THE UNIVERSITY OF CHICAGO

GROWING UP RHESUS: A DYNAMIC SYSTEMS APPROACH TO SPATIAL COGNITIVE DEVELOPMENT AND EARLY EXPERIENCE IN FREE-RANGING RHESUS MACAQUES (*MACACA MULATTA*)

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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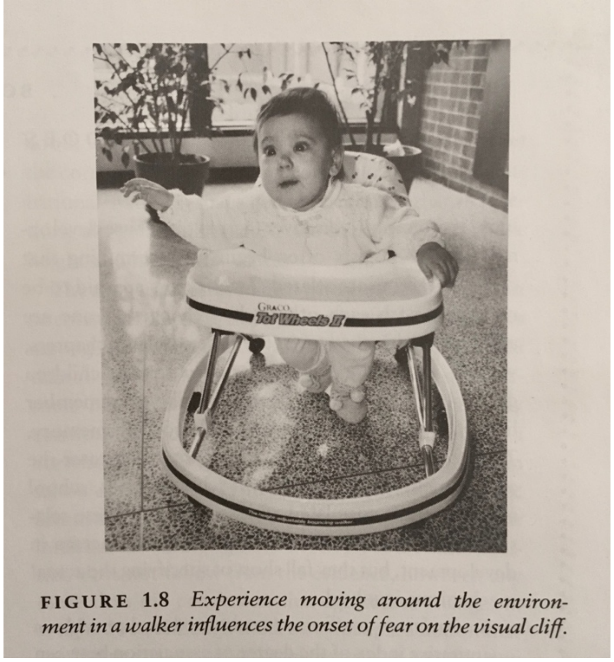

FIGURE 1.8 *Experience moving around the environment in a walker influences the onset of fear on the visual cliff.*

Figure 0.1: Christine Fleener, page 23, Figure 1.8 in Cole, M. & Cole, S. R. (1989). *The development of children*. New York: Scientific American Library.

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You will always matter even when you are gone.

Abstract

Humans exhibit a dynamic system of early development, where shifts in motor development interact with shifts in cognitive development. Milestones in locomotion repeatedly emerge with overlapping milestones in object permanence, spatial representation, reasoning, and attention. Still, we know very little about how these relationships compare in a nonhuman primate with divergent cognitive and motor development but with many analogous skills and developmental sequences. I present longitudinal behavioral and cognitive data from birth through the first years of life in a population of free-ranging rhesus macaque monkeys on the island of Cayo Santiago, Puerto Rico that support dynamic relationships between spatial cognitive development and early experience in a nonhuman primate.

Chapter 2 examines emergent spatial coding systems and whether yearling rhesus macaques will apply a consistent spatial coding strategy to interpret small-scale visuospatial tasks in rotational movement. Participants ($N = 37$) were exposed to two displacement scenarios consistent with either allocentric or egocentric interpretations of space, and while participants appeared to respond to change in both conditions, they did not differentiate between the conditions overall. However, there was variation in individual expectation, and the majority consistently increased their attention to one condition as a possible violation of their expectation and decreased their attention to the other independent of the order of exposure. Individuals could be categorized as “allocentric” or “egocentric” based on these looking time measures. “Egocentric” individuals that increased their attention to the allocentric condition and habituated to the egocentric condition also spent more time investigating a rotated image than “allocentric” individuals, supporting a connection between the spatial coding of multiple objects and the speed of processing a single rotated object.

Chapter 3 uses the same individuals (N = 15 to 39) to examine interactions in cognitive development over the first two years. Participants improved most on gaze following in their first year and improved in their participation on search tasks from their first to second year. Moreover, they exhibited a consistent positive correlation between performance in object permanence and means-ends support problem tasks over the first two years, and “allocentric” coders consistently outperformed “egocentric” coders, illustrating dynamic relationships between these cognitive abilities. Though, participants did not show any overall evidence for advanced object permanence in solving invisible displacements or causal reasoning in support problems.

Chapter 4 continues to examine dynamic cognitive development in the context of early experience. In humans, independent movement and changes in posture can facilitate spatial cognitive development, but it is unclear how this relationship might persist in rhesus macaques with an earlier locomotive onset and quadrupedal gait. Though, rhesus macaques and humans do share a similar early socioemotional environment in which maternal-infant relationships are particularly formative. Over the first year, individuals (N = 38 to 44) exhibited a steady increase in their independent movement, which was highly correlated with maternal weaning behaviors, but high rates of maternal abuse and rejection over the first year consistently corresponded to low participation rates in search and support problem tasks and an “egocentric” attention in the spatial coding looking time task. However, those that consistently recovered the reward and qualified for stage

V object permanence in their first year of exposure to the A-not-B object permanence task exhibited significantly higher rates of independent locomotion and social play in their first year than those that appeared to search randomly, and this was independent of their rates of maternal abuse and rejection.

These collective discoveries support analogous dynamic systems of spatial cognitive development and early experience in nonhuman primates and humans despite some divergence in their cognitive repertoire and early motor development. These results also substantiate novel methods for approaching these questions with spontaneous testing in a free-ranging population.

Chapter 1

Introduction

Primates are characterized by large brains and a slow rate of development relative to other mammals, and this has facilitated a cognitive plasticity that accommodates complex social systems and foraging behavior across large and diverse terrestrial and arboreal home ranges. In particular, primates have evolved a large neocortex that permits advanced sensory perception, motor development, and spatial reasoning (Mandalaywala, Fleener, & Maestripieri, 2015), which both human and nonhuman primates use to navigate between and within changing environments in small- and large-scale spaces. They exhibit advanced abilities to recall the locations of unseen objects and track their occluded movement, they can identify causal relationships and apply the necessary actions to achieve a goal, they investigate and solve novel problems, and they can use social cues to communicate and infer behavior and intentions. Still, there is considerable variation across species.

Locomotion in a dynamic system

Divergence in cognitive abilities is best explored early in development, when individuals undergo the most dramatic shifts in cognition and experience. In mammals, caregivers initially provide all of the necessary resources for the survival of their offspring, and parental care permits a unique period from birth to juvenility in which individuals are most curious, exploratory, and playful with their environment. Prior to the reproductive and foraging demands of adulthood, this transitional phase marks an extremely interesting and understudied critical period of brain development.

In humans, early shifts in cognition overlap and align with shifts in motor development, where milestones in spatial cognition, object permanence, means-ends reasoning, and attention also emerge with milestones in movement and exploration (Acredolo, 1984, 1985; Campos, et al., 2000; Diamond, 1991; Herbert et al., 2007; Horobin & Acredolo, 1986; Oudgenoeg-Paz et al., 2014; Smith et al, 1999; Thelen et al., 2001). Piaget (1952, 1954) was the first to propose a one-sided approach to development, where sensorimotor experience directly facilitates an individual's intellectual development, and where the achievement of one ability has a cascading effect on the emergence of other abilities. It is well known that the onset of independent, self-generated locomotion stimulates proprioception and the construction of visuospatial perspectives that coordinate an infant's visual and vestibular information to improve perception and processing of an environment (Bidell & Fischer, 1997; Edelman, 1987; Gibson, 1988; Thelen & Smith, 1994), but it is unclear how strictly these shifts are contained within circumscribed periods of development or how motor and cognitive milestones might continue to interact throughout development.

There has been a resurgence of interest in the consequences of motor development that was prompted by dynamic systems and ecological approaches to the study of perception and action (Gibson and Pick, 2000; Thelen & Smith, 1994; 2006). These theories introduce a non-linear approach to early development such that critical changes in experience and cognition are constantly interacting with each other to influence shifts in the system as a whole. This has led to an emphasis on embodied cognitive dynamics, where bodies and their movement provide the substrate for psychological activity (Casasanto, 2011; Clark, 1997; Thelen, 2000; Varela et al., 1992; Wilson, 2002). Locomotor infants outperform prelocomotor infants in search tasks, but just changing an infant's posture during a task can also improve their performance (Smith & Thelen, 2003). Neuroscientists have also confirmed anatomical links in brain areas that are involved in cognitive and motor functions (Diamond, 2000), and there is evidence that ongoing experiences and motor activity can continuously shape the brain throughout development beyond specific transitional periods (Doidge, 2007; Gomes da Silva et al., 2012; Oudgenoeg-Paz et al., 20014; Piek et al., 2008). To better understand how dynamic systems might facilitate development, we must first establish analogous cognitive and motor milestones across species and investigate their emergence and interaction.

Humans diverge from other primates in their prolonged locomotive development which improves from quadrupedal crawling to bipedal walking over more than a year, and each of these accomplishments correspond with notable achievements in means-ends reasoning, object permanence, and attention, suggesting that gradual transitions in motor development might play a crucial role in the organization of more complex cognitive abilities (Campos et al., 2000). Alternatively, many nonhuman primates like rhesus macaques do not experience this same gradual transition from crawling to walking, but they achieve many of the same cognitive milestones as humans and only diverge in the complexity of these abilities. Most nonhuman primates maintain quadrupedal locomotion throughout their lives and are locomotive only a few days after birth, which could generate a different cognitive development according to Piaget's strict approach to transitional periods. With a mismatch in the emergence of motor and cognitive milestones in nonhuman primates, it is important to investigate how these systems may still interact and influence each other within the framework of a dynamic system and to further consider how these differences between humans and nonhuman primates might account for variation across species.

Humans also diverge from other primates in the simultaneous emergence and development of language and culture over the first few years, which also interacts with their spatial cognitive development and their mental representation capacity early in life (Gentner et al., 2013; Landau & Jackendoff, 2013; Levinson et al., 2002). Language learning can improve the capacity to understand, visualize, maintain, and apply several complex spatial relationships at a time, which may account for more sophisticated achievements in the higher order object permanence and problem-solving abilities of humans relative to nonhuman primates. Though, even in the absence of language, we observe some capacity for these cognitive abilities in nonhuman animals, which further demands investigation in how these abilities emerge.

Object permanence development

Human and nonhuman primates exhibit similar brain structure and growth and a similar sequence of cognitive events (Goldman-Rakic, 1985). Humans will begin to manually search for a hidden object around 8 to 9 months of age, around the time of locomotor onset, while rhesus macaques will search for occluded objects as early as 2 months (Antinucci, 1990; Piaget, 1954; Williams, 1979), around the time that they also exhibit more independent exploration but have long been locomotive. At this stage, humans do still exhibit an A-not-B perseverance error in which infants will continue to search in an original hiding location even after they have seen an object move. This error is associated with stage IV object permanence and may be due in part to deficits in attention, conditioning to reach for the original location, or an inhibitory conflict between an infant's perception and action that are associated with this age, but this transitional period remains a curious and unexplained aspect of object permanence development that is intimately connected to transitions in motor and cognitive development.

By the time human infants are around 12 months and transition from quadrupedal crawling to bipedal locomotion, they overcome their A-not-B perseverance error and achieve stage V object permanence. Around 18 months, humans achieve the final stage VI of object permanence where they can locate objects that have been hidden outside of their view, and it is this shift from stage V to VI that is thought to be facilitated by the emergence of mental representation, which also develops with linguistic capabilities and more sophisticated social cognition. The circumstances of the transitions from stage IV to stage VI object permanence are not well studied in nonhuman primates. The transition from stage IV to V is subtle and the circumstances of this shift are difficult to detect in nonhuman primates without with shorter early developmental periods and less clear motor milestones. Additionally, due to their linguistic limitations, it is often thought that nonhuman primates are not even capable of achieving stage VI object permanence at all.

Rhesus macaques and other great apes and monkeys do exhibit a capacity for stage V object permanence, but there is disagreement about when the transition from stage IV to V occurs and whether they can fully achieve stage VI object permanence (Call, 2000; De Blois & Novak, 1994; De Blois, Novak & Bond, 1998; Dore & Dumas, 1987; Dumas & Brunet, 1994; Mathieu et al., 1976; Natale et al., 1986; Natale &

Antinucci, 1989; Parker, 1977; Redshaw, 1978; Schino et al., 1990; Wise, Wise, & Zimmerman, 1974; Wood et al, 1980). Rhesus macaques can solve visible displacements and linear transpositions, but they struggle with invisible displacement (De Blois et al., 1994; 1998), though they can show improvement over multiple exposures. Macaques appear to solve mental representation choice and looking time tasks associated with mental representation and stage VI object permanence in the absence of language (Anderson, 2012; Filion, Washburn, Gulledge, 1996; Hughes, 2012; Kohler et al., 2005; Mathieu et al., 1976; Mendes & Huber, 2004; Neiworth et al., 2003; Schino et al., 1990; Vauclair, Fagot, & Hopkins, 1993; Wise et al., 1974), but we must be cautious to differentiate spontaneous versus repeated exposures to a given task and abilities that are measured exclusively by looking time tasks.

Human infants as young as 3.5 months have exhibited looking times that are consistent with stage IV object permanence months before they can solve a search task (Baillargeon & DeVos, 1991), and infants as young as 6 months have exhibited looking times that appear to differentiate between possible and impossible invisible displacement scenarios even when they do not solve these search tasks until 18 months (Baillargeon, 1986). This identifies a crucial distinction between what an individual may perceive and what they can conceive, and the discrepancy between looking time and interactive search tasks must be considered when defining an individual's actual cognitive ability, though it presents a valuable means by which we can compare subtle shifts in cognitive perception even before they inform an individual's interaction with an environment.

