state-of-the-art body pose estimation methodologies (see Pavlakos, 2023 for more information) for both 3D joint evaluation and for 3D mesh evaluation on the FreiHAND (Zimmermann et al., 2019) and the HO3D (Hampali et al., 2020) datasets.



Figure 8. HaMeR visual output examples. Adapted from Pavlakos et al., 2023.

One video per timepoint per participant was analyzed with HaMeR. If the first video submitted followed the specific protocol, it was used for analyses. If it did not, the subsequent video was used (if it followed protocol). If no videos were usable at a specific timepoint, the participating family was contacted and was asked to record new videos. For inclusion into the analysis sample, participants could miss a maximum of 40% of collection timepoints as determined via a scree plot of the frequency of missing videos of the entire study sample (see Figure 9). As there is not a precedent for the amount of acceptable missing video data in an intensive at-home longitudinal design, we opted to

utilize a data-driven method that is commonly used in principal component analyses, the scree plot, to determine the number of components to extract based on eigenvalues (Hubert & Engelen, 2004). The number of components is determined from the ‘elbow’ of the graph, the number that is at the end of the initial decrease in eigenvalues (Hubert & Engelen, 2004). We used the scree plot to visualize the frequency of the number of missing videos and found that the ‘elbow’ of the graph was at 6 missing videos out of 16 possible videos or about 40% of videos. Using this threshold, the number of videos per participant in the current sample varies from 10 to 16 with an average of 13.86 videos per participant. The total number of videos for the sample analyzed is 595. As typical in kinematic analyses and body pose estimation, all 21 joints of the hand were tracked per video frame. The resulting data from HaMeR is then run through a custom Python script to extract the kinematic variables. The quantitative output includes kinematic variables such as distances and angles between fingertips and distances between fingertips and their respective knuckles (see Figure 10).



Figure 9. Scree plot. Frequency of participants by the number of missing videos

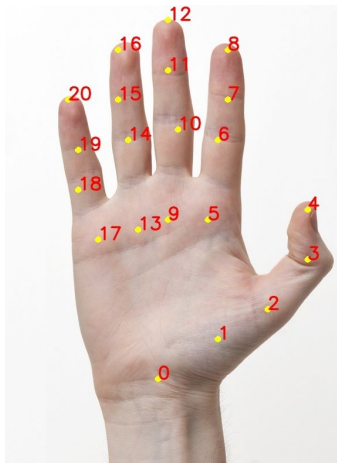


Figure 10. Visualization of hand joints.

Behavioral Coding of Grasping Videos

Behavioral coding was used to derive grasp strategy from the phone-recorded grasping videos. The coding scheme was based on categories used in prior infant reach-to-grasp literature (Karl et al., 2012; Karl & Whishaw, 2014). The base of our coding scheme was adopted from Karl and Whishaw (2014), except that we added another strategy called *emerging preshape*. This strategy was added after we began to use the coding scheme because many infants were starting to tuck their fingers by 13.5 months old, but not to the extent required for a *full preshape* strategy. This onset of slight preshaping seemed to be in between a fully haptic and a fully visual grasp and therefore this strategy could be important for understanding how infants integrate vision and haptics together. Therefore, all grasps were categorized into one of six different strategies: *full preshape*, *emerging preshape*, *touch and release*, *capture*, *adjust*, and *manipulate* (see Table 3 for definitions and Figure 11 for visual examples).

Coders were instructed to code all the strategies the infant used to grasp. For the videos with one strategy used, that strategy is called the main strategy. For videos with two strategies, the first one is called the pre-strategy and the second one, which was used to complete the grasp, is called the main strategy. We expected that touch and release would be used as a pre-strategy only, based on the definition requiring the object to be released, which sets up the hand to try a different strategy (see Table 3). The majority of grasping trials used one or two strategies, but there were occasional cases (2% of all videos) where infants used *touch and release* strategy multiple times then used a different strategy to complete the grasp. Another difference in the coding schemes between the current study and Karl and Wishaw (2014) is that the strategy that Karl and Wishaw used in their analyses was the first strategy the infant used (without differentiating whether that was the strategy that completed the grasp), same as our pre-strategy.

All videos were coded independently by one coder and 20% of the videos were blind coded by a second coder for the purpose of establishing reliability. The KappAcc program was used to calculate kappa statistics (Bakeman, 2023). The omnibus kappa was .82 while individual kappas per strategy ranged from .74 to .91 with a standard error of .06, which indicate an excellent agreement. The raw percent agreement was 87% between coders.

Table 3. Definitions of individual grasping strategies. Based on work from Karl et al., 2012 and Karl and Whishaw, 2014.

Grasping Strategy	Type of Grasp	Definition
Full Preshape	Visual	Full tucking of fingers (middle, ring, little) during reach, no adjustments, smooth grasp
Emerging Preshape	Visual	Evidence of tucking of fingers (middle, ring, little) during reach, or clear use of just the forefinger and thumb to pick up the object (middle, ring, and little can be straight but are separated and not being used to assist in grasp), no adjustments, smooth grasp
Touch and Release	Haptic	Touched object, fully remove finger(s), touch again
Capture	Haptic	Open hand contacted object while the rest of the hand closed from a large aperture, smooth grasp
Adjust	Haptic	Object was grasped then some fingers were adjusted without fully releasing object
Manipulate	Haptic	Object was moved by one or more digits before being grasped or during grasp to aid in stability



6mo Touch and Release



6mo Manipulate



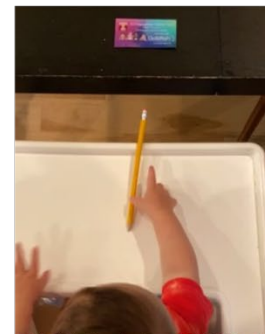
10mo Adjust



12mo Capture



**10mo
Emerging Preshape**



**9mo
Full Preshape**

Figure 11. Grasp Strategy Examples.

In-Person EEG Paradigm

At 14 months of age, participants came to the lab to complete a passive oddball EEG paradigm. Small tactile stimulators are taped onto the infants' thumb, middle, and little fingers and covered with a soft cloth mitten. The adult version of the tactile stimulators had been successfully used multiple times in our lab (Shen, Weiss, et al., 2018; Shen, Meltzoff, et al., 2018, Shen et al., 2020, Horger et al., 2024). We collaborated with CyNexo (CyNexo, Udine, Italy) to design and create tactile stimulators small enough for infant fingers, as our adult sized stimulators were too large. These stimulators consist of a thin plastic membrane in a housing that is connected via flexible tubing to a pneumatic stimulator that delivers a pulse of compressed air to inflate the membrane (see Figure 12). To generate the tactile stimuli, custom software delivers a trigger that serves to briefly open and then close a solenoid. The tactile stimulus feels similar to a light tap. In our prior work using the adult stimulators, expansion of the membrane began 15ms after trigger onset and peaked 20ms later (i.e., 35ms after trigger onset), with a total duration of membrane movement of around 100ms. We expect the characteristics of the infant stimulators to be similar.

The task involves stimulation to all three fingers, where the middle finger receives 80% of the stimuli (standard stimuli), while the thumb and little finger receive 10% each (deviant stimuli). There are a total of 4 blocks of the task, where the first block is the oddball paradigm (800 stimuli to standard, 100 stimuli to each deviant), and the subsequent blocks are individual blocks of 100 stimuli with all stimuli to one site per block. The oddball stimulation order was pseudorandom where deviants were separated by at least two standards. The inter-trial-interval varied between 1200ms and 1800ms.

During the EEG task, infants were on their caregivers' lap and were distracted by videos, bubbles, and/or snacks, with the goal to keep them content



Figure 12. EEG task set up. Tactile stimulator for infant fingers and a participant wearing both an EEG cap and tactile stimulators. Shared with permission.

As in our prior sMMN studies in infants (Shen, Weiss, et al., 2018; Shen, Meltzoff, et al., 2018, Shen et al., 2020) and adults (Shen, Smyk, et al., 2018; Horger et al., 2024), we are using the “identity MMN” method, which involves subtracting the ERP elicited from the control block of stimulation to one location from the ERP elicited from that location when it was a deviant within the oddball paradigm (e.g., the ERP from the thumb deviant minus the ERP from the thumb control). This method was previously utilized in MMN research (e.g., Möttönen et al., 2013; Pulvermuller et al., 2006), its key

advantage being that it controls for potential differences in perceptual sensitivity between individual stimulation sites.

EEG Acquisition

EEG data were collected using a James Long Company system. The data were digitized at 512 Hz using Snap-Master data acquisition software (HEM Data Corp., Southfield, MI). Signals were acquired from 32 electrodes that were mounted in a stretch cap (Ant Neuro, Germany) according to the International 10-20 placement system, including electrodes Fp1, Fpz, Fp2, AFz, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P3, Pz, P4, P8, POz, O1, Oz, O2, M1, and M2). Each electrode was filled with conductive gel (Electro-Gel, Electro-Cap International, Eaton, Ohio). During collection, the EEG signals were referenced to Cz with an AFz ground. All signal impedances were kept under 30 k Ω . EEG signals were amplified by optically isolated, high input impedance (>1 G Ω) bioamplifiers from SA Instrumentation (San Diego, CA) and digitized using a 16-bit A/D converter. The amplifier gain was 4,000 and the hardware filter was set at .01 Hz (high-pass) and 100 Hz (low-pass) with a 12 dB/octave rolloff. Out of the 59 participants who attempted the task, ten participants' data were lost to technical equipment problems, due to the equipment not performing all trials. An additional two participants' data were not usable due to a finger stimulator falling off during collection.

EEG Preprocessing and Cleaning

Physiological data was preprocessed in MATLAB (R2022b) using a custom script utilizing EEGLAB (Delorme & Makeig, 2004) functions to complete actions including resampling data to exactly 512 Hz, merging the event file with the EEG data file,

referencing to the average of the mastoids, and adjusting event times. Event times were adjusted by 20ms due to the time lag between the event trigger and the solenoid opening. Prior to referencing, signals from the mastoid electrodes were visually inspected for quality, which is typical in EEG studies. Participants with one mastoid electrode deemed unusable were referenced to the usable mastoid ($n = 2$), while participants with both mastoids as unusable were not used in the final sample ($n = 0$).

To decrease instances of human error within visual artifact deletion, EEG channels were cleaned using the low-density pipeline within HAPPE+ER v3.3 (Gabard-Durnam et al., 2018; Lopez et al., 2022; Monachino et al., 2022). The HAPPE+ER pipeline utilizes third-party software functions, including EEGLAB (Delorme & Makeig, 2004), Cleanline (Mullen, 2012), and FASTER (Nolan et al., 2010). Wavelet thresholding was performed for artifact detection, we used HAPPE+ER's "hard" threshold because the current study was on young children. Bad channels were identified using HAPPE's default functioning. The filters used were two FIR filters at 30 Hz low-pass, .1 Hz high-pass, and a 60 Hz line noise within the Cleanline program. Data were separated into epochs of 100ms before the event and 500ms after (-100 to 500ms), and were baseline corrected from -100 to 0ms. Segments affected by artifact or low-quality data were interpolated using the FASTER program, while entire epochs were rejected based on amplitude (-150 to 150 μ V) and joint probability. Channels identified earlier as poor quality or flatlined were interpolated, then the data were split into separate files by event marker and were saved as text files. The HAPPE+ER pipeline provides quality assessments and output information on the data that can be used for inclusion criteria. We used three variables for inclusion criteria: correlation of the data pre/post line noise

removal (above or equal to .90 for 59 and 61Hz), the percentage of usable epochs per condition (40%), and which specific channels were unusable, where a maximum of one channel in the region of interest could be unusable.

Identification and Scoring of ERP Components

Based on work by Scharf and colleagues (2022), a temporal principal component analysis (tPCA) was conducted on the EEG data. The goal of the tPCA was to identify and score separate ERP components in a more data-driven way compared to visually inspecting the grand mean waveforms, where time windows are selected in a relatively arbitrary manner, which can cause distorted effects or introduce artifact (for discussion see Luck and Gasepelin, 2017). We have successfully used this method on EEG data recorded during a tactile oddball paradigm in adults (Horger et al., 2024). The tPCA identifies factors that are present within the data, which each have their own topography and waveforms. The resulting ‘parts’ of a tPCA are usually called components, but here we will refer to them as factors, so they are not confused with traditional ERP components. The tPCA was conducted on the amplitudes of the difference conditions resulting from the oddball paradigm. As EEG has low spatial resolution due to the mixing of signals as the signals pass through the brain and scalp, the factors resulting from a tPCA will be correlated (Dien et al., 2005; Scharf & Nestler, 2018; Scharf et al., 2022). A parallel analysis (Horn, 1965) and an Empirical Kaiser Criterion (Braeken and van Assen, 2017) determined that the number of factors to extract was 13. As recommended from Scharf and colleagues (2022), we used a Geomin rotation (Yates, 1987) with 30 random start values and a rotation epsilon parameter of 0.01 (Bernaards & Jennrich, 2005). Geomin may be a better option than the more traditional Promax rotation (Hendrickson

and White, 1964) in separating factors that are highly overlapping, as we expect with all ERP data (Scharf & Nestler, 2018, 2019). To visualize the resulting tPCA factors, waveforms and topography plots were created for each individual factor. Expected sMMN component characteristics, including peak latency, amplitude directionality, and topography, were matched with the resulting tPCA factors.

Study Procedure

Following initial participant consenting and onboarding (both done online via video call and Research Electronic Data Capture (REDCap)), there were two parts to data collection: Longitudinal in-home video collection from 6 to 13 months, and one in-person lab visit at the conclusion of study participation, at 14 months of age. Interested families contacted the researchers via email, calling, or texting and scheduled an onboarding Zoom call with an undergraduate research assistant (RA) for the consenting and training process. In addition to the in-home video collection from 6 months to 13 months, caregivers filled out a temperament questionnaire, the Infant Behavior Questionnaire-Short Form, at 8, 10, and 12 months old (IBQ-S; Gartstein & Rothbart, 2003). The in-person lab visit at 14 months includes an EEG recording (for the sMMN) and various other tasks (see below).

For the onboarding zoom call, the RA explained the entire consent form, obtained electronic consent via REDCap (Harris et al., 2009; 2019), answered all questions, and trained the caregivers on how to record the videos with their cell phone using a semi-standardized procedure. Caregivers were also instructed to have specific materials ready for this call including standard unsharpened wooden pencil, a credit-card-sized-card such as a membership card, and a cutting board or sheet pan to be used as an occluding screen.

After caregivers downloaded the TrHandy cell phone app, they were then asked to place their infant in a highchair with a tray, or to seat the infant at a table in an appropriate booster seat. The first step of recording a video is to make sure the card is in view of the phone, then use the screen (cutting board or sheet pan) to block the infants view of the tray, and then place the unsharpened pencil vertically in front of the infants' midline. After all of that is set up, caregivers can start recording on the app and remove the screen and record until their infant grasps the pencil. Once the caregivers stop recording, the app will prompt them to watch the video and if it looks good then they can click "Yes, send" and if not, they can click "No, take a new one" and then are prompted to record a new video. Caregivers recorded and sent researchers videos until their infant is 14 months old. They were reminded biweekly via email or text (whichever method they prefer) by an RA to send a set of videos (2-3 videos).

At 14 months of age, participant families came into the lab for the final part of data collection. This lab visit included the oddball EEG paradigm (see above), the fine motor scale of the Bayley Scales of Infant and Toddler Development to evaluate the extent of the infants' fine motor skills (Bayley, 2006), the Early Motor Questionnaire, a parent-reported motor skills measure (EMQ; Libertus & Landa, 2013), and recording of the infant grasping a pencil and a vertical rod using cellphone video as well as an Intel RGB depth camera. The vertical rod was similar to that used in Karl and Whishaw (2014). The present investigation does not involve the IBQ-S, Bayley results, EMQ, or the task involving infant prehension in the lab setting.

Participant families were compensated \$10 for the initial set of videos, \$5 for subsequent biweekly sets of videos, and \$80 for the lab visit at 14 months. Participants

were also mailed a set of stacking cups at 8.5 months old and a study-specific onesie at 10.5 months old.

Data Analysis Plan

All analyses were conducted using R Statistical Software (v4.3.0; R Core Team, 2021) and RStudio (RStudio Team, 2020; "Cherry Blossom" Release) via various packages. The data were imported, organized, and inspected with various packages including *readr* (Wickham et al., 2024a), *psych* (Revelle, 2023), *dplyr* (Whickham et al., 2023), and *tidyr* (Wickham et al., 2024b). Outliers present in the continuous variables were visualized by the *Routliers* package (Klein & Delacre, 2024) and identified as values more extreme than the confidence interval derived from median ± 3 *median absolute value (Leys et al., 2013). Using those most extreme points as the thresholds, the values outside of the threshold were considered outliers and were winsorized using the *datawizard* package (Patil et al., 2022). Graphs were created with multiple packages including *ggplot2* (Wickham, 2016), *eegUtils* (Craddock, 2022), *effects* (Fox & Weisberg, 2018, 2019), *performance* (Lüdecke et al., 2021), *paletteer* (Hvitfeldt, 2021), *rcartocolor* (Nowosad, 2018), and *patchwork* (Pedersen, 2024).

For the grasp strategy analyses, multiple packages were used. The *nnet* package (Venables & Ripley, 2002) was utilized for the multinomial linear regression. The *lmtest* package (Zeileis & Hothorn, 2002) was used for a likelihood ratio test. The predicted probabilities were extracted using the *ggeffects* package (Lüdecke, 2018). For the kinematic analyses, the latent growth curve model was conducted using *lavaan* (Rosseel, 2012).

For analyses including the EEG data, the region of interest included electrodes F3, F4, C3, C4, FC1, and FC2, based on prior sMMN work on infants by Shen and colleagues (2020). The multilevel models were conducted using *lme4* (Bates et al., 2015) and *lmerTest* (Kuznetsova et al., 2017) packages. An unconditional model (without interactions) was always conducted prior to a conditional model (with interactions) and the models all had a random intercept of participant. To probe significant main effects of variables with more than two levels, Tukey-adjusted pairwise *t*-tests were performed to assess directionality. The *emmeans* package (Lenth, 2023) was used for simple effect and simple slope analyses to understand directionality of the relations between the variables. Graphs were created using the packages mentioned above.

CHAPTER 3

RESULTS

Aim 1: To Investigate the Fine-Grained Development of Grasping from 6 to 13 Months

Aim 1a: Longitudinal Examination of Grasping Strategy Usage

We examined the usage of grasping strategies using a behavioral coding scheme that was based on the published scheme by Karl and Whishaw (2014). Our coding scheme included six different grasping strategies and coded the pre-strategy and main strategy, where the pre-strategy was the first strategy used, and the main strategy was the strategy used to complete the grasp (see Methods for more information).

To investigate whether there are any trends in either pre-strategy or main strategy use, we explored the descriptive statistics and frequencies of use. Infants may use all the strategies in relatively the same order throughout development or strategy usage order could be more individual. For pre-strategy usage, the most common strategy used was *touch and release*, where 95% of infants used *touch and release* at least one time. As expected, the *touch and release* strategy was only used as a pre-strategy. The pre-strategy frequency of use of *touch and release* was highest at 7, 8, and 8.5 months old with 17 (40%), 14 (33%), and 20 (47%) cases, respectively. After 8.5 months old, the frequency decreased. Interestingly, *capture* was used as a pre-strategy at various timepoints for two different infants and always preceded the usage of *adjust* (0.5% of all videos). Overall, *touch and release* was most frequently used and three instances of a *capture* strategy required an *adjust* strategy prior to grasp completion (see Figure 13).