Spatial coding in visuospatial tasks

Shifts in spatial attention also emerge with shifts in object permanence. Shifting from egocentric (self-to-object) to allocentric (object-to-object or object-to-environment) spatial coding can eliminate frequent search errors, and this change in attention has been detected around the same time that humans transition into stage IV and V object permanence. Piaget (1954) suggested that the construction of a referential environment facilitates search behavior and the onset of locomotion and exploration must be driving these shifts in spatial attention. Infants can only build a dynamic, allocentric perspective of space after moving through it and encoding it from multiple angles (Campos et al., 2000).

Acredolo and colleagues (1978) first investigated the development of spatial perspectives by testing infants on a position constancy task where participants were conditioned to find a stimulus on their left. After repeated trials, infants were then moved to the opposite side of the array so that the stimulus would now appear on their right, but in the same location relative to the room. Infants less than 9 months consistently continued to look and search to their left, which was consistent with their original egocentric motor response and similar to the perseverance error found in stage IV object permanence around the same age, while older infants were able to update their perspective with their movement. Bai and Bartenthal (1992) later confirmed the role of locomotion in this transition by showing that locomotor infants were significantly better at updating their perspective than prelocomotor infants independent of their age.

Furthermore, when the array of objects moved rather than the observer, there was a sudden increase in error. Even though the relative motion between observer and array was identical, the participant's active movement around the array appeared to facilitate the necessary feedback to update their perspective and solve the task. Individuals were only consistently successful at this task around 3 years of age, but infants did show improvement on this task with repeated exposures and with visual access to distinct landmarks cues in the array (Barth & Call, 2006; Bremner, 1978; Lasky et al., 1980; Okamoto-Barth & Call, 2008). These results show how locomotor onset and movement during the task can facilitate the ability to update spatial perspectives, but they also reveal how rotational displacement can elicit a greater attention to allocentric associations, which is crucial for designing experiments that measure attention to landmark cues and determine how exactly motor development might improve attention to allocentric information in these tasks.

Great apes exhibit the same capacity to update their perspective after movement, and they also exhibit the same difficulty with solving rotational displacement without access to landmark cues (Acredolo & Evans, 1980; Albiach-Serrano, 2010; Anderson, 2012; Barth & Call, 2006; Beran & Minahan, 2000; Beran, Beran, Menzel, 2005; Bremner, 1978; Call, 2003; Collier-Baker, 2006; Haun et al., 2006; Okamoto-Barth & Call, 2008; Roojjakkers et al., 2009). Apes are most successful in these tasks in the presence of landmark cues, but they still struggle to use cup features alone to reorient themselves and often require multiple exposures before mastery. Haun and colleagues (2006) used these results to suggest that human and nonhuman primates must differ in their attention to and application of allocentric spatial relationships. However, comparable tasks have indicated that even monkeys are capable of searching between landmarks after a change in display (Dolins et al 2004; 2009; Garber 7 Brown, 2005;

Deipolyi, Santos, & Hauser, 2001; MacDonald, Spetch, Kelly & Cheng, 2004; Marsh, Spetch, & MacDonald, 2011; Poti, Bartolommei, & Saporiti, 2005; Poti et al., 2010; Sutton, Orthof, & Roberts, 2000), and additional looking time methods have supported that adult rhesus macaques can discriminate between possible and impossible rotational displacement scenarios (Hughes & Santos, 2012).

Attention to spatial relationships and perspectives may only emerge after locomotion onset, but there is still evidence that individuals continue to differ in their preference to attend to allocentric or egocentric information in different contexts even later in life. Kozhevnikov and Hegarty (2001) found that humans generally prefer to use an egocentric coordinate system to navigate large-scale spaces but will apply an allocentric coordinate system to describe small-scale rotation. Hegarty and Waller (2004) also found that while different contexts and scales may be more likely to elicit a particular frame of reference or spatial coding strategy, measures of perspective taking and efficiency in mental rotation are highly correlated, and differences in individual spatial strategies can account for a significant proportion of the variance in overall test performance. These differences in individual spatial attention and coding support a dynamic system in which multiple factors might influence an individual's attention to spatial information, and these factors have never been captured in a nonhuman primate.

Shifts in attention and means-ends abilities

Patterns of attention are intimately involved in the development of spatial cognition and motor milestones. Human infants with locomotor experience maintain a longer attention span than prelocomotor infants and more commonly attend to objects, people, and motion in distant space, while prelocomotor infants do not appear to attend to anything in particular (Acredolo, Adams, Goodwyn, 1984; Acredolo, 1985; Freedman, 1992; Gustafson, 1984; Horobin & Acredolo, 1986). Locomotor infants also exhibit a greater tolerance for delays between initiating and completing a behavior (Herbert et al., 2007; Tao & Dong, 1997), and more efficiently discriminate relevant information and means-ends behaviors than prelocomotor infants (Smith et al., 1999; Thelen et al., 2001).

Evidence of means-ends and causal reasoning at young ages can be measured with a support problem task, where participants are introduced to a reward that is out of reach, but in contact with a cloth support that is within reach. Pulling the cloth to access the distant reward requires a capacity to identify and maintain a goal while completing the intermediate actions that achieve that goal (de Mondonca-Furtado & Ottoni, 2008; Hauser et al., 1999; Piaget, 1952; Range, Hentrup, & Viranyi, 2011; Spinozzi & Poti, 1989; Willatts, 1984, 1990; Yocom & Boysen, 2010), though it does not necessarily require an understanding of the efficacy of those actions. Additional support problem tasks comparing a choice between pulling a functional support and nonfunctional support further clarify the extent to which participants attend to action efficacy.

Human infants as young as 6 months can identify inconsistencies in causal relationships and differentiate between possible and impossible scenarios in looking time tasks (Baillargeon, DeVos, Black, 1992), but they do not yet apply these concepts in practice (Willatts, 1997; 1999). Infants may not have achieved the attentional demands required to execute a sequence of means-ends behaviors or they may not yet be capable of inhibiting their desire to reach for the reward to attempt the intermediate steps in problem solving (Baillargeon, 1993; Bushnell, 1985; Freedman, 1992; Willatts, 1984). It is not until around 9 months of age that humans pull a support to access a distant reward (Diamond, 1985), which comes at the same time that they begin searching for fully occluded objects. They also begin to recognize and apply causal reasoning around the same time that they overcome the A-not-B error in object permanence development (Piaget, 1952). Maintaining the goal of a hidden reward while searching and maintaining the goal of a distant reward while pulling a support are conceptually very similar, though additional studies have not found a clear causal relationship between these object permanence and means-ends abilities (Matthews, et al., 1996). Kowaguchi and colleagues (2016) have also suggested that basic reaching and pulling behaviors are still primarily a function of an egocentric spatial coding system and infants can only begin understanding causal connections with the emergence of attention to object-to-object relationships.

Many species of nonhuman primates will pull a cloth support only when there is a reward in physical contact with the support and not when there is a reward placed just next to it, suggesting some causal understanding (Albiach-Serrano et al., 2015; Hauser, Kralik, and Botto-Mahan, 1999; Hauser et al., 2002; Weiss et al., 2007; Yocom & Boysen, 2010). Adult rhesus macaques can identify function actions in looking time tasks and will pull a causally relevant support to access a distant reward (Rochat et al., 2008; Spinozzi & Poti, 1989). Still, it is important to note that there is a great deal of variability in the flexibility of problem-solving behaviors and learning requirements across primates as the majority of species do not exhibit spontaneous tool use behaviors in the wild. Accordingly, we must acknowledge how a divergence in cognitive adaptations might continue to play a role in the dynamic development of cognitive and motor systems in a nonhuman primate.

Joint Attention

Both human and nonhuman primates will respond to head turns and eye gaze cues (Ferrari et al., 2000), which is fundamental to inhabiting complex social environments and a prerequisite for more complex perspective taking and theory of mind. Humans will respond to gaze cues in the first few months and exhibit a steep increase in their frequency of gaze following around the same time that they become locomotive and begin searching for fully occluded objects and solving means-ends tasks. Around 12 months, they will follow gaze to target objects, and this occurs around the same time that they begin walking independently, overcome the A-not-B object permanence error, and exhibit causal reasoning. By 18 months, infants will follow gaze toward objects that are beyond their immediate view (Butterworth, 1991; Moll & Tomasello, 2004; Scaife & Bruner, 1975; Shepherd, 2010), which also corresponds to a shift into stage VI object permanence. Rhesus macaques exhibit human-like changes in gaze following across the lifespan (Rosati et al., 2016), but they do not show any evidence of using gaze information to improve their performance on search tasks (Anderson, Montant, & Schmitt, 1996; Hare & Tomasello, 2004; Miklosi & Soproni, 2006; Ruiz et al., 2008).

In humans, responsiveness to communicative and referential gestures improves with locomotion experience, which can be a function of exposure to more unique patterns of maternal signaling that incite more sophisticated views of others' intent in relation to distal objects (Zumbahlen, 1997). This further prompts a closer look at the role of maternal caregivers in the development of these cognitive abilities. Parents are the first point of contact with an environment and can facilitate an infant's exploration and exposure within that environment. In both humans and nonhuman primates, there is variation in maternal behavior which either encourages or delays and infant's independence (Fairbanks & McGuire, 19877; Fairbanks, 2003; Maestripieri, 1994; 1995). Mothers vary from protective or restrictive to laissez faire, and they can differ in the intensity and timing of their weaning behaviors, which influence earlier onset and regularity of infant locomotion that would not occur in the absence of maternal encouragement (Maestripieri, 1995). This mother-infant dynamic can impact an infant's interaction with an environment in multiple ways, where premature weaning behaviors or extreme abuse and rejection can result in cognitive and emotional deficits (Glaser, 2000; Kaufmen et al., 2000; Maestripieri, 2006; McEwen, 2001; Newport et al., 2002), increased anxiety in novel environments (Lyons & Parker, 2007), and lasting consequences on an individual's physiological development (Mandalaywala et al., 2014). This further emphasizes the dynamic relationships that can impact domains of development from multiple angles, but additional research is required to fully capture how these early experiences enrich or delay cognitive development in nonhuman primates.

Questions

In this dissertation, I address three central questions: 1) Do rhesus macaques exhibit a consistent spatial coding system when attending to the features of small-scale visuospatial tasks in rotation in the first year?, 2) Is there an interaction between spatial coding, object permanence performance, means-ends behavior, and gaze following early in rhesus macaque development?, and 3) What interactions exist between early experiences and cognitive development in rhesus macaques in their first year? Together, these methods seek to contribute to a better understanding of the dynamic systems involved in the early development of a nonhuman primate species.

Chapter 2

Interpreting spatial coding from rotational displacement and mental rotation looking time tasks in yearling rhesus macaques

Abstract

Humans can use both egocentric (self-to-object) and allocentric (object-to-object) frames of reference to orient, navigate, and locate objects in dynamic space. Human infants first employ an egocentric frame of reference and develop allocentric reasoning over time, but little research has been done on how these spatial coding systems have evolved and developed in nonhuman primates. This chapter addresses 1) whether yearling rhesus macaques consistently attend to and make predictions based on egocentric or allocentric information as they track and recall the movement and location of multiple objects in a small-scale array, 2) whether yearling rhesus macaques can successfully differentiate between a single rotated image and an altered image in a mental rotation task, and 3) whether the spatial coding strategies applied to identifying the rotational movement of multiple objects in an array corresponds to looking in response to the rotation and alteration of a single object.

Two small-scale visuospatial tasks were introduced to 37 rhesus macaques between 14 and 16 months. One task involved the rotational movement of multiple objects and measured attention to either egocentric or allocentric spatial cues. The other involved the rotation and alteration of a single continuous image. There was no significant overall preference to attend to conditions in the multiple object task based on egocentric or allocentric coding, but there was a significant negative correlation between

looking time in each condition that was independent of the order of exposure. This suggests that individuals may consistently predict the location of the reward based on a particular coding strategy, but that individuals may differ in the frame of reference they employ. Those that appeared to make “egocentric” predictions in this looking time task also significantly increased their attention to a rotated image, while “allocentric” coders decreased their attention, supporting a possible connection between spatial coding and the speed of processing rotation.

These results fail to reject the prediction that yearling rhesus macaques will consistently apply the same spatial coding strategies to solving the rotational displacement of multiple objects, and they introduce a novel use of looking time tasks to investigate individual differences when attention in a population is not uniform. Additionally, these results support a possible interaction between the systems that are applied to tracking the location and rotational movement of multiple objects and identifying a single object after rotation. Though, attention to spatial associations does not necessarily impact attention to the relative positioning of features on a single, continuous object.

Introduction

Both human and nonhuman primates have exhibited the capacity to accurately navigate complex environments and large-scale spaces, moving between locations with goal-directed efficiency (Garber & Brown, 2006; Hughes et al., 2013; Janson, 1998; Kanngiesser & Call, 2010; Menzel, 1973; Menzel, 1991; Normand et al., 2009; Presotto & Izar, 2010). They can also successfully track the location and movement of objects in small-scale spaces or from different angles of approach or occlusion (Albiach-Serrano, Call, Barth, 2010; Antinucci, 1990; Beran et al., 2005; de Blois et al., 1999; Diamond, 1990; Okamoto-Barth & Call, 2008; Piaget, 1954; Poti, 2000). These abilities represent an impressive system of spatial reasoning, but little is known about the mechanisms involved in the development of spatial reasoning and how it differs between human and nonhuman primates. Here, I focus on how frames of reference may emerge and inform spatial reasoning in visuospatial tasks using yearling rhesus macaque monkeys as a model to compare human and nonhuman development.