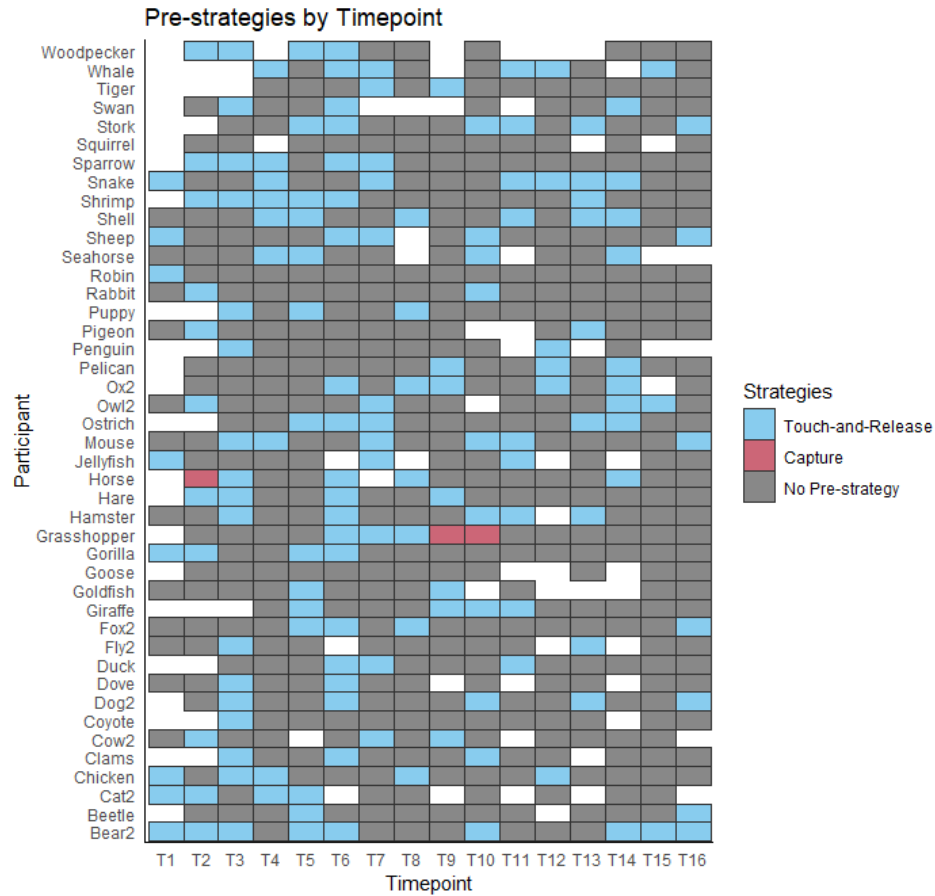


Figure 13. Pre-strategy usage by timepoint. Empty squares indicate missing data. Each animal name refers to one participant.

For main strategy usage, there also were no overt patterns and not all infants used all the different strategies. For example, all infants used a *manipulate* strategy at least once while only 58% used *adjust*. 5% of infants did not use *capture* at all, but interestingly, those infants did use *emerging preshape*, providing evidence that the *capture* strategy is not a required precursor to using the *emerging preshape* strategy. 88% of infants used *emerging* or *full preshape*, which shows that most infants did start preshaping their fingers by 13.5 months old, but there is still variability and individual differences in strategy use. 28% of infants used *full preshape* at least once. Overall, the

majority of infants used all of the different grasping strategies, but infants did not have to use one strategy to progress to the next and there were no specific orders that emerged of main strategy use over time (see Figure 14).

A multinomial logistic regression analysis was conducted to predict the main grasp strategy from infant age. The likelihood ratio test for the fitted model indicated that the one predictor model provided a better fit than the null model without any predictors, $\chi^2_{(4)} = 75.96, p < .001$. The odds ratios indicate the probability of using one strategy vs the probability of using the reference category, *manipulate*, and they are calculated in terms of a one month increase. The odds ratio is 1.72 for using *full preshape* vs *manipulate*, $p < .001$, therefore, over time the odds of using *full preshape* is higher than using *manipulate*. The odds ratio is 1.53 for using *emerging preshape* vs *manipulate*, $p < .001$. The odds ratio is 1.23 for using *capture* vs *manipulate*, $p < .001$. The odds ratio is 1.13 for using *adjust* vs *manipulate*, $p = .17$. Taking these odds ratios together, it is significantly more likely for an infant to use *full preshape*, *emerging preshape*, and *capture* as they age compared to *manipulate*.

For visualization purposes, we extracted the probabilities from the regression and predicted the probabilities from 14 to 36 months old using the trends (see Figures 15-16). Examining the predicted probabilities allows us to visualize how the strategy usages change over time and when haptic grasp strategies are predicted to be phased out.

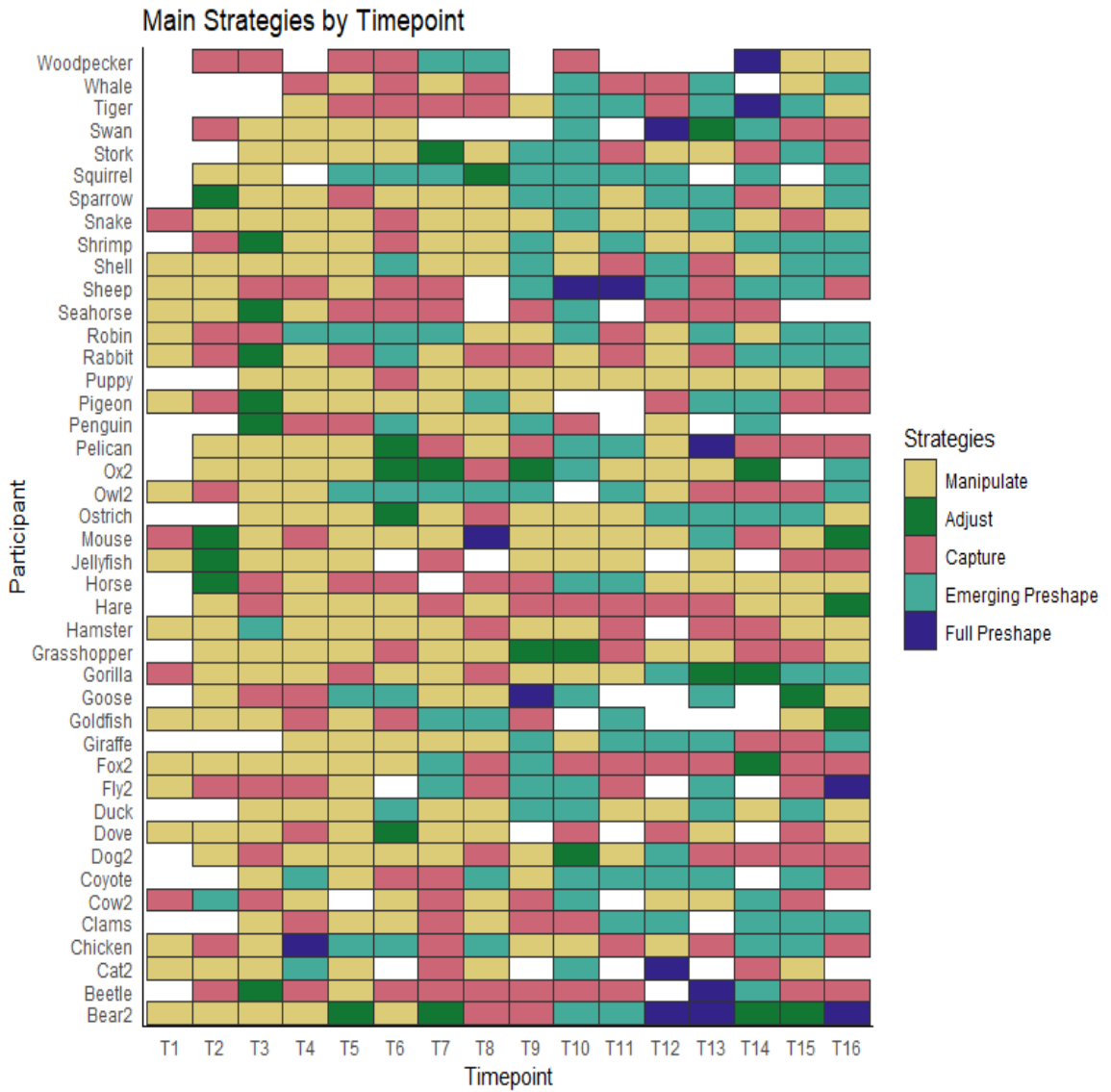


Figure 14. Main grasping strategy usage by timepoint. Empty squares indicate missing data.

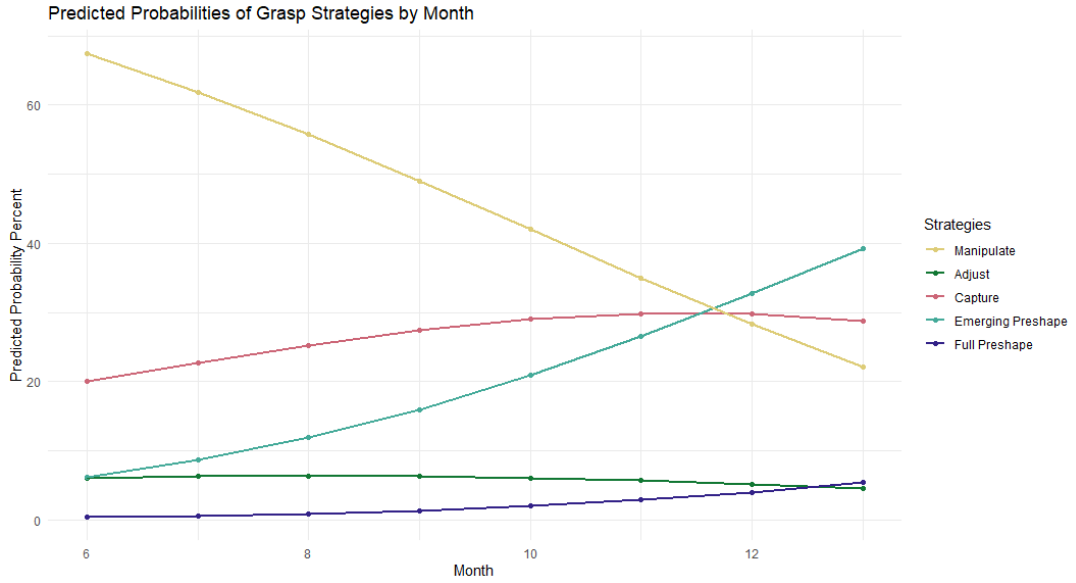


Figure 15. Predicted probabilities of grasp strategies by month.

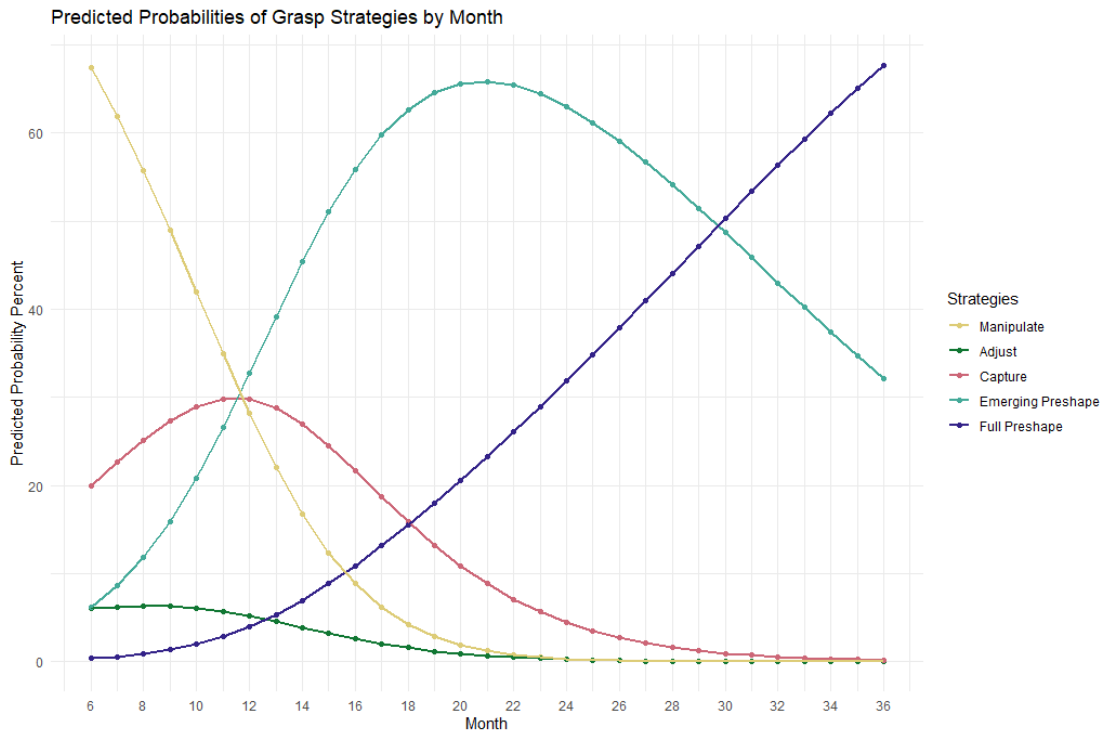


Figure 16. Predicted probabilities to 36 months old of grasp strategies.

Aim 1b: Longitudinal Investigation of Grasp Proficiency

We developed a variable called grasp proficiency to investigate how preshaping changed longitudinally that included both the distance from the middle fingertip to the middle finger knuckle and little fingertip to the little finger knuckle at the instance of first contact with the pencil. To ensure that changes in these distances are not due to hand growth, we tested hand size from each infants' first and last grasping videos. Hand size was measured as the distance between the index finger knuckle and the little finger knuckle at first contact with the pencil, as the hand is most likely to be outstretched at this point. Hand size did not significantly differ from the first video (including ages 6 to 7.5 months) ($\beta = 34.3\text{mm}$, $\text{SE} = 1.1$) to the last video (including ages 12.5 to 13.5 months) ($\beta = 36.8\text{mm}$, $\text{SE} = 1.1$) of the study, $\Delta\beta = 2.45$, $\text{SE} = 1.56$, $t(84) = 1.57$, $p = .12$. We investigated grasp proficiency over time with a latent growth curve model to examine both the starting point and growth trajectory of preshaping. The degree of grasp proficiency at 6 months is significantly different between infants, $\beta = 58.67\text{mm}$, $\text{SE} = 2.22$, $z = 26.4$, $p < .001$. The growth from 6 to 13.5 months old is significantly different between infants, $\beta = -.95\text{mm}$, $\text{SE} = .25$, $z = -3.86$, $p < .001$. We also included a dichotomous covariate into the model that tested whether infants who used a visual grasp (either *emerging preshape* or *full preshape*) during the 13.5-month video (timepoint 16) had different proficiency slopes than the infants who used a different strategy. Infants who used a visual grasp at 13.5 months ($n = 14$, slope = -1.52) did not have a significantly different grasp proficiency trajectory than those who did not preshape ($n = 29$, slope = $-.64$), $z = -1.86$, $p = .06$.

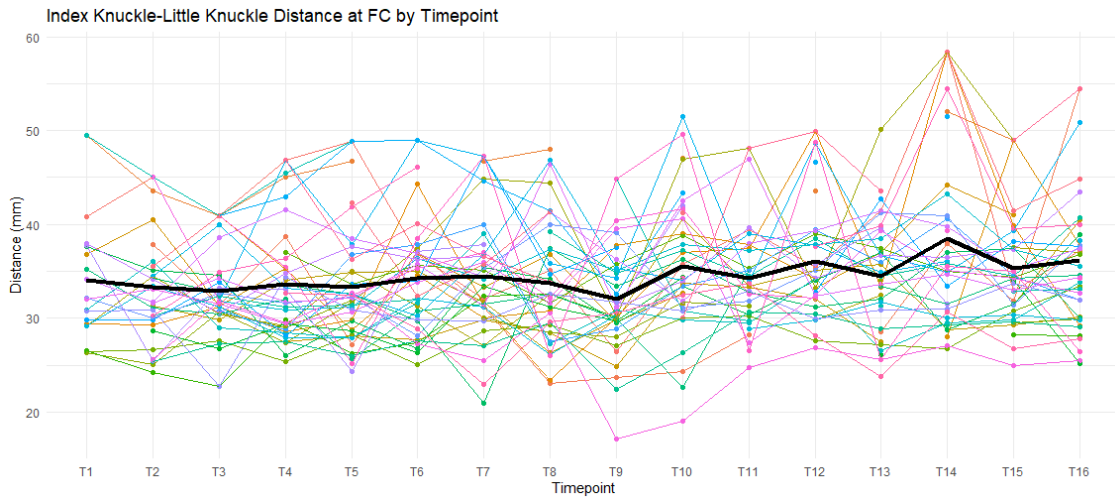


Figure 17. The proxy for hand size at each timepoint. The distance between the index knuckle and the little knuckle at first contact (FC).

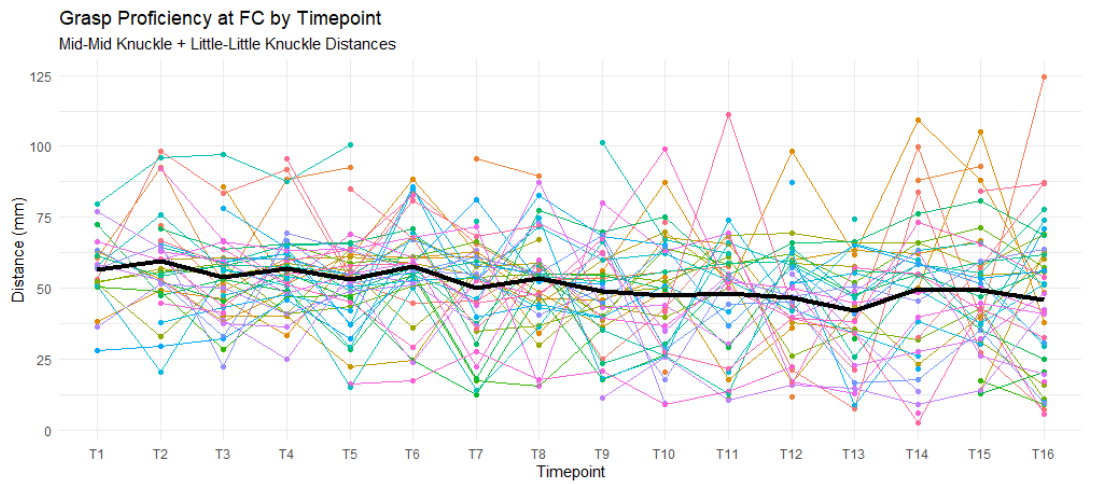


Figure 18. Grasp proficiency over time. Separated by individual (colors) and the average proficiency (in black). Smaller values indicate higher proficiency.

Aim 2: To Relate the Neural Correlates of the Relations between Infant Fingers at 14 Months Old to the Longitudinal Development of Grasp Proficiency from 6 to 13 Months

Aim 2a: Identification of the sMMN ERP Component and Multilevel Regressions

We examined the topography and timing of each factor identified by the tPCA to find the best match with the component of interest, the sMMN. In lieu of manually scoring ERP amplitudes, we used a tPCA to extract the ERP component. A typical tPCA extracts around 8-12 major factors, while the rest of the factors are minor factors and usually represent noise or latency jitter between participants (Scharf et al., 2022; Dien, 2012). In general, there is not a cut-off based on the amount of variance explained by each factor. The tPCA included only the little finger and thumb difference conditions (deviant – control waveform), which led to 13 factors being identified. One factor (factor 6; amount of variance explained: 3%) was matched to the sMMN component through a peak latency at 126ms and a maximal amplitude in the difference waveform over electrode C3. This peak latency and topography were similar to previous research using the manual extraction method (individual 15ms averaged peak latency between 60-180ms, frontocentral topography; Shen et al., 2020) and matches a previously analyzed sMMN component using a tPCA on the same task in adults (peak latency: 130ms, peak electrode: C3; Horger et al., 2024).