Humans appear to be capable of applying multiple frames of reference in order to specify the spatial structure of an environment. For one, individuals can retrace a route using an *egocentric* spatial reference frame, encoding locations in an environment relative to axes of self and recalling them based on a sequence of left-right, front-back, or up-down body turns. For example, if an egocentric coder walks down a hallway and enters a door on their left, they will always recall the location of that door as being “on their left.” If an egocentric coder walks down a hallway, passing a potted plant on their left, they will always confirm their route when the potted plant is on their left. Individuals can accurately track, integrate, and update their visuospatial information using this egocentric spatial coding strategy, and when they only need to encode and consider the position of the objects relative to self, this can have a relatively low impact on working memory.

However, egocentric coding has its limitations. Egocentric spatial coders must maintain continuous visual and physical awareness as they move through an environment in order to accurately update their information, and the reliability of this system breaks down when there are changes to the environment that are unseen or the environment is entered from a different angle of approach. Additionally, as paths get longer and more complex, the sequence of information can become too demanding for an individual's working memory. In these circumstances, humans can also interpret and recall environmental information using *geocentric* or *allocentric* spatial reference frames. Geocentric reference systems define spatial relations with respect to features of the environment, such as the cardinal directions north, south, east, and west or the perceived direction of gravity, the Sun's azimuth, or the Earth's magnetic field. Allocentric reference frames more specifically emphasize the relative locations of landmarks, encoding positions based on the relationships *between* objects rather than object locations relative to self. This allows an individual to construct a mental map of their environment, which can be applied to more complex navigation that permits reliable re-orientation when a space is entered from multiple angles and supports the formulation of new and more efficient routes and short cuts.

When one walks down a hallway and passes a door or potted plant on their left, they should not only encode the location relative to self, but also attend to the locations relative to other features of the hallway or the world outside. Individuals can then recall that the potted plant is ten feet north of a certain door; or there is a potted plant near the correct door; or there is a potted plant *to the left* of the correct door; or in a hallway full of multiple plants and doors, the correct door is always *between* a blue plant and a red plant. Now, the correct door can be identified regardless of the angle of approach and without having to track all sequential movement through the space.

In the aforementioned examples, the use of one spatial coding strategy does not necessarily exclude the capacity for the other, and different frames of reference can be applied to navigation through large-scale space or locating objects in small-scale space. The application of egocentric, geocentric, and allocentric systems can even occur simultaneously, where individuals can imagine seeing space form multiple egocentric perspectives even as they construct an allocentric map. Multiple species exemplify the integration of multiple coding systems to corroborate their spatial awareness. In insects, for example, species of bees and ants navigate using egocentric path integration while they apply an allocentric system to recognize shapes and relative locations of landmarks, and then confirm their orientation geocentrically using polarized light or magnetic fields (Gallistel, 1990; Gothard, Skaggs, McNaughton, 1996; Wehner, Michel, Antonsen, 1996). In birds, black-capped chickadees will first search for a reward based on its geocentric location relative to a room, and then use allocentric information like relative geometry and featural differences in landmarks when there is insufficient information to rely on a geocentric reference (Brodbeck, 1994).

Humans also appear to regularly apply both sequential egocentric and allocentric strategies during navigation (Bullens et al., 2010; Igloi et al, 2009), though some studies have shown that humans will often prioritize egocentric information when retrieving and reporting on novel, large-scale, virtual environments (Bryant & Tversky, 1990; Scholl & Nolin, 1997; Wang et al., 2005; Werner & Schmidt, 1999), while others have found that people form multiple allocentric representations of space when they first encounter an environment (Graziano & Gross, 1994; Mou et al., 2004; O’Keefe & Nadel, 1978, Tipper & Behrmann, 1996; Tversky, Lee, Mainwairing, 1999). Research in nonhuman primates has shown that many species are capable of attending to multiple types of spatial information (Mishkin, 1982; Newcombe & Huttenlocher, 2003; Sutton, Olthof, & Roberts, 2000), but little is known about the systems used to encode this spatial information and the development of different frames of reference.

Human infants primarily integrate and encode their environment from an egocentric reference initially and incorporate allocentric referencing with age as they begin to locomote (Campos et al., 2000). At birth, infants only experience a proximate world that largely comes to them and attends to their needs, and they only need to interact with the world in relation to themselves. Even the visual system of newborn infants can only interpret distance information within a range of one to two meters from themselves. As they age and begin to walk, crawl, and interact more with their environment, infants develop a more dynamic perspective that facilitates more accurate calibration of distance information and relationships between objects (Berti & Frassinetti, 2000). Around this point, infants establish and improve their ability to apply multiple reference frames to encode and solve small-scale and large-scale spaces, and these abilities can be evaluated using a battery of visuospatial search and looking time tasks.

To test the development of spatial coding in humans, Acredolo and colleagues (1978) conditioned infants to expect a stimulus to appear on one side of a room whenever a sound was played. Infants were then moved to the opposite side of the room, so the stimulus would now appear on the opposite side of the infant, but the same side of the room. If the infants were only relying on their original egocentric motor response to orient toward the stimulus, they would turn in the original, and now incorrect, direction, but if they were updating their perspective during movement, they would turn in the correct, revised direction. Infants between 6 and 9 months fail this test by consistently predicting the location of the stimulus based on their initial egocentric motor response, while older infants were able to correctly update their expectation.

Bai and Bertenthal (1992) further explored the emergence of spatial coding in human infants by introducing a *search task* in which infants were shown the location of a reward under one of two hiding containers in an array, and they were then moved to the opposite side of the array and given an opportunity to search again from a different vantage point. Again, they found that older infants more often selected the correct container, and moreover, infants with locomotor experience were more successful than prelocomotor infants. These methods were able to illuminate a developmental milestone in spatial updating, but this still did not completely clarify what spatial strategy infants were using to solve this problem. Because infants maintained continuous visual awareness throughout their movement, they likely updated their egocentric perspective rather than necessarily attending to any allocentric cues. Though, this does show a measurable shift in spatial coding development as a function of proprioceptive experience, and egocentric updating is still complex in is requirement to track multiple target positions in the room relative to the observer. Still, this result does not necessarily represent an emergence of object-to-object spatial coding.

Many researchers further explored how subject movement influenced performance on spatial coding tasks. Bai and Bertenthal, as well as many others (Barth & Call, 2006; Bremner, 1978; Lasky et al., 1980; Okamoto-Barth & Call, 2008), modified the experiment so that the array rotated instead of the subject. They found that infants of all ages now struggled with this *rotational displacement task*. The relative movement between the subject and the array was identical, but when the subject was not the one moving, they had more difficulty keeping track of changes and were unable to successfully update their perspective. Only participants over three years of age were able to improve their performance and successfully track the movement of a reward in a rotating array, and performance on this task was improved when there were obvious landmark cues available. These results suggest that while human infants improve at egocentric updating in their first year, relying on bodily movement to update their egocentric perspective, they may not be capable of using allocentric information until much later. These methods also reveal that rotational displacement tasks elicit attention to allocentric cues and have a demand for mental transformation, and Campos and colleagues (2000) noted that the use of allocentric strategies are most likely in conditions where landmarks are close to each other in a small-scale array, landmarks are salient, and when no training trials are used prior to testing.

Haun and colleagues (2006) ran a series of tests similar to those of Acredolo (1978), Bai and Bertenthal (1992), and others using trained great apes (orangutans, gorillas, chimpanzees, and bonobos). Participants were shown a reward hidden under a cup on either the far right or left side in an array of three separate cups. The participants were then moved to the opposite side of the array and given the opportunity to search for the reward. All participating species selected the correct location of the reward, showing that they were not prioritizing egocentric information and were able to attend to other cues to update and reorient their perspective after movement. Haun and colleagues used these results to conclude that both human and nonhuman primates must use environmental cues more readily than self and suggested that there may be phylogenetic inheritance of a preference for allocentric spatial strategies. However, this task still primarily evaluates one’s capacity for egocentric updating.

Additionally, when the array was rotated instead of the subject, participants more commonly made the error of searching in the location that was consistent with their original egocentric motor response. When the cups were replaced with visually distinct containers to encourage the use of features or landmark cues to solve the task, adult apes were still unable to locate the reward, which indicates a possible divergence in attention to landmark information across primates. Haun et al (2006) also emphasized that human spatial cognition appears to vary with language and culture, and that the complexity of allocentric reasoning may be intimately connected with language acquisition that allows humans to cognitively represent spatial relationships, which may account for the divergence in the spatial cognition development of human and nonhuman primates.

However, multiple methodologies have shown that many species of nonhuman primates can learn to solve this type of rotational displacement task after additional training when they have repeated visual access to landmark information and substrate rotation. (orangutans and capuchins: Poti et al, 2010; apes: Barth & Call, 2006; Beran, Beran, Menzel, 2005; Call, 2003; Okamoto-Barth & Call 2008, rhesus macaques: Hughes & Santos, 2012). Further, the capacity to apply allocentric cues may not be limited to great apes and humans. Dolins and colleagues (2009) trained five cotton-top tamarins to locate 11 hidden food rewards among three distinct landmarks in a small-scale array that was 2.5 by 2.5 feet. The array of rewards and landmarks was then rotated by 90 degrees behind a barrier, so the rewards and landmarks were in the same locations relative to each other, but different locations relative to the grid. If participants were able to successfully locate the rewards after rotation, this would indicate that they were indeed attending to spatial relationships among the stimuli and were able to apply knowledge about relationships in the first configuration to the rotated configuration, rather than just identifying a landmark as a “beacon” and searching around it indiscriminately. The tamarins successfully recovered the rewards at above chance levels, which confirmed that they must have attended to the spatial relationships between multiple landmarks and not just to basic associations (Dolins, 1994), and similar results were also found in capuchins (Garber & Brown, 2005).

Numerous studies have confirmed that nonhuman primates are capable of applying allocentric cues to large-scale foraging scenarios (Deipolyi, Santos, & Hauser, 2001; MacDonald, Spetch, Kelly & Cheng, 2004; Marsh, Spetch, & MacDonald, 2011; Poti, Bartolommei, & Saporiti, 2005; Poti et al., 2010; Sutton, Orthof, & Roberts, 2000). In these studies, a reward is hidden at a certain distance and direction from a particular landmark, and once the participant is familiarized with the location of the reward, the landmark is moved when the participant is out of sight, and the participant's searching behavior is observed. Nonhuman primates continue to search at the same distance and direction from a landmark rather than in original hiding locations, which further confirms that individuals are attending to relationships between objects and locations. Especially in instances where individuals must leave, return to, and recall locations in large-scale space, it appears that allocentric information can be encoded and applied in nonhuman primate species.

Additional research has further expanded on the way human and nonhuman primates attend to and apply allocentric, object-to-object associations using the *expansion test*. In this test, a reward is hidden between two landmarks and the landmarks are gradually expanded out and away from each other while the reward remains proportionally equidistant from each landmark (MacDonald, Spetch, Kelly & Cheng, 2004; Marsh, Spetch, & MacDonald, 2011; Poti, Bartolommei, & Saporiti, 2005; Poti et al., 2010; Simms & Genter, 2008; Spetch & Parent, 2006; Sutton, Orthof, & Roberts, 2000; Uttal, Sandstrom, & Newcombe, 2006). Both adult nonhuman primates and young human children appear to preferentially use vector and distance information in these scenarios, consistently searching at a certain distance and direction from both landmarks, rather than attending to the relative locations of objects and searching *between* two landmarks. In the wild, there will rarely be a condition in which two landmarks gradually move away from each other, and moving landmarks are not the most reliable at marking land. So, the concept of *betweenness* might be less salient or ecologically valid without the confirmatory integration of vector and distance information. While we can confirm that both human and nonhuman primates are capable of attending to allocentric information, they likely do not exclusively rely on the relative positioning of objects to encode a mental representation of space.

Still, search tasks are often used to investigate spatial coding systems, and these types of cognitive tasks have limited scope. For one, search tasks require participation, which can bias samples by excluding data from more reluctant individuals. Second, search tasks rely on an interpretation of behavior at the level of decision-making and action, which do not always represent an individual's immediate cognitive response. These complications can be avoided and improved on by using *looking time methods*, which are designed to evaluate an individual's immediate reaction to different scenarios. This method was established for use in nonverbal participants and compares habituation trials and attention to novel stimuli in order to determine whether individuals are able to differentiate between scenarios or react to change across trials. An increase in looking time for one scenario over another is often interpreted as a *violation of expectation*. Participants develop an expectation for what they will observe based on previous exposures, and if they are shown a scenario that conflicts with their expectation, they will often investigate it for longer (Fantz, 1964; Groves & Thomson, 1970; Spelke, 1985). Differences in looking time can exist on scale of a fraction of a second but are a statistically robust way of comparing immediate reactions before individuals are even conscious of their preference.

Hughes and Santos (2012) adapted the rotational displacement task as a looking time method and tested a population of rhesus macaque monkeys. Participants were first shown a reward hidden in one of two differently colored boxes in a small-scale array, and the array was then rotated 180 degrees. Finally, the boxes were opened to reveal the reward in either the correct box after rotation or the incorrect box after rotation. Adults looked significantly longer at the incorrect event than the correct event, suggesting that rhesus macaques were indeed discriminating and making accurate predictions about the rotational movement of the hidden reward. Contrary to the null results from previous rotational displacement search tasks, this looking time paradigm revealed that adult macaques do potentially have the cognitive capacity to solve the historically challenging rotational displacement task without training. Knowing this, we can adapt this methodology to further investigate the possible coding systems applied to cognitive tasks.