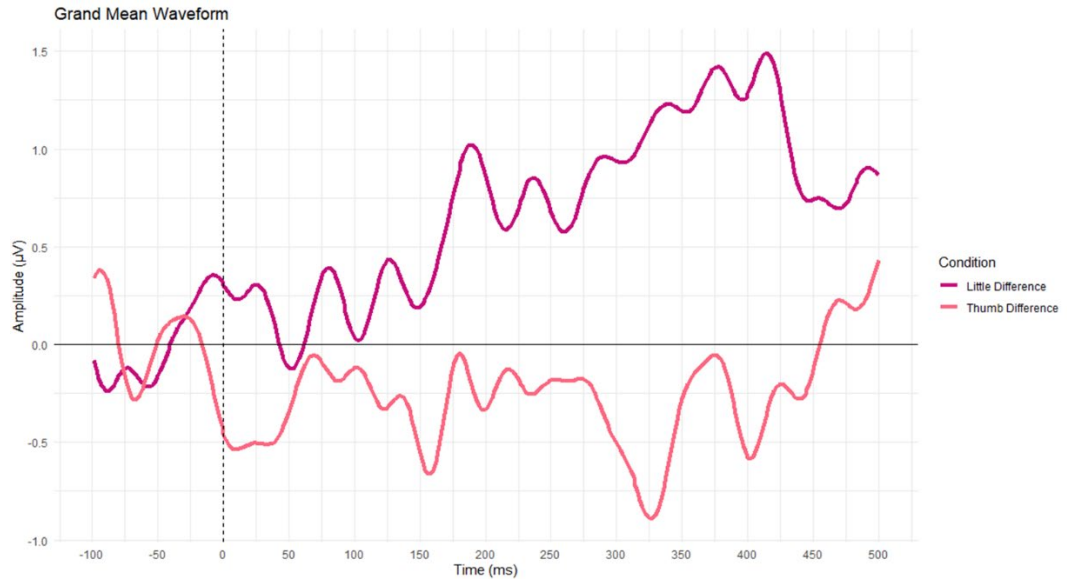


Figure 19. Grand mean waveform of difference scores.

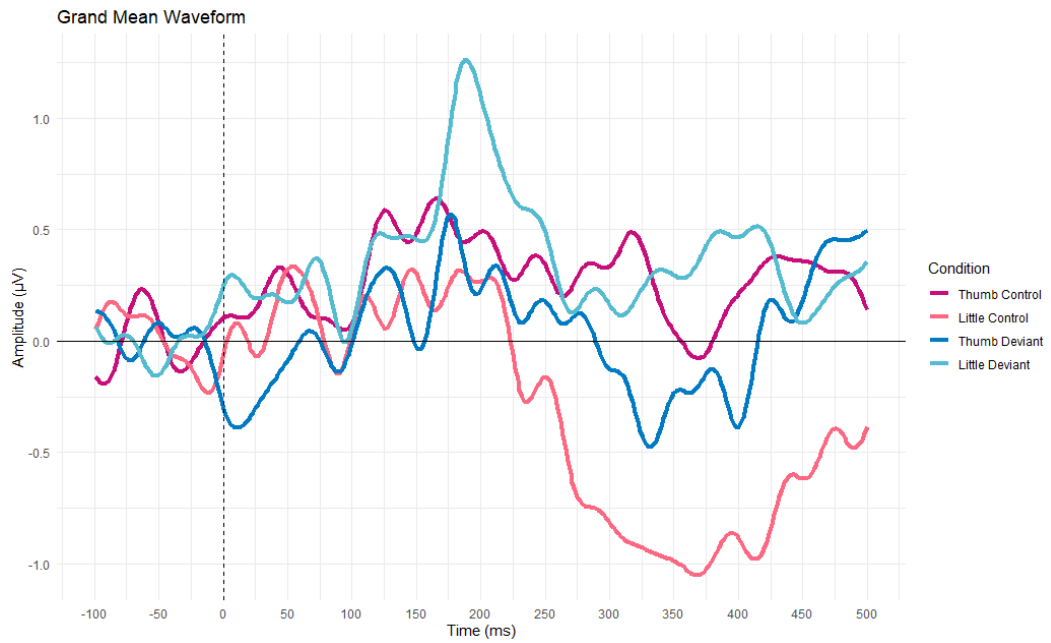


Figure 20. Grand mean waveform with all conditions.

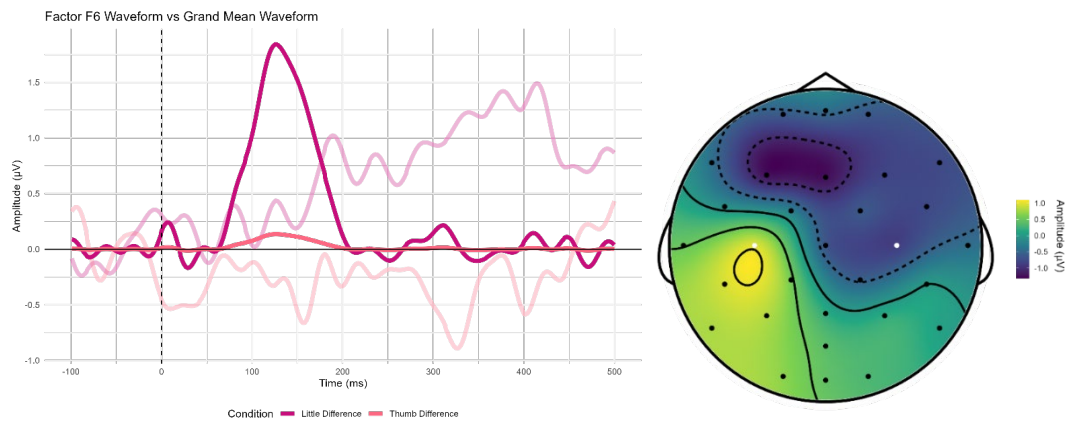


Figure 21. sMMN Plots. sMMN at C3 vs grand mean waveform; sMMN topography

The unconditional multilevel model with a random intercept of participant, including the predictors task condition (little difference/thumb difference), hemisphere (right/left), and region (frontal/central/frontocentral), predicting the raw sMMN amplitude showed significant main effects of all predictors. sMMN amplitude was significantly enhanced (more negative) over the right hemisphere than the left ($\Delta\beta = -.62$, $SE = .30$, $t(499) = -2.05$, $p = .04$) and over the frontal region as compared to the central region ($\Delta\beta = -1.08$, $SE = .37$, $t(499) = -2.93$, $p = .004$). The thumb difference condition amplitude was enhanced ($\beta = -.80$, $SE = .39$, $CI = [-1.57, -.04]$) in comparison with the little difference condition ($\beta = -.14$, $SE = .39$, $CI = [-.91, .63]$), $\Delta\beta = -.67$, $SE = .3$, $t(495) = -2.23$, $p = .026$. There were no significant interactions present in the conditional model. The interactions were tested separately and included task condition by hemisphere and task condition by region.

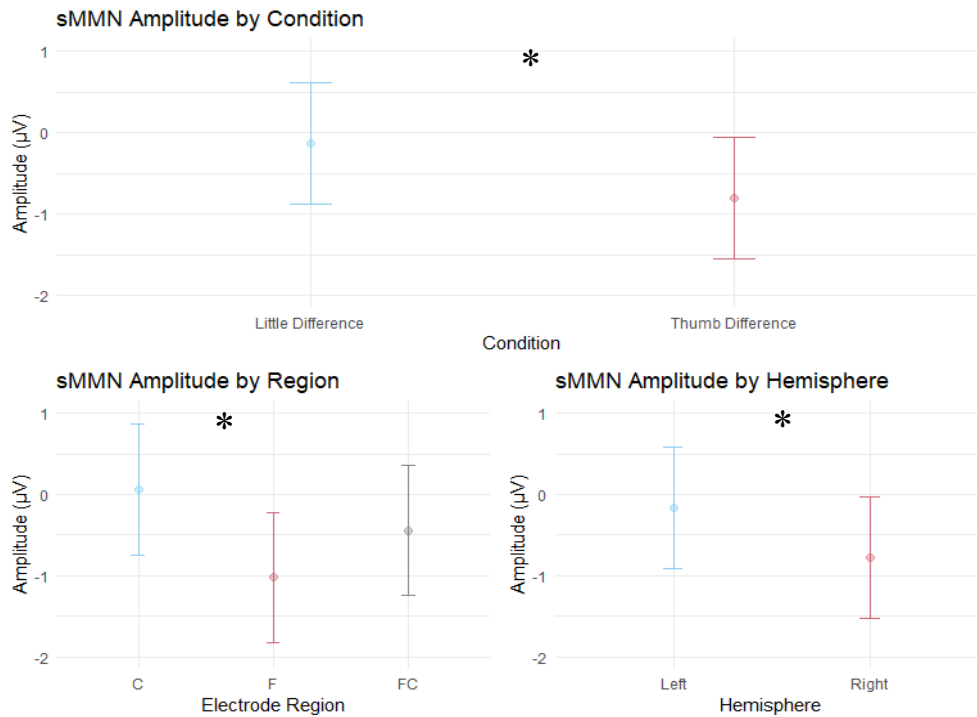


Figure 22. sMMN multilevel model results. Significant contrasts indicated by asterisks.

Aim 2b: Relations between Behavioral Grasping and sMMN Amplitude

We conducted a series of multilevel models to investigate the overall relations between kinematics, behavioral grasping strategies, and the sMMN amplitude. The first model, the unconditional model, predicted the raw sMMN amplitude and included the following predictor variables: EEG task condition, the standardized proportion of timepoints that were coded as a visual grasp (*emerging or full preshape* strategies), a dichotomous variable of whether timepoint 16 (13.5 months of age) was coded as a visual grasp, and the standardized individual grasp proficiency growth trajectory slopes (extracted from aim 1b). The model’s random intercept is participant. The only

significant main effect was the EEG task condition. The sMMN amplitude during the thumb difference condition ($\beta = -.66$, $SE = .44$) was significantly enhanced compared to the little difference condition ($\beta = -.04$, $SE = .44$), $\Delta\beta = -.62$, $SE = .32$, $t(463) = -1.94$, $p = .05$.

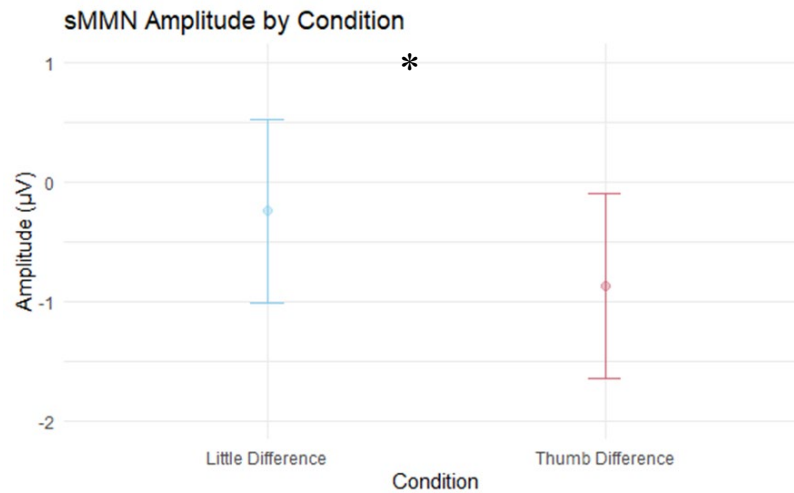


Figure 23. Main effect of EEG task condition.

The conditional models tested one interaction each, involving the EEG task condition and one of the other predictors. There is a significant interaction between task condition and the proportion of behavioral preshaping, where a higher proportion of preshaping was related to enhanced thumb difference condition ($\beta = -.57$, $SE = .44$, $CI = [-1.46, .33]$) amplitudes compared to the little difference condition ($\beta = .26$, $SE = .44$, $CI = [-.63, 1.15]$), $\Delta\beta = -.82$, $SE = .32$, $t(462) = -2.59$, $p = .01$. This interaction was not influenced by one condition over the other as the thumb difference condition and the little difference condition slopes are not significantly different from zero, as evidenced by the

confidence intervals. This interaction revealed that a higher proportion of preshaping over time is related to the presence of two inferred categories of the hand (inferred from an enhanced thumb difference condition compared to the little difference condition). There was also a significant interaction between task condition and grasp proficiency growth trajectory, where a more negative grasp proficiency trajectory was related to enhanced little difference ($\beta = .86$, $SE = .41$, $CI = [.05, 1.67]$) amplitudes compared to the thumb difference ($\beta = .17$, $SE = .41$, $CI = [-.64, .98]$) amplitude, $\Delta\beta = -.67$, $SE = .32$, $t(462) = -2.15$, $p = .03$. This interaction was driven by the little difference slope, as it is significantly different from zero. Interestingly, this interaction revealed that a more negative grasp proficiency trajectory is related to the presence of two inferred categories of the hand. There were no other significant interactions.

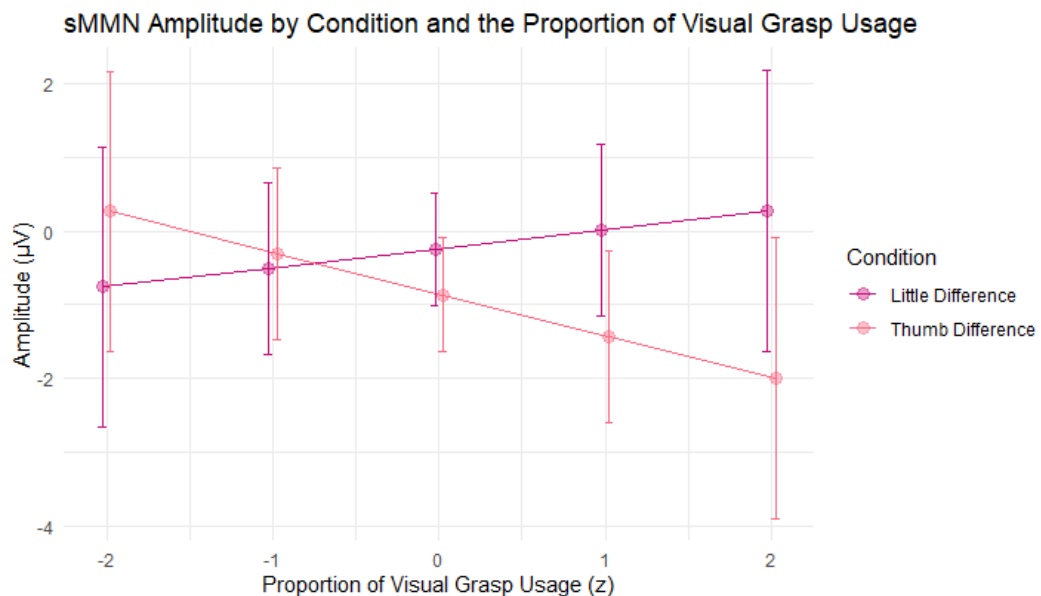


Figure 24. sMMN amplitude by condition and the proportion of visual grasp usage.

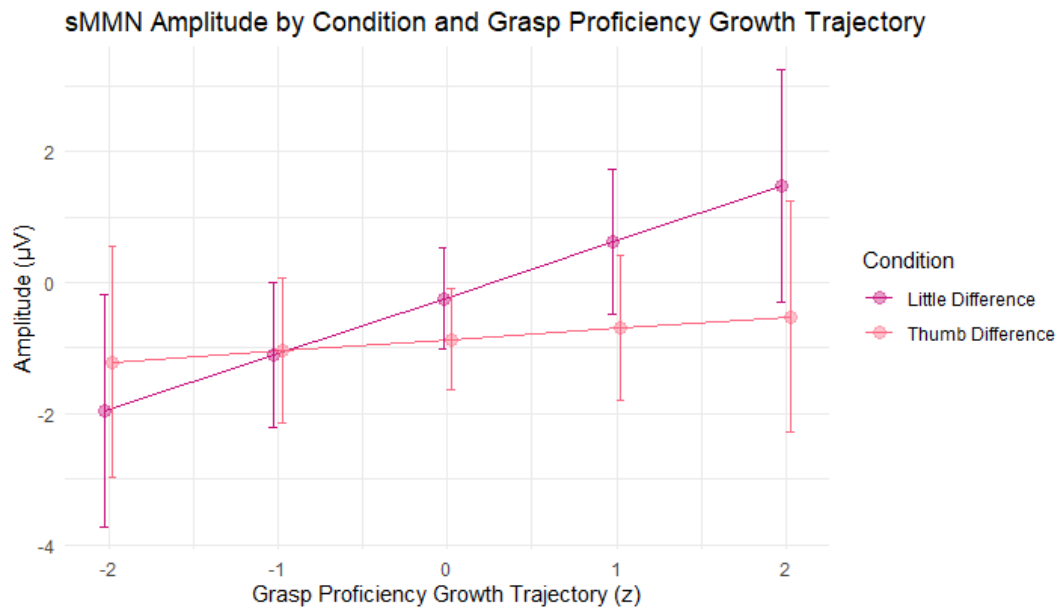


Figure 25. sMMN amplitude by condition and grasp proficiency growth trajectory.

CHAPTER 4

DISCUSSION

The purpose of this study was to uncover how preshaping emerges over infancy and whether longitudinal behavioral indices of grasping are related to a neural index of finger relations. Infancy is marked by rapid change and growth in skills, but these processes are highly individualized and dependent on context and culture (Hadders-Algra, 2018). As young infants practice grasping, they are learning about their environment, their body, and the interplay between the two. During this process, the infant brain is fine-tuning the way the body and the relations between all body parts are represented in the brain, called a body map. Until now, there was a gap in understanding the relations between the developing infant grasp and the neural body map of the hand.

We started by examining the longitudinal changes of infant prehension from 6 to 13.5 months old, using both behavioral coding (aim 1a) and kinematic analysis (aim 1b). We found that grasping strategies are highly variable both inter-individual and intra-individual, but most infants showed signs of learning to preshape their hand on approach of grasping an object. Likewise, kinematic analyses indicated that infants were progressing in their maturation and precision of grasping. Each infant had a slightly different starting position, growth rate over time, and pattern of growth.

We then investigated the somatosensory mismatch negativity (sMMN) (aim 2a), which can be used to examine the neural relations between the body parts stimulated, in our case, the thumb, middle, and little fingers. From those relations between fingers, we can infer the categorical boundaries present in the hand at 14 months old. A boundary

location is assumed depending a comparison of the magnitude of the response between one set of body parts (one deviant location to the standard location) to the other set body parts (other deviant location to the standard location). The sMMN response will be enhanced when crossing a boundary. We found that the sMMN response was enhanced for the thumb deviant to middle finger standard location compared to the little deviant to middle finger standard location, therefore, we infer that there is a boundary between the thumb and the middle finger on the infant hand at 14 months old. Interestingly, prior work using this paradigm on adults yielded similar results (Horger et al., 2024; Shen, Smyk, et al., 2018a; 2020), therefore, the neural body map of the hand is matured to mimic adult-like performance at 14 months old.

To address our primary question, we examined the relations between the longitudinal change in infant grasping using both behavioral coding and kinematic analysis from 6 to 13.5 months old to predict the sMMN response at 14 months old (aim 2b). We found that only behavioral coding predicted the magnitude of the sMMN response, suggesting that infant grasp strategy usage and change over time is important for the development of the relations between the individual fingers.