Rotational displacement tasks also require that an observer track the trajectory of a hidden object within an array of multiple hiding locations, and also track the substrate supporting the array as it is rotated to a new position. Previously mentioned work has established that it can be difficult to follow rotational movement when the observer does not have access to some "allocentric" information and can use relative locations, landmarks, or features to identify the correct hiding location. When movement is occluded, observers must also be able to recall and match past and present views of the array and mentally represent multiple versions of the array as it moves, which is a highly advanced skill in object permanence development (Piaget, 1954; 1971). Mental representation and manipulation is not well studied in nonhuman primates, but may be an important aspect of the development of primate spatial reasoning. In an effort to understand how perspective taking and spatial coding might influence each other, we can introduce other small-scale visuospatial tasks that elicit mental manipulation and compare their attention and performance.

One notable type of small-scale visuospatial task that evaluates the capacity for mental manipulation and recognition is the *mental rotation* task. *Mental rotation* tasks were designed by Shepard and Meltzer (1971) to test how long it takes an individual to discriminate between two views of a single complex object and determine whether they represent two views of the same object or two completely different objects. Often, participants are shown a 2-dimensional representation of a 3-dimensional object and are then shown several images of that same object slowly rotated about the x, y, or z-axis. They are then shown a completely novel image and asked to identify whether it matches the original image. In contrast to violation of expectation looking time methods, mental rotation studies will often use *speed of processing* methods (Carroll, 1993) that evaluate performance based on the time it takes for a participant to solve a matching test rather than whether they are able to differentiate between novel and familiar stimuli. In these circumstances, individuals can increase their attention to familiarity when the cognitive demands of recognition are greater than or equal to identifying novelty, showing the importance of multiple approaches to looking time results.

In order to identify an image as a rotation or a completely novel image, participants may attempt to mentally rotate the original image or the new images until they match each other. They may also imagine taking a different perspective around the images until they match each other, or they may attempt to compare and match specific featural information on each image until they identify a difference. These strategies share many similarities with the spatial coding systems applied to rotational displacement tasks insofar as individuals may mentally manipulate the image from an egocentric perspective, attend to allocentric, featural information, or both.

However, they differ where rotational displacement requires a representation of a space containing relationships between multiple objects and mental rotation requires the representation of a single, continuous object. The question remains whether the spatial coding strategies applied to solving the rotational displacement of multiple objects in an array relate to solving the rotation and identification of a single object in a nonhuman primate.

Previous experimental paradigms have attempted to compare performance on mental rotation and perspective-taking tasks to spatial coding skills in humans (Kozhevnikov et al, 2001; Kozhevnikov et al, 2006). Kozhevnikov and Hegarty (2001) found that overall, participants most commonly reported the direction of a particular object within an array with respect to self, indicating that they were first mentally manipulating their egocentric coordinate system rather than using objects in an array as a reference. Alternatively, when participants were asked to match and identify rotated objects, they more commonly reported attendance to an object's relative parts and features, applying an allocentric representational system to identify whether an image was a rotated version of a previous image or a completely novel image. These results show an interesting dissociation in the preferred overall strategies applied to different spatial contexts, but they did not fully explore consistency within individual strategies.

The strategies applied to solving mental rotation tasks may also influence the speed with which participants can solve the tasks. Identifying a rotated image by continuing to mentally rotate the image to complete a sequence of rotations should be more efficient than attempting to mentally visualize taking several different perspectives about multiple images (Kozhevnikov et al, 2001; Kozhevnikov et al, 2006). Kozhevnikov and colleagues categorized these strategies in terms of spatial coding, where allocentric coders more efficiently manage spatial visualization, manipulating objects from a stationary point of view, and egocentric coders update their spatial orientation, taking longer to identify rotation when they have to imagine taking multiple perspectives about an image. Previous research has confirmed that measures of perspective taking and mental rotation appear to be highly correlated across experiments, and differences in strategy likely accounts for a significant proportion of the variance in test performance (Carroll, 1993; Hegarty & Waller, 2004; Just & Carpenter, 1985; Kyllonen, Lohman, & Woltz, 1984; Lohman, 1988).

Many researchers also use violation of expectation looking time methods to compare and interpret mental rotation results (Aslin 2007; Roder, Bushnell, Sasseville, 2000). In these studies, participants are habituated to multiple, increasingly rotated views of an image and then shown either a) a more dramatic rotation of that same image, b) an altered or chiral image rotated to a matching degree, or c) both a rotated and mirror image simultaneously. If the participant exhibits a significant increase in attention from baseline for one condition relative to the other, this suggests they are indeed discriminating between the two images based on a strategy that identifies the rotated image as familiar and the different image as novel. Using these methods, human infants as young as 3 months old appear capable of successfully discriminating between rotated and mirror images in a mental rotation task (Moore & Johnson, 2008; Quinn & Liben, 2008). When Quinn and Liben (2008) exposed infants to seven rotated perspectives of an image and then revealed a rotated view of the stimulus and its mirror image simultaneously, infants tended to look longer at the mirror image.

Limited studies have also tested mental rotation in nonhuman primates and have demonstrated some capacity to compare and match different views of an image (Hughes, 2012; Kohler, Hoffmann, Dehnhardt, & Mauck, 2005; Vauclair, Fagot, & Hopkins, 1993). Vauclair and colleagues (1993) were the first to use a match-to-sample task to show that baboons can distinguish between a rotated image and its mirror image. Kohler and colleagues (2005) ran a match-to-sample task with a small sample of rhesus macaques, where the monkeys had to identify a figure from a choice between a rotated view of that figure or a mirror image of that figure using a touch screen, and their analyses showed that at least one participant exhibited reaction times that were consistent with successful identification of a rotated image. They proposed that rhesus monkeys might be employing different information processing systems to identify the rotated images, but they did not pursue this possibility any further and the results were inconclusive due to the small sample size and the reliance on a touch screen apparatus. Additionally, most of these methods tested a choice between one or more answers, which does not necessarily clarify whether individuals were identifying rotation or whether they were simply eliminating incorrect choices.

Later, Hughes (2012) tested a larger sample size of 67 adult, free-ranging rhesus macaques at the Caribbean Primate Research Center on Cayo Santiago, Puerto Rico. Hughes habituated participants to three 45-degree rotations of an image and then showed participants a novel test event where the image was either rotated an additional 90 degrees or replaced with a mirror image rotated to the same degree. Hughes' results showed that overall, participants appeared to differentiate between conditions as evidenced by a significant difference in average looking time between the rotated image and the mirror image test condition. However, unlike the human literature, the macaques looked longer at the 90-degree rotation than the mirror image condition. This result may be consistent with the interpretation that participants will look longer at familiarity when it takes more time to process, match, and identify than novelty (Aslin, 2007; Roder, Bushnell, & Sasseville, 2000). Additional research is required to establish how spatial coding might be interacting with attention in this task.

Quinn and Liben (2008) also found notable sex differences in mental rotation performance in humans, where the increase in attention to the mirror image was more likely in males than females, though Hughes (2012) did not find any sex difference in rhesus macaque attention and discrimination between rotated and mirror image conditions. This reinforces the importance of testing abilities early in development to determine at what point rhesus macaques might begin to exhibit shifts in abilities and possible differences by sex, age, rank, or other skills or experiences.

The current study seeks to determine if rhesus macaques in their first year of life make predictions about the location of a reward among multiple objects in a rotating array based on egocentric or allocentric spatial coding strategies, and to further investigate whether the spatial coding system applied to tracking a reward among multiple objects corresponds to attention in tracking a single, continuous image through rotation and manipulation. In this chapter, I focus on two small-scale visuospatial tasks that assess the use of spatial cues and mental manipulation by recording looking time: a rotational displacement task comparing “allocentric” and “egocentric” conditions for locating a reward among three distinct landmarks and a mental rotation task that compares a “rotated” view and an “altered” view of a single, continuous image.

The rotational displacement task was designed to evaluate whether participants were consistently applying a spatial coding strategy to monitoring and solving the location of a reward among three distinct landmarks in an array after rotation. In one condition, the reward is rotated with the array and appears in a different location relative to the observer, but the same location relative to the array and landmarks, and participants that prioritize allocentric information should expect the reward to appear in this location. In the other condition, the reward does not rotate with the array and appears between two different landmarks, but in the same location relative to the observer, and participants that neglect relationships between the reward and the landmarks and prioritize egocentric information should expect the reward to appear in this location. Consistent allocentric coders should increase their attention or looking time in the *egocentric* condition as it is conflicts with their expectation of where the reward will appear, and they should show a greater habituation to the *allocentric* condition as it is consistent with their expectation of where the reward will appear. On the contrary, consistent egocentric coders should increase their looking time in the *allocentric* condition as it violates their expectation and habituate to the *egocentric* condition that is consistent with their expectation. Consistent with previous literature, participants should react to change and reveal a consistent preference to identify each scenario as possible or impossible based on the same spatial coding strategy.

The mental rotation task was designed to engage egocentric and allocentric attention in identifying and differentiating the rotational movement of a single, continuous image. The task involves habituation to three gradually rotated views of an image followed by a more dramatically rotated view of the original image or a more dramatically rotated view or the original image *with an alteration to the relative positioning of its features*, encouraging individuals to identify and differentiate the images by attending to relative features as well as by employing different strategies of spatial visualization and orientation. We expect to see significant differences in attention to a rotated and altered image. However, because previous literature has shown that human infants as young as 3 months exhibit a significantly longer looking time at a novel, mirror image than a rotated image while adult rhesus macaques exhibit significantly longer looking at the rotated condition than the novel, mirror image condition, we must consider that both the rotated and altered condition may elicit an increase in attention due to some change in the display. Accordingly, it is important to investigate processing time for each condition individually as well as to compare attention between conditions.

If the coding systems used to process each of these small-scale visuospatial tasks are highly correlated, then the differences in attention and discrimination between the rotated and altered views of the images should correspond to the spatial coding system indicated by looking time in the rotational displacement task. Allocentric and egocentric preferences in the rotational displacement task may not influence discrimination between the rotated and altered image, but it may instead influence the speed of processing rotated and altered images. Therefore, we expect to see differences in how individuals that prioritize allocentric or egocentric information respond to the rotated and altered views of an image independently, where allocentric coders are more efficient at rotating images from a stationary point of view while egocentric coders take longer to imagine taking different perspectives about an image, and where allocentric coders are better at identifying changes to relative features on a continuous object than egocentric coders. Alternatively, no indication of differentiation or reaction to change in either the rotational displacement or mental rotation task may indicate that yearling rhesus macaques are not capable of mental representation and manipulation at this age. If there are significant differences in attention to each task but no relationship, this would also indicate that there is no apparent interaction between the systems that are applied to processing each scenario.

This comparison of multiple, dynamic, small-scale spatial tasks enables a more accurate interpretation of how primates encode and apply spatial coding strategies to tasks involving rotational movement on multiple contexts and scales. Pursuing this comparison in a nonhuman primate in particular will help us identify factors that may contribute to similarities and differences in primate cognition, and by testing nonhuman primates early in development, we can better understand when and why these abilities emerge.

Methods and Results

Participants and Data Analysis

Data were collected at the Caribbean Primate Research Center on Cayo Santiago, Puerto Rico, a 15.2-hectare island 1 kilometer off the east coast of Puerto Rico and home to over 1,500 free-ranging rhesus macaques (Rawlins & Kessler, 1986). This colony has naturally divided into approximately seven social groups comprised of between 100 and 350 individuals. The macaques on Cayo Santiago are provisioned with Purina monkey chow once a day from three locations on the island and are provided with multiple basins that pump rainwater from cisterns that collect rainwater. The monkeys also forage on naturally occurring vegetation, flowers, berries, and soil, and otherwise spend their time moving and interacting freely about the island.

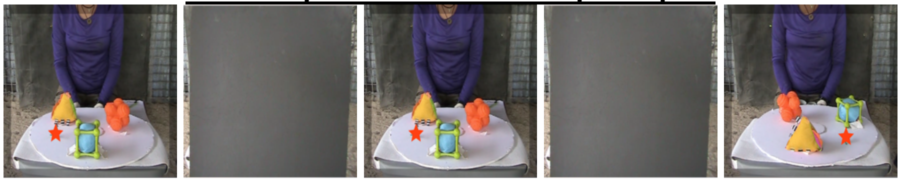
Rhesus macaques are seasonal breeders (Gordon, 1981), and the population on Cayo Santiago currently mates between March and August (Hoffman et al., 2008) and gives birth between September and January. From the months of October to December, select individuals are trapped and temporarily caged for testing. From this population, I randomly selected the first 51 infants born between July and September of 2013 from mothers of varying ages and rank and three different social groups of varying size (8 from group S that has approximately 150 individuals; 18 from group R, an alpha group with approximately 325 individuals; and 25 from group KK that has approximately 175 individuals). Infants of mothers that were being followed for a different longitudinal study were not included, resulting in the exclusion of 15 individuals from group R and 5 individuals from group S that were also born between July and September of

2013. Focal behavioral data was collected on these individuals from birth throughout their first 3 years of life, and they had only limited exposure to random cognitive testing on the island outside of the three isolated testing periods where participants were trapped at 3-6 months of age, 14-16 months of age, and 25-30 months of age for cognitive testing. Of the 51 infants that had been followed from birth, 41 were successfully trapped for testing at 60 weeks (approximately 14 months) to 70 weeks (approximately 16 months) of age, while the other 10 evaded trapping or passed away before the trapping period. Of the 41 that were trapped, 37 were tested on cognitive tasks, while four were excluded due to time constraints. This group included 21 females and 16 males.

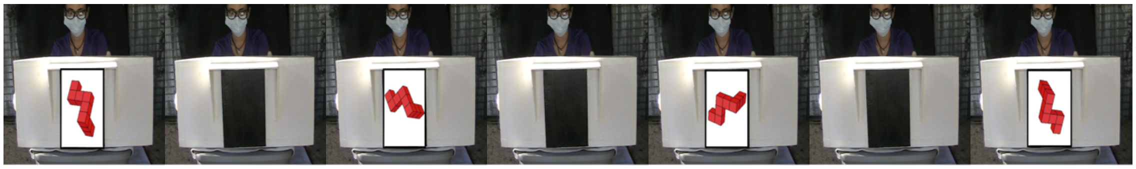
Participants were trapped individually and temporarily housed in a 2' by 2' by 2' squeeze cage and given at least 15 minutes to habituate to their cage before testing. Each individual was tested in isolation while confined to their cage (see Figure 2.1), and tests were presented approximately 2 feed away from the participant's cage. Testing lasted approximately 15 minutes. Due to the infrequency of trapping and the limited time for testing during trapping, participants were not previously trained or exposed to any of the cognitive testing protocols. Additionally, because the participants are so infrequently trapped for testing, it may be a stressful experience relative to the daily lives of the monkeys. As a result, we might expect individuals to be more reluctant to participate in testing than if tests were conducted while the individuals were free ranging in their natural environment. However, testing in isolation reduces interference from other social group members and natural distractions associated with their free ranging environment, and captures more spontaneous measures of performance. Accordingly, tests were adapted to accommodate limited training time and participation and relied on a looking time paradigm developed for nonverbal participants that compared 2-3 10-second habituation trials and one 10-second test trial. Looking time was recorded by a video camera on a tripod positioned behind the presenter. As soon as each trial was revealed, the presenter yelled "now," which alerted coders to the exact start of trial exposure, and a naïve coder recorded the number of frames (60 frames per second) that each participant directed their gaze at the apparatus for 10 seconds (600 frames) after hearing "now." Videos were coded frame by frame using QuickTime Player 7, and differences in trial times were analyzed using SPSS Statistics Software.

I used the same 37 individuals in both conditions of a rotational displacement and a mental rotation looking time task but discarded the data from 2 participants in the mental rotation task due to poor visibility in the video. Each participant was exposed to each condition in randomized order but received the same order of tasks. First, participants were exposed to the three trials of one of the two rotational displacement conditions, followed by the four trials of one of the two mental rotation conditions, followed by three trials of the other rotational displacement condition, followed by four trials of the other mental rotation condition (Figure 2.1). Each trial was revealed for 10 seconds each, with 3 seconds between trials when a barrier was placed between the observer and the apparatus so the array could be manipulated or the image could be changed.

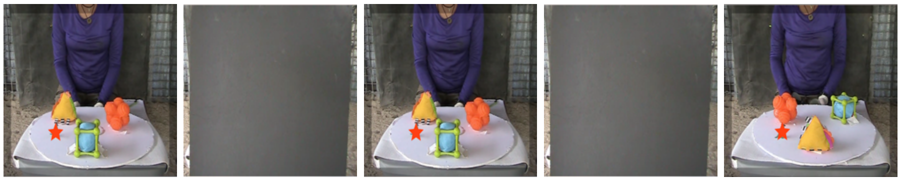
Order of presentation for each participant



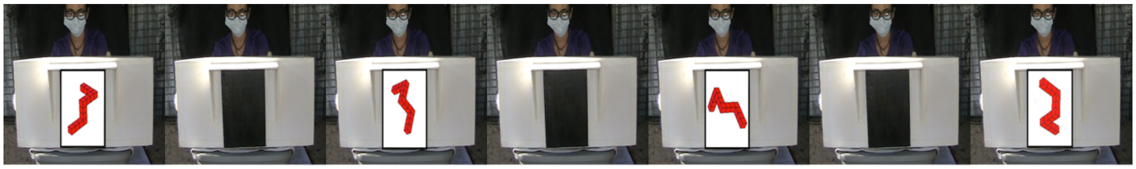
Rotational Displacement Task Condition 1:
10 seconds Trial 1 → barrier → 10 seconds of identical Trial 2 → barrier → 10 seconds of *allocentric* or *egocentric* Test Trial



Mental Rotation Task Condition 1:
10 seconds of Trial 1→ barrier → 10 seconds of 45° rotated Trial 2 → barrier → 10 seconds of 45° rotated Trial 3 → barrier → 10 seconds of *rotated* or *altered* Test Trial



Rotational Displacement Task Condition 2:
10 seconds of Trial 1 → barrier → 10 seconds of identical Trial 2 → barrier → 10 seconds of other Test Trial



Mental Rotation Task Condition 2:
10 seconds of Trial 1→ barrier → 10 seconds of 45° rotated Trial 2 → barrier → 10 seconds of 45° rotated Trial 3 → barrier → 10 seconds of other Test Trial

Figure 2.1: Order of presentation for each participant. Each participant received one of the two rotational displacement conditions followed by one of the two mental rotation conditions followed by the other of the two rotational displacement conditions followed by the other of the two mental rotation conditions. Rotational displacement conditions also differed in the starting location of a reward and mental rotation conditions also differed in the object image used.

Rotational Displacement Task: Apparatus, Design, and Procedure

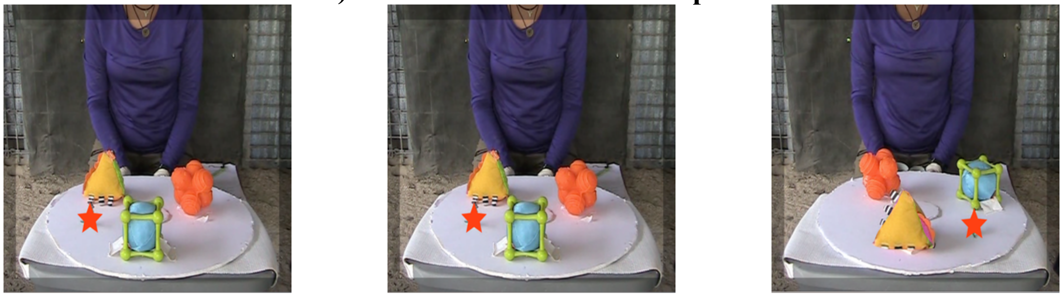
In the rotational displacement task, each participant was exposed to two conditions evaluating allocentric versus egocentric spatial coding memory and attention involved in tracking the location of a reward among three distinct objects in an array. In both conditions, participants were shown two identical 10-second habituation trials followed by a 10-second test trial. A significant difference in attention between the test trials would determine whether individuals were differentiating between the two scenarios and favoring one over the other based on their expectation.

The apparatus was a flat, white, circular array with a diameter of approximately 20 inches, circumference of approximately 63 inches, and an area of approximately 314 inches^2 that contained three distinct objects that were roughly 4” by 4” by 4” each and evenly spaced around the edge of the circle. The objects included an orange, rubber toy made up of six bulbous balls, a plush yellow pyramid, and a green rubber cube with a plush blue ball inside (see Figure 2.1). The reward was a small piece of papaya, a fruit that the participants cannot otherwise find on the island but is used as a special treat during the trapping period and is widely enjoyed by the monkeys. As a looking time task, participants were not given access to grab and eat this reward. The array was set up behind a barrier that was placed between the participant and apparatus, which was approximately 2 to 3 feet away from the participant. When the barrier was removed, the trial time began.

In the first trial, the reward was located between two of the three objects in the array, and the starting location of the object was randomized for each individual and differed by condition. The reward was always located in one of the two positions closest to the participant. After 10 seconds (600 frames) of exposure, I rotated the array a full 360 degrees back to its starting location to represent the full range of motion of the array and then placed a black barrier between the participant and the array. After waiting approximately 3 seconds, I lifted the barrier to start the second trial, which was identical to the first and served to measure habituation to the first exposure. After 10 seconds, the array was then rotated 360 degrees back to its starting location and a barrier was placed between the participant and the apparatus. Behind the barrier, the array was modified to reflect either an *allocentric* test condition or an *egocentric* test condition.

In the *allocentric* test trial, the reward was rotated 120 degrees with the array so that it now appeared in a different location relative to the participant, but in the same location relative to the objects in the array (Figure 2.2a). If the reward started on the left the array, it was rotated 120 degrees, so it now appeared on the right of the array relative to the observer, and if the reward started on the right of the array, it was rotated 120 degrees so it appeared on the left of the array. Then the barrier was lifted and looking time was recorded for 10 seconds. In the *egocentric* test trial, the array was rotated either 120 degrees to the left or right behind the barrier, but the reward was not moved with the array, so it appeared in a different location relative to the objects in the array, but the same location relative to the participant (see Figure 2.2b).

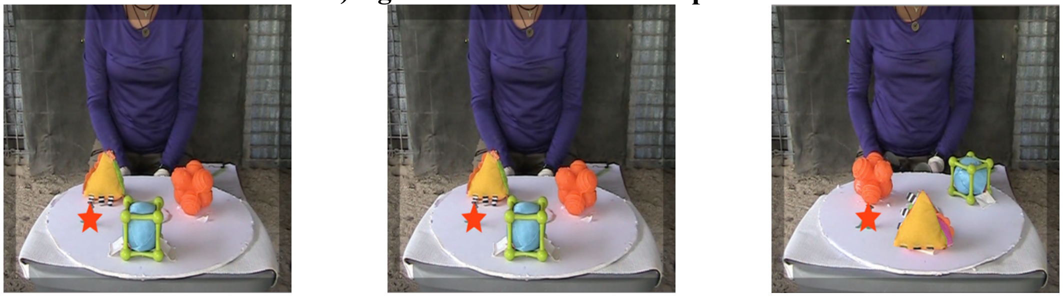
a) Allocentric condition example:



Trial 1 **Trial 2: Habituation** **Test Trial: Allocentric**

Reward location *same* relative to objects, *different* relative to observer

b) Egocentric condition example:



Trial 1 **Trial 2: Habituation** **Test Trial: Egocentric**

Reward location *different* relative to objects, *same* relative to observer

Figure 2.2: Presentation for the rotational displacement looking time task. The star indicates possible starting and ending locations of the reward, but for each individual the starting location differed between the two condition exposures. All participants received both conditions, and the order of exposure was randomized. In Trial 1, participants saw a food reward between two of three objects in an array for 10 seconds (600 frames) before a barrier was placed between participant and array. In Trial 2, participants were shown the same display again for 10 seconds to measure habituation. In the test trial, participants were shown a change in display that was either consistent with a) allocentric or b) egocentric attention for 10 seconds.

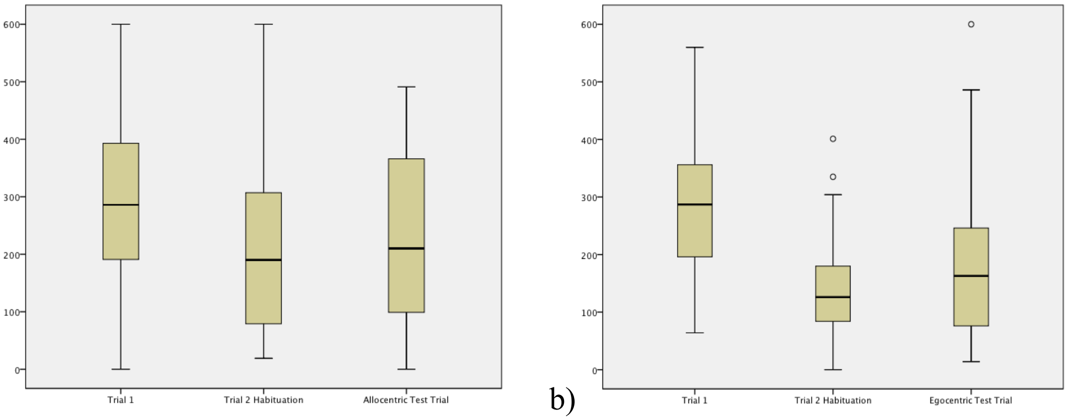
Looking time should decrease between habituation trials 1 and 2 as both conditions are identical and should be less interesting over time. There may be a slight increase in looking time from habituation to test trial due to a change in display, but a greater increase in looking time for one condition relative to the other is interpreted as a *violation of expectation,* which is established based on either an egocentric or allocentric prediction about the resulting location of the reward. If an individual is only attending to the location of the reward relative to themselves, they should expect the reward to appear in the same location on their left or right despite other changes in the display and should exhibit a decrease in looking time from habituation to test trial for the egocentric condition and an increase in looking time for the allocentric condition. Alternatively, if individuals are attending to the relationships between object locations, they should expect the reward to appear in the same location relative to the other objects in the array when it moves and should therefore exhibit a general decrease in looking in response to the expected, allocentric test trial and an increased attention in response to the egocentric test trial the violates these expectations.

If an individual is only associating the reward with being in front of, to the left, or to the right of a particular object in the array, this may still be insufficient to accurately predict the location of the reward following rotation, since these views change when the array is rotated. With three objects in the rotating array, the reward might first appear in front of the yellow triangle, to the left of the green-blue box, and between the yellow triangle and the green-blue box, but when the array is rotated 120 degrees, from the observer's perspective, the reward now appears to the right of the yellow triangle, in front of the green-blue box, and between the yellow triangle and the green-blue box (see Figure 2). The only consistency across both views is that the reward exists between the same two objects. So, unless the individual can recognize this association from a different angle, they may still increase their looking time in both conditions as neither are consistent with their expectation. If an individual is encoding the location of the reward as being *between* two particular objects in the array, they should be able to identify the correct location of the reward even after rotation and should exhibit a decrease in looking time from habituation to test trial for the allocentric condition that is consistent with their expectation while increasing looking time for the impossible, egocentric condition.