Behavioral Development of Grasping (Aim 1a)

We utilized behavioral coding to investigate changes in grasping strategy usage between 6 and 13 months of age. Infants seated in their highchair at home were presented with a pencil vertically flat on the tray while their caregivers recorded them grasp the pencil. We behaviorally coded the strategy used to grasp the pencil. The strategy used to complete the grasp was taken as the main grasping strategy, which was used in the primary analyses. Any strategy used prior to successful grasping was coded as a “pre-

strategy,” since as during the development of a mature grasp, infants often require several touches before achieving a successful grasp (Gordon, 1994). This is consistent with the theoretical approach of NGST (Hadders-Algra, 2018), which includes a phase of secondary variability in development where trial and error learning is an important aspect of grasp development as it leads to being able to functionally adapt motor movements.

To remind the reader, the foundation of our coding scheme was the scheme used by Karl and Wishaw (2014), with two main differences: 1) the coded strategy that Karl and Wishaw used in their analyses was the first strategy the infant used, which may not have resulted in a successful grasp; 2) We also added another strategy called *emerging preshape* to their coding system. When we initially began to use the coding scheme of Karl and Wishaw on our videos, it was evident that most infants were not progressing to using a *full preshape* strategy by 13.5 months old, but many infants were starting to tuck their (non-index) fingers during the reach, in readiness to grasp the object. This strategy did not fit into the original coding scheme of Karl and Wishaw, which led us to add the *emerging preshape* strategy. Importantly, this represents a transitional phase between fully haptic strategies (*touch and release, adjust, manipulate, capture*) and the fully visual strategy (*full preshape*) that has been overlooked in prior work.

As expected, the predominant pre-strategy used by infants in our sample was *touch and release*, with the frequency of this strategy decreasing at older ages. Surprisingly, there were multiple instances where infants used *capture* as a pre-strategy then *adjust* for the main strategy. For the main strategy usage, younger infants used *manipulate* more frequently and older infants used *capture* more frequently. The probability of using *capture* increased over time but plateaued around 11 months old then

decreased. *Emerging preshape* and *full preshape* strategies both increase over time, with 28% of infants successfully progressing to using *full preshape* and the majority of infants (88%) progressing to using the *emerging preshape* strategy. Although most infants used *emerging preshape* by 13.5 months old, there was much intra- and inter-individual variability in strategy use over time. Our intensive longitudinal design can reveal variability in a way that cross-sectional or longitudinal designs with wider spaced data collections cannot (Siegler, 1996). The extent of variability on the path of developing stable behavioral abilities also aligns with studies of infant development in other domains, such as self-recognition (Courage et al., 2004).

Using the trends examined with the multinomial regression, we predicted the strategy usage probabilities into the future and found interesting results. *Capture* would continue to decrease steadily until 30 months old when it would not be used anymore. *Emerging preshape* would continue to increase in use until around 21 months old then decreases, while *full preshape* would increase steadily until it is the most common strategy, which is predicted to happen around 30 months old. These estimates are especially interesting as they are the first estimates of strategy usage beyond 13.5 (current study) or 24 months old (Karl & Whishaw, 2014) and provide information for later development on the process where pincer grasps become more adult-like.

Considering that our coding scheme was based off Karl and Whishaw's (2014) coding scheme, it is important to note that the object's orientation in our study compared to Karl and Whishaw's study is different. In our study, the 0.72cm diameter pencil was placed vertically flat on the highchair's tray, while in the other study, the 1.65cm diameter rod was vertically positioned in the air on an acrylic stand in front of the

participant. The placement of the pencil in the current study was chosen because of the 2D nature of the videos (recorded from above to effectively remove the depth dimension) that were recorded in an particular environment. In contrast, Karl and Whishaw (2014) used an optoelectronic lab setup with multiple cameras. These differences in orientation could provide different affordances to the infants to grasp, where the pencil lying flat could elicit a more natural pincer grasp than a rod positioned vertically in the air.

These differences in object placement can explain some of the differences in variability and strategy use trends between our study and that of Karl and Whishaw (2014). The difference in target object orientation provides different challenges for the infants. When the pencil is flat on the highchair, infants do not need to rotate their arm from a resting position as they would if the pencil was vertically in the air. This arm rotation requires more muscle coordination and timing than if it was not necessary. However, the rod was considerably thicker than the pencil, where a thinner object requires more precision to grasp. Both tasks were designed to elicit precision grasping, but they ended up being difficult in separate ways.

Comparing strategy frequencies from Karl and Whishaw (2014) to the current study shows that even though the grasp tasks were distinct, and the coding schemes were not identical, the reported frequencies of strategy use are not vastly dissimilar. For example, our frequencies for 11-12 months old for *emerging preshape* and *full preshape* are 30% and 3% respectively, while Karl and Whishaw reported a *preshape* frequency of 12%. Our predicted frequencies for *emerging preshape* and *full preshape* at 24 months old are 63% and 32% respectively, while the reported frequency for the *preshape* strategy in Karl and Whishaw is 25%. For the *touch-and-release* pre-strategy, Karl and Whishaw

found that 33% of infants were still using the strategy at 11-12 months old while we found that only 21% of infants used *touch-and-release* as a pre-strategy. The biggest difference between the two studies comes from our inclusion of the *emerging preshape* strategy, which was not included in the Karl and Whishaw *preshape* strategy. In their study, what we called *emerging preshape* may have fallen within the *capture* strategy or among the haptic strategies without reported frequencies in their paper (*manipulate* and *adjust*). Despite the broad similarities in frequencies, our grasping paradigm (involving a pencil lying flat) showed growth trajectories where 33% infants progressed to using a visual strategy between 11 and 12 months (either *emerging* or *full preshape*) compared to the grasping paradigm from Karl and Whishaw (involving a rod vertically placed in the air) where only 12% of infants progressed to using a visual strategy between 11 and 12 months (see Tables 4 and 5 for strategy usage frequencies).

Table 4. Prior grasp strategy frequency percentages. Adapted from Karl and Whishaw (2014)

Age	<i>Preshape</i>	<i>Touch & Release</i>	<i>Capture</i>
4-6mo	3%	56%	25%
7-8mo	5%	41%	44%
9-10mo	6%	28%	56%
11-12mo	12%	33%	51%
24mo	25%	0%	75%
Adults No Vision		56%	38%
Adults Vision	72%		28%

Table 5. Grasp strategy frequency percentages.

Age	<i>Emerging Preshape</i>	<i>Full Preshape</i>	<i>Capture</i>	<i>Adjust</i>	<i>Manipulate</i>	<i>Touch & Release (Pre-Strategy)</i>
6mo	6%	0%	20%	6%	67%	41%
7-8mo	10%	1%	24%	6%	59%	35%
9-10mo	18%	2%	28%	6%	46%	28%
11-12mo	30%	3%	30%	5%	32%	21%
13mo	39%	5%	29%	5%	22%	17%
24mo (predicted)	63%	32%	4%	0%	0%	3%

Kinematic Analysis of Grasp Proficiency (Aim 1b)

We employed computer vision methods to quantify physical hand and finger movement during prehension, and we derived a variable to index grasp proficiency, or the infants' degree of preshaping prior to object contact. While reaching for an object for a pincer grasp, the middle, ring, and little fingers will tuck into the palm and the thumb and index finger will be positioned just wide enough to allow for a smooth contact and grasp of the object. This tucking of the fingers, called preshaping, increases the chances of a stable grasp by increasing the fingertip forces of the thumb and index finger (Gordon, 1994).

Overall, we found differences in grasp proficiency over time, specifically, there were individual differences in both the first timepoint of grasp proficiency (at 6 months old) and the overall rate of change, or growth trajectory. The average of the grasp proficiency index decreased from 56.45mm (SD = 12.81) to 45.98mm (SD = 26.82) over the age range of the study, from 6 to 13.5 months of age. This suggests that infants have

started preshaping their hand over this age period. This finding confirms some previous reports, but sheds light on the overall trajectory of development. In their review paper, Corbetta and Santello (2018) report that finger preshaping begins between seven and eight months of age to adapt to the objects' characteristics (the second phase of prehension development), while the results of empirical work from Whishaw and Karl (2014) indicate that preshaping starts between nine and 12 months. There are other empirical reports that the integration of visual and haptic perceptions while grasping begins as early as five months through hand orientation changes only (von Hofsten & Fazel-Zandy, 1984) or between six to nine months for individual finger adjustments to a concave or convex object (Bonniec, 1985). However, in the current sample, there does not seem to be a specific starting age of preshaping beginning between six to 14 months old, and the onset seems gradual.

Neural Aspects of Relations between Fingers (Aim 2a)

To investigate neural aspects of grasp development, we employ an EEG-based measure of the relations between fingers, which allows for inference into the categorical boundaries of the hand. Prior work has suggested that the categorical boundaries may be related to functional usage of the digits. The tactile stimulation task in our study was previously used in adults, but this was the first instance of applying it to infant fingers. We used a data-driven technique (tPCA) to score the sMMN component, which limits the instances of human biases and errors. We successfully elicited the sMMN in infants for the first time, and the ERP component characteristics were similar to prior studies in both infants (Shen et al., 2020) and adults (Horger et al., 2024; Shen, Smyk, et al., 2018a).

We hypothesized that 14-month-old infants would have two categories of their hand, which are based on the functional usage of the hand where the thumb and index are in a separate category than the other fingers. The presence of two categories would be evidenced by an enhanced (more negative) sMMN amplitude for the thumb difference condition (thumb deviant condition – thumb control condition) compared to the little difference condition. In accordance with our hypothesis, we found that the thumb difference amplitude average was significantly enhanced compared to the little difference. This suggests that the thumb is in a separate category because the neural response was larger as the categorical boundary (between the thumb and middle finger) was crossed. This finding provides evidence that there are at least two body map categories of the hand at 14 months old and the findings are consistent with the proposal that the categories are based on hand usage, although further developmental work is needed to clarify the developmental origins of these categories.