Rotational Displacement Task: Results

In the allocentric condition (Figure 3a), there was a nearly significant decrease in overall looking time from the first trial (m = 283.14 frames, se = 26.23) to the second identical trial (m = 216.68 frames, se = 25.28); t(36) = 1.86, p = 0.07, which indicates some habituation to viewing the same array twice, and there was no significant increase in looking from the second trial to the test trial (m = 226.22 frames, se = 24.58); t(36) = -0.354, p = 0.73. Additionally, there was no significant difference between the change in looking time from trial 1 to trial 2 (m = -55.46 frames, se = 35.80) and the change in looking time from the second habituation trial to the test trial (m = 9.54 frames, se = 26.98); t(36) = 1.407, p = 0.168. 22 individuals exhibited a higher change in looking between habituation and test trial than between habituation trials, and 15 individuals exhibited a lower change in looking between habituation and test trial than between habituation trials, showing an inconsistent overall response to change.

For the egocentric condition (Figure 2.3b), there was a significant decrease in looking time between the first trial (m = 284.49 frames, se = 19.35) and the second, identical trial (m = 138.11 frames, se = 15.32); t(36) = 6.447, p < 0.001, indicating successful habituation, but no significant increase from the second trial to the test trial (m = 186.78 frames, se = 23.54); t(36) = -1.615, p = 0.12. There was also a significant difference between the change in looking from the first to the second habituation trial (m = -146.38 frames, se = 22.70) and the change in looking from the second habituation trial to the test trial (m = 48.68 frames, se = 30.15); t(36) = -4.390, p < 0.001, supporting a significant shift in attention in the egocentric condition that was not present in the allocentric condition. 31 individuals exhibited a higher change in looking between habituation and test trial than between habituation trials, while only 6 individuals exhibited a lower change in looking between habituation and test trial than between habituation trials, suggesting that the majority appeared to respond to the change in display.



a) b)

Figure 2.3: Looking time across trials for the allocentric and egocentric condition. Distribution of looking time in frames (60 frames = 1 second) for all participants (N=37) across Trial 1, Trial 2, and the Test Trial for the a) allocentric condition and b) egocentric condition.

I compared overall looking time in the test trials of the allocentric and egocentric conditions using a paired-samples t-test, and found no significant difference between the two conditions; t(36) = 1.217, p = 0.23, and I found no significant difference in the change in looking from habituation to test trial for the egocentric and allocentric conditions; t(36) = -0.78, p = 0.43, indicating no clear preference to increase attention to one condition over the other. Though, when I compared the 16 individuals that exhibited a change in attention from habituation to test trial that was higher than the change in attention between habituation trials, I found a significantly higher change in attention to the allocentric test trial (m = 101.4 frames, sd = 130.6) than the egocentric test trial (m = 11.69 frames, sd = 64.97); t(15) = 2.16, p = 0.047 and no significant difference in their change in attention to habituation trials; t(15) = 0.03, p = 0.98, which may support longer investigation of the allocentric test trial compared to the egocentric test trial among those individuals that detected change in both conditions.

Due to time restrictions, I did not include a control condition with a test trial in which no change occurred, which made it difficult to compare reaction to change against a natural loss of attention. I could only compare the two conditions against each other. With no significant difference between the mean response to the two conditions, I expected to find individual consistency in their attention to both conditions, where some individuals would more or less attentive in general. However, when I compared the change in looking from habituation to test trial for the egocentric and allocentric condition, I discovered a negative partial correlation ($r = -0.474$, $p = 0.004$) between the two conditions even when controlling for the order in which individuals were exposed to the conditions (Figure 2.4). This suggested that the insignificant difference in overall looking time between conditions may have been due to individual differences in expectations. This was a completely novel approach to analyzing looking time data, which is designed to evaluate mean looking time in large data sets rather than individual differences. However, by comparing these looking time profiles to other tasks, we can investigate whether these individual differences in attention are consistent and potentially representative of individual cognition.

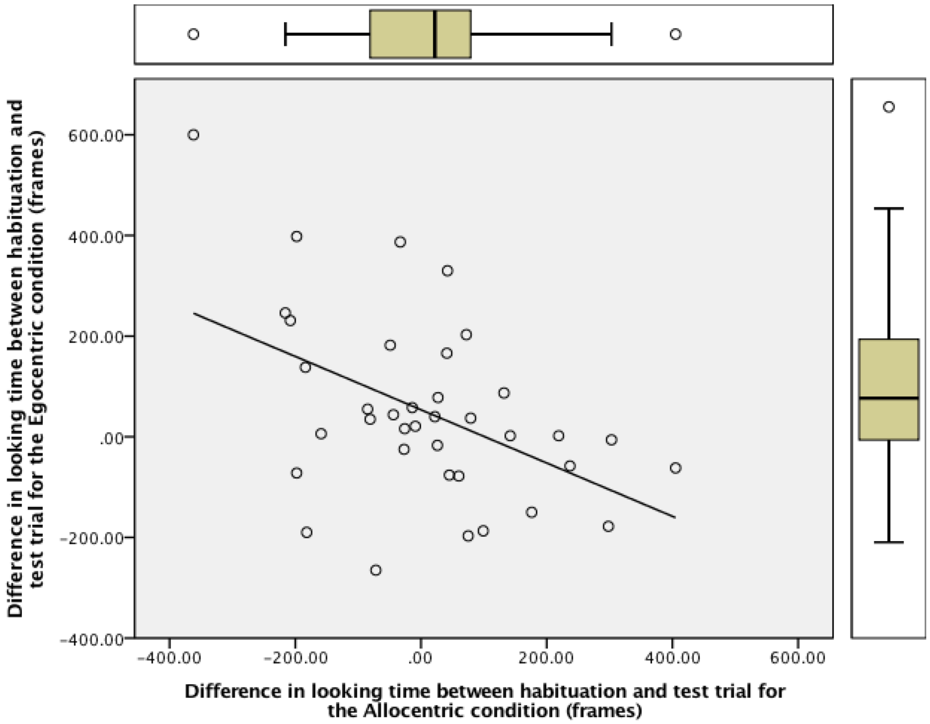


Figure 2.4: The relationship between looking response in the allocentric and egocentric conditions. The relationship between the change in looking time from the second habituation trial and the test trial for the allocentric and egocentric conditions was negatively correlated after controlling for order of presentation (r = -0.474, p = 0.003).

The majority of participants (24 out of 37 and 65%) exhibited an increase in attention from habituation to test trial in one condition and a decrease in the other that was independent of the order in which they received each condition. Of these individuals, 14 decreased their looking time in the allocentric test trial and increased looking time in the egocentric test trial, which is consistent with predicting location and movement based on allocentric information, and 10 participants decreased their looking time in the egocentric test trial and increased looking time in the allocentric test trial, which is consistent with predictions based on egocentric information. The remaining 9 (24.3%) participants increased looking time in both conditions and only 4 (10.8%) individuals decreased looking time for both conditions. These results are consistent with an interpretation that individuals may be consistently prioritizing spatial information based on an egocentric or allocentric coding strategy, and they may make predictions about the location of the reward accordingly.

Mental Rotation Task: Apparatus, Design, and Procedure

The same participants were tested on a mental rotation task, where each individual was exposed to two conditions that evaluated attention to the rotation of an image and the capacity to differentiate an image based on an alteration of its relative features. In both conditions, participants were shown three 10-second trials of an image rotating at 45-degree intervals followed by a 10-second test trial. In one test trial, participants saw an image rotated dramatically around the z-axis and in the other test trial, participants saw an image rotated dramatically around the z-axis, but with one of its features altered to point in the opposite direction. A significant difference between the response to test trial and response to the other trials within a condition would indicate that individuals were identifying a change by mentally matching past and present views, and a significant difference in response to the test trial between conditions would indicate that individuals were differentiating between the two conditions and identifying novelty based on mental rotation and attention to relative object features.

Stimuli were adapted from 2-dimensional representations of 3-dimentional models of simplified Shepard-Metzler (1971) objects scaled to 8” by 8” images. Object ‘A’ consisted of 8 blocks and four connected arms and object ‘B’ consisted of 13 blocks and four connected arms. All images were red to increase visual salience. Both image ‘A’ and ‘B’ depict a 2-dimensional “w” shape, which includes two ends situated so they appear to be facing out of the same side of the image despite pointing along different axes (see Figure 2.5).

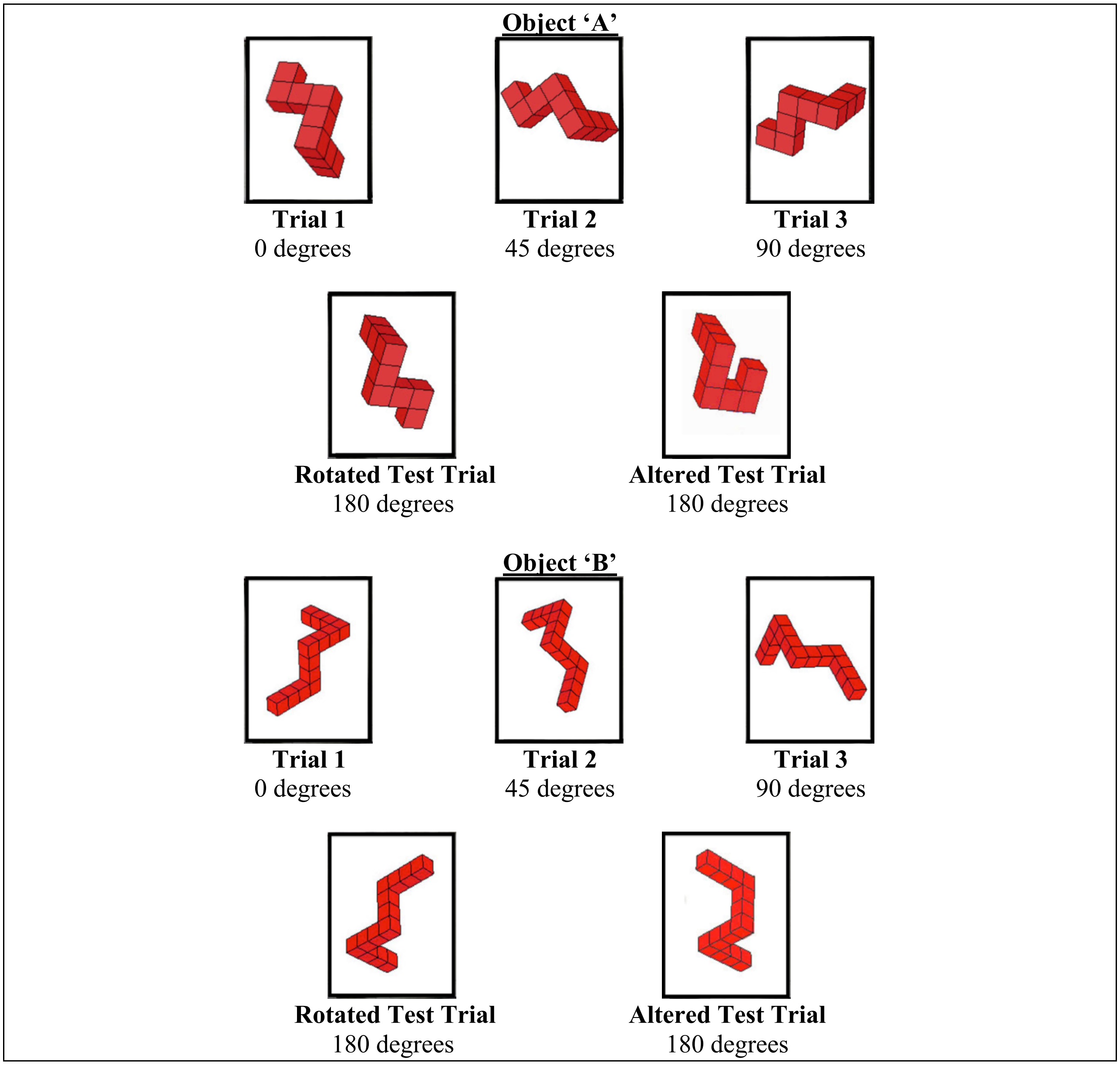


Figure 2.5: Presentation for the mental rotation looking time task. All participants received both conditions, the order exposure was randomized for each individual, and the object used was randomized for each condition. If they received object 'A' for one condition, they received object 'B' in the other, and each trial was 10 seconds (600 frames) long. In Trial 1 participants were shown an image, in Trial 2 they saw the previous image rotated 45 degrees, In Trial 3 they saw the previous image rotated an additional 45 degrees, and in the test trial they saw either the rotated test condition, where the previous image was rotated another 90 degrees, or an altered test condition, where the previous image was rotated 90 degrees but with one altered feature.

In the first trial, participants were shown either image A or B at 0 degrees of rotation for 10 seconds (600 frames). At the end of the 10 seconds, a barrier was placed between the participant and the image, and the image was removed and replaced with a new image through a window in the back of the apparatus. These transitions took approximately two seconds, and then the barrier was lifted, and the next trial began immediately. In the second trial, participants saw the same image rotated 45 degrees to the left around the z-axis for 10 seconds, and then a barrier was placed between the participant and observer and the image was replaced with a new image. In the third trial, participants saw the same image rotated another 45 degrees to the left around the z-axis and 90 degrees from the first trial for 10 seconds before a barrier was again placed between the participant and image. Participants only saw stills of each image orientation and did not witness any rotational movement.