In our prior work in adults utilizing the same EEG task, the average difference between the little difference and thumb difference conditions in only electrode C3 was .11 μV (Horger et al., 2024) and in electrodes F3, F7, FC1, and FC5 the difference was around .90 μV (Shen, Smyk et al., 2018a). In the current study, the average difference between the little difference and thumb difference conditions in electrodes F3, F4, C3, C4, FC1, and FC2 was .67 μV . As the magnitude of response in infants was similar to the responses of adults in the same task, this is evidence that the categories present in the hand are adult-like at 14 months old. Taking these findings in conjunction with the grasp strategy and grasp proficiency findings, we can assume that the neural categories mature into two categories prior to the behavioral grasping being fully matured. One important

next step is that sMMN amplitudes need to be assessed during the first year of life, preferably at multiple timepoints, to understand the plasticity and development of the categories of the hand.

Linking Neural and Behavioral Measures (Aim 2b)

Our final aim was to assess whether longitudinal changes in behavioral grasping from 6 to 13.5 months predicts the sMMN amplitude at 14 months old. Contrary to our hypotheses, there was no overall impact of behavioral grasping on the amplitude. However, there were multiple interactions between various aspects of behavioral grasping and the EEG task condition in predicting the sMMN amplitude. Infants who had a higher proportion of timepoints where they used a visual grasp strategy, either using an *emerging preshape* or *full preshape* strategy, also had evidence of a presence of two neural categories of the hand, where the sMMN amplitude for the thumb difference was enhanced. There was no interaction between whether infants used a visual grasp strategy at 13.5 months old. It is interesting that the overall proportion of behavioral preshaping was predictive, but strategy usage only at 13.5 months was not. In bringing these results together, it is evident that the overall process of grasping has a larger impact on prehension development than the specific hand configuration at the point of first contact with an object at one timepoint.

There was also an interaction between grasp proficiency, derived from the kinematic data, and the EEG task condition. Infants with a positive growth trajectory of grasp proficiency and those with modestly negative growth trajectories have evidence of a presence of two neural categories, as the thumb difference sMMN amplitude is enhanced compared to the little difference. This is surprising because infants with a zero

or positive growth trajectory are not changing the degree of preshaping they use over time or they are preshaping less and those who have a steep negative trajectory, who change their degree of preshaping substantially, do not have evidence of two categories. One reason could be that some infants' grasp proficiency values were steady over time while others started out with a higher proficiency, so they had less opportunity to change. Our grasp proficiency variable inherently takes less information into account compared to our behaviorally coded grasp strategy variable, as the grasp proficiency includes distance data only from the point of first contact during prehension. We speculate that this interaction could be a result of the grasp proficiency variable measuring something different than the behaviorally coded grasping strategy variable.

Limitations

Our main limitation is the use of only at-home videos when the previous literature used more controlled and likely more precise in-lab videos with multiple cameras, exclusively. The collection of 2D cellphone videos in the home setting introduced variability in task set up, lighting, and camera view. This decision was made to allow for at-home data collection by caregivers for multiple reasons, including feasibility of data collection during COVID-19, feasibility of recording with a cell phone (given advances in cell phone camera technology), and more flexibility for families in terms of when to participate in recording videos. However, this limitation is somewhat offset by recent developments in kinematic methods for inferring 3D from a single 2D video, such as the HaMeR tool that is being applied in the current analyses. There are prior research that infers 3D from two 2D videos in the lab (von Hofsten & Lindhagen, 1979), but not any with only one video.

One important additional limitation is that the sample is highly skewed towards Caucasian families with relatively high household income. A homogeneous sample falls short in terms of representing of all possible children and may limit the extent of the generalizability of the results. This could be due to various reasons, including the time commitment of the study and that the study mostly took place during the COVID-19 pandemic. This study was the first intensive longitudinal study completed in our lab, so we do not have a precedent regarding whether this sample could reflect an artifact due to the longitudinal nature or due to the COVID-19 pandemic. However, in earlier cross-sectional studies in our lab, using similar recruitment methods, we achieved more diverse samples using the same recruitment methods as we used here, so it was surprising to not replicate those sample characteristics for this study. Further examination of these issues is necessary to better understand factors that may have reduced the diversity of the sample in the current study. There is evidence supporting the idea that differences between cultures impact development (Hadders-Algra, 2018), however, replication with more diverse samples is still necessary to fully understand how infants learn to reach and grasp an object that they choose to.

Conclusion and Future Directions

In this study, we examined how infants learn how to grasp through a longitudinal multimethod approach combining at-home video collection, behavioral coding, kinematics, and EEG. As expected, we found that there were individual differences over time in both grasping strategy usage and in kinematically-derived grasp proficiency. We also investigated the inferred body map categories present in the infant hand using an EEG measure called the sMMN. Then, putting all three methods together, we uncovered

novel relations between grasping behavior and the neural correlates of finger categorization. This comprehensive approach to fine motor development provides new insights into the developmental integration of sensory and motor systems, particularly pincer grasp development and preshaping.

Through both behavioral coding and kinematic analysis, we found that the grasping skills in infancy were maturing, but the developmental trajectory was different from previous research. The reported age of the first instance of preshaping is variable, either as early as 5 months or as late as 12 months (Corbetta & Santello, 108; Whishaw & Karl, 2014; von Hofsten & Fazel-Zandy, 1984; Bonniec, 1985). In theory, a specific onset time of preshaping would be indicated by a significant increase in the evidence of preshaping at a specific timepoint. However, our data did not show a specific increase of preshaping at a certain timepoint within 6 to 13.5 months, but rather that preshaping skills increased gradually over time (see Figures 14 and 18). Future directions should include a wider time range to explore the onset of preshaping skills as well as utilizing multiple kinematic variables.

The growth in preshaping skills is indicative of an integration between visual and tactile sensory experiences. In early infancy, before this integration, infants rely on haptic feedback about their environment and cannot use their vision to adapt to their environment (Corbetta & Santello, 2018). Later in infancy, through this integration, infants begin to be adaptive agents in their environment, using their haptic and visual feedback together (Corbetta & Santello, 2018; Hadders-Algra, 2018). Maturation in both systems is required before they can be utilized simultaneously. We propose that a novel grasping strategy, *emerging preshape*, captures a point in development after the full

separation of touch and vision but before the systems can be integrated. The emerging *preshape grasping* strategy is present when infants begin to slightly tuck their non-index fingers, but without using a full pincer grasp, using only the thumb and index finger to grasp. We found that most infants have begun this integration process by 13.5 months old, as evidenced by grasp strategy usage (see Figure 14 and Table 5).

Utilizing a novel EEG paradigm, we investigated the relations between fingers of the infant hand and the neural body map categorization of the hand at 14 months old. The body map categories separate body parts, where joints are the typical boundary, such as the wrist is a boundary between the hand and forearm (Tamè & Longo, 2023; de Vignemont et al., 2009; Knight et al., 2016). Generally, this categorical perception is mutually exclusive where the categorical bounds are explicit (Damper & Harnad, 2000). For example, when asked whether two locations of tactile stimulation on the arm are closer or farther apart from each other, the answer is dichotomous—closer or farther (Tamè & Longo, 2023; de Vignemont et al., 2009; Knight et al., 2016). There is no continuous aspect to that categorical perception. However, using our EEG paradigm, our measure is a continuous measure of the relations between the fingers, where we then can infer the categories. We found evidence that the thumb and the little finger are not in the same category, as the sMMN amplitude for the thumb difference condition (see Methods for condition explanations) was significantly enhanced compared to the little difference condition. This pattern of results is the same as prior research with adults (Horger et al., 2024; Shen, Smyk, et al., 2018a). We speculate that the thumb and index finger are in one category while the middle, ring, and little fingers are in another category as used in the

pincer grasp, but further research is needed to elucidate the specific categorical bounds and development of these bounds.

We also found interesting relations between the longitudinal grasp development from 6 to 13.5 months old and the inferred categories of the hand at 14 months old. The amount of timepoints where a visual grasp strategy was used, which is indicated by any preshaping skill present, was related to whether infants had evidence of two inferred categories of their hand. The infants with a higher proportion of preshape usage also had evidence of the two inferred categories, while the infants with a lower proportion did not. Combining these results with the separate behavioral and neural results paints a unique picture of grasp development as preshaping skills evolve gradually over time, but the pincer grasp is not mature at 13.5 months old, but the inferred neural categories of the hand at 14 months old show a similar pattern to prior work in adults. Our results highlight the highly individualized nature of infant development and illustrates the heterogeneous paths infants take towards common outcomes. This notion aligns with the secondary variability phase in NGST, which is when infants use trial and error to learn to adapt their behaviors (Hadders-Algra, 2018). Future directions should include multiple types of objects and a more heterogeneous sample in terms of demographics.

Our kinematic analysis was carried out through a novel machine-learning algorithm called HaMeR, which introduces a new method in study of infant motor development. In our study, HaMeR was validated against similar computer vision and machine learning algorithms (see Methods section). However, HaMer has not been validated against methods common in infant literature. The gold standard for movement quantification involves the use of an optoelectronic device, where multiple cameras

record movements from different angles to create a 3D representation. This approach typically involves the placement of physical markers attached to the body. To our knowledge, there are no studies where an optoelectronic device was used to study infant fingers, since the markers used are generally too large for infant fingers, which could impact grasping. Further, there would be challenges related to maintaining visibility of all markers throughout grasping movements. Most of the kinematic research using optoelectronic methods to study infant movements has used markers on joints that are more widely spaced, whereas infant fingers are very small and very close to each other. One solution to this issue would be to use HaMeR with multiple cameras from different angles and integrating the resulting video signals to examine the accuracy of deriving hand pose from a single-camera setup. Future directions should include a validation study between HaMeR and an optoelectronic system along with using HaMeR on a wider range of infant ages.

As the current study paired multiple novel methodologies to uncover nuances on grasp development, it is important to use the data and methodologies to advance science. The current data and results can inform developmental timelines for fine motor development. Also, this study sets a precedent for future research to extract usable kinematics from cell-phone videos in the infants' environment. As our multimethod approach was fruitful, new fine motor intervention strategies can be developed that use multiple aspects of development, including both video and neurological data. There is also the possibility of applying this methodology to identify developmental delays and differences and to inform interventions. In all, the path to the pincer is both universal and

unique in diverse ways, therefore a multimethod approach is the only way to fully understand the nuances.

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