In the fourth trial, participants either saw a *rotated* test trial or *altered* test trial for 10 seconds. In the *rotated* test trial, participants saw the image from the previous trial rotated more dramatically 90 degrees to the left around the z-axis and 180 degrees from the first trial (Figure 2.5a). In the *altered* image test trial, participants saw the image the image from the previous trial rotated another 90 degrees to the left around the z-axis and 180 degrees from the first trial, but altered so one of its ends was now pointing in the opposite direction so that the ends of the object no longer appeared to be facing out of the same side, where the image as a whole no longer appeared to make a “w” shape (Figure 2.5b). If a participant saw object ‘A’ for one condition series, they saw object ‘B’ for the other condition series, and the object assigned to each condition and the order of each condition was randomized for each individual.

Looking time should decrease or stay the same across the first three trials as participants recognize the image as it gradually rotates about its z-axis. The difference in response to the test trials should be greater than the change in looking time between the first three trials for both conditions as the test trials involve twice as much rotation and should require longer assessment to mentally rotate and identify the image as being the same as or different from previous views. A significant difference in response to the test trial would indicate a capacity to identify change and attempt matching. If participants are using mental rotation and object features to identify novelty, we should observe a significant difference in the looking time response to the test trials between the *rotated* and *altered* condition, where looking time is higher for the novel, altered image.

Mental Rotation Task: Results

The single image mental rotation task differs from the rotational displacement looking time task in that each trial portrays some change in display as the image gradually rotates in 45 degree increments in the first three trials and changes more dramatically in the test trial. Accordingly, while we expect to see a decrease in looking time across trials, the differences between trials may not be as evident. We only expect to see a significant difference in the change in response to the test trials. In the rotated condition, there was no significant difference in looking time between trial 1 (m = 96.58 frames, se = 13.53) and trial 2 (m = 65.36 frames, se = 9.27); t(32) = 1.837, p = 0.076, and there was no significant difference between trial 2 and trial 3 (m = 79.85 frames, se = 13.20); t(32) = -0.0947, p = 0.351. There was also no significant difference between trial 3 and the test trial (m = 60.42 frames, se = 10.44); t(32) = 1.147, p = 0.26 (Figure 2.6a). In the altered condition, there was no significant difference in looking time between trial 1 (m = 120.71 frames, se = 15.10) and trial 2 (m = 94.71, se = 19.17); t(33) = 1.251, p = 0.22, and there was no significant difference in looking between trial 2 and trial 3 (m

= 88.38 frames, se = 17.53); t(33) = 0.321, p = 0.75. Additionally, there was no significant difference between trial 3 and the test trial (m = 70.41 frames, se = 17.63); t(33) = 0.726, p = 0.473 (Figure 2.6b).

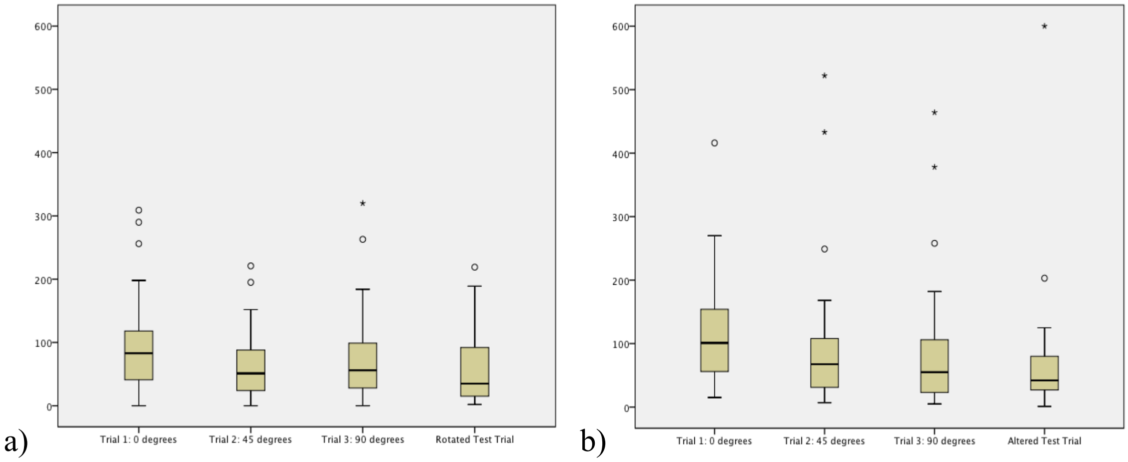


Figure 2.6: Looking time across trials for the rotated and altered condition. Distribution of looking time in frames for all participants (N=33) across Trial 1, Trial 2, Trial 3, and test trials for the a) rotated and b) altered conditions.

While there was a nearly significant difference between looking time in the first trial for the rotated and altered condition; t(32) = -1.896, p = 0.067, participants exhibited the same change in looking from one trial to the next for both conditions. There was a comparable change in looking from trial 1 to trial 2 for the rotated condition (m = -31.21 frames, se = 16.99) and the altered condition (m = -27.30); t(32) = -0.193, p = 0.848, and a comparable change in looking from trial 3 to the test trial for the rotated condition (m = -19.42 frames, se = 16.93) and the altered condition (m = -20.15, se = 25.41); t(32) = 0.023, p = 0.982. Accordingly, these results do not support an obvious reaction to the more dramatic change in either condition of the single image rotation task and do not support an overall differentiation between the two conditions.

Because there was no significant change in overall looking time for the mental rotation task, I investigated possible individual differences in looking time using similar methods that I applied to the rotational displacement task. I found that 13 (37.1%) of the 35 participants increased their looking from the third trial to the test trial in the rotated image condition, and 18 (50%) of the 36 participants showed an increase in attention from the third trial to the test trial in the altered condition, but there was no apparent correlation in looking in the rotated and altered condition ($r = -0.154$, $p = 0.409$) when controlling for order of exposure. Additionally, only 5 (14.3%) of the 35 participants showed a consistent decrease in attention across the first three incrementally rotated habituation trials in the rotated condition and only 10 (27.8%) of the 36 participants showed a consistent decline in looking across the first three trials in the altered condition, further suggesting that participants were not successfully habituating to the incrementally rotated image and did not react to the change and were not attempting to match the final test trial. These results alone are inconclusive, but we may reveal more about how to interpret these data by comparing performance across this single image rotation task and the multiple object rotation task.

Overlap in response to the rotational displacement of multiple objects and the rotation of a single object

Due to the variability in looking time across individuals and contexts, looking time tasks are most often used to evaluate average overall attention across large sample sizes and are rarely used to assess individual differences. However, due to the consistency in individual looking time and the multiple tasks and conditions conducted within each individual, I wanted to explore whether these individual differences were further supported in comparisons between looking time tasks. I took the 24 of 37 participants in the multiple object rotational displacement task that exhibited an increase in looking for one condition and a decrease in looking for the other condition and compared their attention to the rotated and altered condition in the single image rotation task.

Using a paired samples t-test, I found no significant difference in how "allocentric coders" reacted to change in the rotated condition (m = -14.25 frames, se = 19.73) relative to the altered condition (m = 3.00 frames, se = 28.53); t(11) = -0.610, p = 0.55, and I found no significant difference in how "egocentric coders" responded to change in the rotated condition (m = 6.60 frames, se = 38.67) relative to the altered condition (m = -48.30 frames, se = 77.66); t(9) = 0.573, p = 0.581, which does not indicate that individuals designated as either "allocentric" or "egocentric" were necessarily better at differentiating between the altered and rotated test trials. Though, a Fisher's exact test revealed that all of the individuals that increased their looking time in response to both the egocentric and allocentric test trials also lost interest in the rotated test trial, while those that decreased their attention to both the egocentric and allocentric test trials all increased their attention in response to the rotated test trial ($\chi^2 = 11$, p = 0.006).

Using an independent samples t-test, I noted a significant difference in attention to the rotated condition between "allocentric coders" and "egocentric coders" (t(20) = -2.802, p = 0.011), where "allocentric coders" more commonly decreased their looking from the first trial to the rotated test condition (m = -82.33 frames, se = 22.41) and "egocentric coders" more commonly increased their looking from the first trial to the test trial in the rotated condition (m = 11.60 frames, se = 25.00). The relationship between the multiple object and single object tasks was further confirmed with a chi-square that indicated that individuals that increased their looking in response to the egocentric test condition more commonly decreased their looking in response to the rotated test condition and vice versa ($\chi^2 = 10.01$, p = 0.002). Though, I found no significant difference in reaction to the altered condition between "allocentric coders" (m = -76.83 frames, se = 39.45) and "egocentric coders" (m = 16.50 frames, 55.14); t(20) = -1.408, p = 0.174, but "allocentric coders" did decrease their looking time on average while "egocentric coders" increased their looking.

The apparent association between looking in the rotational displacement task involving multiple objects in an array and looking in the single image rotation task offers interesting evidence for a relationship in how these different types of rotational movement are processed and validates some consistency in task measurement. Additionally, these results provide substantive support for the use of looking time tasks to evaluate patterns in individual differences, where a comparison of overall average looking times may be inconclusive due to individual variation in response to different conditions. The significant relationships in response to multiple rotation conditions supports systematic individual consistency and differences in how individuals may process and respond to spatial rotation information.

Discussion

Looking time tasks were developed to compare mean differences in response to change in possible and impossible conditions, and researchers primarily use these methods to determine whether a group or population overall is capable of differentiating between two scenarios. Generally, these methods are not used to compare individual differences, as variation in subtle looking time behaviors and isolated measurements are difficult to validate. However, in instances where a group or population does not uniformly respond to change in the same way, it is important to investigate whether this may be due to differences in how individuals are processing the stimuli. Because these experiments used the same 35 individuals on multiple looking time tasks, they introduced ideal conditions in which to explore individual comparisons in attention and longitudinal cognitive performance. Due to the novelty of this methodological approach, it is important to be cautious with any interpretation, but finding significant correlations that are consistent with predictions and previous literature offers compelling evidence for the reliability of these results.

These results provide some support that individual rhesus macaques in their first year of life may exhibit a consistent spatial coding strategy to track and predict the location of a reward among multiple objects in a small-scale rotating display. There was a significant inverse relationship between looking time in the egocentric condition and the allocentric condition of the displacement task that was independent of the order in which participants received the conditions. This indicated consistent individual differences in looking time preferences that could be interpreted as consistent differences in their expectations. This result was predicted given that individuals are consistently prioritizing the same spatial information to make predictions in both conditions, where one condition violates their expectation and elicits greater investigation while the other is consistent with their expectation and therefore reflects a loss of attention.

There was no significant overall preference for one condition, but 14 individuals increased their attention to the egocentric condition and decreased their attention in response to the allocentric condition, which I used to designate them potential "allocentric coders," and 10 individuals increased their attention to the allocentric condition and decreased their attention in response to the egocentric condition, which I used to categorize them as possible "egocentric coders." About a third of participants showed no obvious preference between the two conditions, which may indicate that individual differences were a product of random effects and instead demonstrate how yearling rhesus macaques struggle to differentiate between conditions in rotational displacement. With only three trials per condition, it is difficult to interpret variation in looking time, especially when there is variability in attention to the habituation trials across conditions. Unfortunately, there was not enough time to introduce a control condition that compared their reaction to no change in display, so analyses relied on a comparison of differences in looking between habituation and test trials. However, there is such a consistent and significant majority that exhibits looking time consistent with predictions that we cannot reliably reject the results as random, and of the participants that showed no preference in looking time between the conditions, the overwhelming majority (9 of 13) increased their attention to both scenarios, which is expected given that both conditions involve some change in display. By comparing trends in attention to multiple related small-scale visuospatial tasks, we can better validate these measures of individual consistency.

Previous research has expressed conflicting results about whether nonhuman primates are capable of applying allocentric coding to solve complex spatial problems, and there is even more controversy about whether nonhuman primates can encode spatial relationships by remembering the location of an object as *between* two other landmarks rather than just recalling a simple association. The rotational displacement looking time task from this study not only compares expectations based on self-centered or object-centered spatial memory, but it also encourages the concept of *between,* where participants must imagine the objects moving together and how they will look from an updated angle in order to accurately track the movement. Both humans and nonhuman primates struggle with rotational displacement tasks even when there are only two objects in the array. The fact that there is such an increase in errors when the array moves rather than the observer suggests that egocentric updating is a preferred means by which most primates process space, but the fact that both humans and nonhuman primates can improve their performance with landmark cues also means that we can confidently say that these tasks encourage to attention to allocentric information. Since since there was no consensus or significant overall difference in looking time between the two conditions, we cannot conclude that these yearling rhesus macaques are generally capable of differentiating between egocentric and allocentric scenarios, but consistent individual differences are extremely interesting to find in the first year of development when participants have no prior or repeated exposure to these types of tasks.

While looking time tasks allow for more flexibility in methods, there is still considerable disagreement in interpreting looking time data, which means we cannot confirm that preferential looking time necessarily corresponds to either an egocentric or allocentric spatial coding strategy. An increase in attention to the egocentric condition may not necessarily indicate surprise, but rather an increase in attention to the location in which they expect the reward to appear. Though, if this were the case, reactions would remain constant over the habituation trials as well. We can also rule out the possibility that participants are simply increasing their attention to novelty, since both the allocentric and egocentric conditions involve a change in display. Again, this would be improved by including a “no change” condition in which participants receive three identical trials, but unfortunately these tasks were constrained by the amount of time allotted for cognitive testing. Instead, I compared the change in attention between habituation trials and habituation and test trials. These tests may also be improved by introducing both test conditions simultaneously to more accurately target relative attention to each scenario.

We must also consider that errors in presentation can account for insignificant differences in overall looking time between the two conditions. These results may be more conclusive with repeated exposures and variations in the types of rewards and landmark information available to determine how spatial coding strategies and preferences change when multiple cues are present. Unfortunately, these questions could not be addressed in this particular study due to time constraints on data collection. However, we can compare looking time on this task with performance in other visuospatial tasks collected from the same individuals at the same time and across early development to provide better support for these novel approaches.

When comparing looking times in the single image rotation task, there was a gradual loss of interest in the incrementally rotated image in the first three trials and an equivalent loss of interest in response to the more dramatic change in the test trials for both conditions. Furthermore, there was no significant difference or correlation in looking time between the rotated and altered test conditions. This suggested that yearling rhesus macaques overall were not identifying any change and were not differentiating between the two conditions in any meaningful way. However, when I compared looking time in the multiple object task, I found that individuals that were designated “allocentric coders” based on the consistency in their looking time also more commonly decreased their attention to the rotated image condition, while “egocentric coders” more commonly increased their attention to the rotated image condition. In particular, there was an inverse relationship between response to the egocentric condition and response to the dramatically rotated image that was independent of the order in which they received the conditions. There are many ways to interpret these results, but they present an interesting intersection between the two small-scale visuospatial rotation tasks despite insignificant differences in looking time overall. This provides additional support for extracting and comparing trends in individual attention to each scenario.

If participants increase their looking when a condition contradicts their expectations and decreases their looking when a condition is consistent with their expectations, then those who did not expect the egocentric test condition and did expect the allocentric test condition were spent less time investigating the dramatically rotated image than those the expected the egocentric condition and did not expect the allocentric condition. Of course, it is difficult to interpret looking time in the single image rotation task when an increase in attention can be interpreted as a violation of expectation or a longer time to process familiarity. These tasks attempt to clarify this distinction by comparing looking times with another rotated and modified image, but there was no significant difference in attention to the rotated and altered conditions by individual or coding preference.

“Allocentric” individuals did not exhibit any notable differences in response to the altered image condition despite involving a change in relative features, which fails to support the hypothesis that individuals that prioritize relationships between objects in one task are also attending to the relationships between features on a single object. Thought, recognizing relative features in a continuous image may not be mechanically analogous to recognizing spatial relationships between multiple objects, or the rotated images may not have been distinct enough to elicit a response. Regardless, we cannot conclude that attention to egocentric or allocentric information interacts with an ability to differentiate between rotated and altered images.

Nevertheless, if we just consider reaction to the rotated image alone, these results are consistent with the theory that egocentric coders will be less efficient at identifying a rotated image because they must imagine taking a different perspective in space rather than attempting to mentally manipulate the image from a stationary point of view as an allocentric coder might. Those that lost interest in the egocentric condition attended more to the rotated image, and those that increased their attention to the egocentric condition looked less at the rotated image. This particular method of comparison may have failed to produce a significant difference between conditions because the rotated condition encouraged the same amount of investigation as the altered condition, since identifying the familiarity of the rotated image and identifying the novelty of the altered image would both elicit an increase in attention.

This task compares two discrete looking time conditions using different shapes, which also made it difficult to accurately discern preference to look at one image over the other and may not have necessarily conveyed a capacity to discriminate between the two images. In the future, it may be more informative to also present this mental rotation task as a preference option test, in which participants are shown a series of gradually rotated habituation images, and then shown the rotated view and altered view images simultaneously. It would also be beneficial to include a condition which compares a mirror image test condition to discern whether individuals were attending to novelty or the relative positioning of object features.

While these results do not support the capacity for yearling rhesus to discriminate between conditions in invisible rotational displacement or mental rotation tasks, they do provide interesting consistency in individual differences and a possible intersection between the spatial coding strategies that are applied to tracking the rotation of multiple objects and a single, continuous object. In general, allocentric and egocentric spatial strategies are difficult to define and differentiate in different contexts and scales, and some propose that allocentric, object-centered, and world-centered reference frames still fundamentally rely on egocentric information (Filimon, 2015), where individuals mentally shift an object to line up with the egocentric midline, imagine the self in new orientations, and encode egocentric object, landmark, or scene recognition from multiple angles. Regardless, these results measure a meaningful relationship between different degrees of spatial complexity and are noteworthy in the conversation about the development and evolution of spatial cognition.

Moving forward we must ask how these differences in cognitive processes might impact other diverse cognitive skills that involve spatial associations. In particular, object tracking tasks like object permanence require mental manipulation as participants track the movement of an unseen object or the location of an occluded object and match past and present views of an experimental array. Abilities in the domain of social cognition can also employ attention to relationships between others. To follow the gaze of another social group member or to consider a theory of mind, one must recognize that there exist relationships between others that are independent of one's self. Additionally, these results introduce the question of what developmental factors and experiences might be influencing the emergence of these individual differences in spatial cognition. If human infants employ more allocentric reasoning as a function of their motor development, how might locomotion experience influence spatial cognition in a species of primate that is born fully locomotive? I will address these questions and more in the coming chapters.

Chapter 3

Interaction of object permanence, means-ends reasoning, gaze following, and spatial attention in rhesus macaques from infancy to juvenility

Abstract

There is a large body of research that studies the presence of cognitive abilities in nonhuman primates, but less attention is given to how they influence each other throughout early development and how this compares to early development in humans. In this chapter I introduce search tasks, support problem tasks, and a gaze following task to address 1) how cognitive abilities emerge and improve across the first two years; 2) how cognitive abilities involved in the development of object permanence, means-ends actions, and gaze following interact in the first two years; and 3) how consistent attention in a spatial coding looking time task at one year interacts with performance on interactive search and problem solving tasks from 1 to 2 years of age.

Participants improved most on gaze following in the first year and appeared to improve in their participation in an A-not-B object permanence task and support problem task from the first year to their second year, though they did not appear to solve causal support problem choice tasks or invisible displacements at above chance. There was a positive correlation between performance on the A-not-B object permanence task and the support problem task when individuals were tested as yearlings and juveniles, and individuals that exhibited "allocentric" attention in a rotational displacement task as yearlings were also more successful in an A-not-B object permanence task in their first

year, a support problem task over the first two years, and an invisible transposition task after their second year.

These results support an interaction in the development of object permanence, means-ends reasoning, and spatial attention over the first two years as well as a correlation between looking time and search behavior that persisted up to a year after looking time was first recorded. The directionality of this correlation further supports a novel approach to interpreting individual differences in a looking time task conducted in the first year.

Introduction

Piaget (1954) defined six stages of object permanence development in humans that occur in the first two years of life and align with the sensorimotor period of cognitive development. Just after birth and in the first few weeks, infants are only capable of the first stage of object permanence, where they display no apparent response to disappearances and only exhibit simple reflexive reactions to their environment. Within the next four months, infants enter stage II, where they will search for the source of a sound or maintain gaze in the last place they saw an object before disappearance, but they will not yet search for it. Around 4 months, infants achieve stage III object permanence, where they begin to attend more to external objects, will look ahead to where a moving object will land, and will retrieve objects that are partially obscured, but do not yet respond to fully occluded objects.

It is not until 9 months of age that infants achieve stage IV object permanence, in which they will now intentionally search for and recover objects that have been fully hidden. However, this stage is defined by the persistence of an A-not-B perseverance error, in which infants consistently search for a reward that they have seen hidden in location ‘A,’ and even when they have seen the reward move to a location ‘B,’ they continue to search in location ‘A.’ This phenomenon has been explained as an over-reliance on basic associations or an inability to inhibit the desire to reach in a conditioned location, but it is still unclear what specifically limits an individual’s ability to update their associations at this stage.

Around 12 months, infants reach stage V object permanence, where they no longer commit the A-not-B error. It has been posited that this transition from stage IV to V may be due in part to a shift in attention to object-to-object relationships, means-ends reasoning, and an increase in exploration that accompanies these ages. However, research conducted since the introduction of Piaget's model has revealed a more dynamic interpretation to the A-not-B task (Smith & Thelen, 2003), revealing that changing infant posture from sitting to standing can improve performance in younger, 10-month old infants, and that age only appears to influence how well participants perform after delay. Due to the disagreement surrounding the developmental transition from stage IV to stage V object permanence, it is important to explore multiple, co-occurring developmental milestones to better understand what may facilitate this cognitive shift.

Around 18 months, humans reach stage VI object permanence, in which they will not only consistently recover hidden objects, they can also track occluded movement and solve invisible displacements. The improvement from stage V to VI object permanence has been associated with the emergence of representational thought, where infants can now visualize what is not physically present, track unseen movement, and deduce and update the locations of hidden objects. This stage completes the development of object permanence in humans, which takes place during a formational time in which humans are simultaneously learning to walk, speak, and interact with their social and physical environment. Considering the many dramatic changes that occur in these first two years of human development, this begs the question of whether nonhuman primates exhibit a similar early development and where exactly they differ.

The achievement of an errorless A-not-B task is commonly used to measure object permanence milestones, and numerous variations have been used to study brain development in nonhuman primates (Diamond, 1985; Goldman-Rakic, 1985; Greenough & Black, 1992). Rhesus macaque monkeys have a similar brain structure and analogous brain growth to humans (Goldman-Rakic, 1985) and appear to exhibit a similar sequence of object permanence development (de Blois & Novak, 1994; Wise, Wise, Zimmermann, 1974), but many of these studies have focused on small sample sizes of captive individuals either in the first few months or exclusively in adulthood, and they reveal variation in individual rates of development that fails to pinpoint the timing of important developmental shifts.

Rhesus macaques have a shorter life course than humans and develop more quickly, and can achieve stage IV object permanence, where they will attempt to uncover occluded objects, around 2 to 4 months of age (Antinucci, 1990; Cornell, 1981; Munakata et al., 1994). Accordingly, these studies have concluded that one month of rhesus macaque development must be proportional to around four months of human development, though it is unclear how this relationship persists for later stages. Based on this rate of development, rhesus macaques should achieve stage V object permanence as early as 3 to 6 months and stage VI just after that. In this chapter, I focus on multiple tasks evaluating stage V and VI object permanence in the first two years to determine how these cognitive abilities may emerge and develop in a large sample of free-ranging rhesus macaques.

Stage VI object permanence in particular has been a commonly cited point of divergence between human and nonhuman primate development. Previous research has supported that great apes are capable of achieving stage VI object permanence, but there is conflicting evidence that monkeys can exceed stage V (Call, 2000; De Blois & Novak, 1994; De Blois, Novak & Bond, 1998; Dore & Dumas, 1987; Dumas & Brunet, 1994; Mathieu et al., 1976; Natale et al., 1986; Natale & Antinucci, 1989; Parker, 1977; Redshaw, 1978; Schino et al., 1990; Wise, Wise, & Zimmerman, 1974; Wood et al., 1980). De Blois and colleagues (1994; 1998) as well as many others attempted to address whether nonhuman primates can internally represent unperceived motion to pass stage VI object permanence, and they found that adult macaques struggle to track the location of an object when its displacement is occluded. Macaques were successful in visible displacement tasks, where a reward is hidden in a box, that box is moved next to a second box, and the reward is then transferred from the first to second box in full view of the participant. Additionally, participants were equally successful on “no transfer” control conditions, where the boxes move but the reward is not transferred from one box to another, which further confirms that they are not simply searching in the last box that moved. However, in an invisible displacement task, where participants are shown a reward hidden in a small box that is moved into larger box where the reward is dropped and the small box is then revealed to be empty, participants show greater variability in their recovery of the reward from the larger box.

These results support that adult macaques may not be capable of achieving stage VI object permanence at all, though it is unclear why. It has been proposed that rhesus macaques do not possess the capacity to maintain a mental representation of the reward while it is in the container and throughout its unperceived displacement. Though, Filion, Washburn, and Gulledge (1996) claim that rhesus macaques are capable of mental representation and can extrapolate occluded movement in computerized tasks. Several other researchers have also found that many species of monkey can pass invisible displacement tasks that demonstrate at least an intermediate understanding of stage VI object permanence (Mathieu et al., 1976; Mendes & Huber, 2004; Neiworth et al., 2003; Schino et al., 1990; Wise et al., 1974). These conflicting results demand further investigation of the capacity for stage VI object permanence in rhesus macaques, and a closer examination of the cognitive factors that may limit or enhance an individual’s performance.

While a deficit in mental representation most commonly explains the difficulty with invisible displacement tasks, it is inconclusive whether monkeys are completely incapable of mental representation in all scenarios. For one, the experiments conducted by De Blois and colleagues (1994; 1998) found that while adults did not succeed in invisible displacements at above chance levels, they did show improvement over time, which may have been because participants were learning to use other associative rules to complete the task or because they were improving in their efforts to mentally represent the occluded movement. Some researchers have also suggested that monkeys may struggle with invisible displacement due to limitations in memory capacity, but the experiments conducted by De Blois and colleagues (1994; 1998) were careful to include visible, invisible, and no transfer tasks that had a comparable number of steps in order to eliminate potential differences in working memory demands. Additionally, research in humans has shown that 8-month old infants can recall object locations after delays of 70 seconds or longer even when they still exhibit the A-not-B error (Baillargeon et al, 1989; Diamond, 1985; Nelson, 1995; Wallman et al., 1986), which suggests that memory is likely not a central factor of search errors.

Monkeys have also passed other types of occluded search (Anderson, 2012), looking time (Hughes, 2012), and match-to-sample (Kohler et al., 2005; Vauclair, Fagot, & Hopkins, 1993) visuospatial tasks that demand mental representation and manipulation, and looking time tasks in particular appear to consistently reveal cognitive abilities that were not previously thought possible based on search tasks alone. In humans, Baillargeon (1986) found that infants as young 6 months will increase their looking at an impossible object permanence condition that is associated with stage V or VI object permanence even though they are only capable of passing search tasks involving stage III object permanence. These results suggest that the capacity for object permanence may be present, but other factors are interfering with the way infants interact with their environment in practice, and this further emphasizes the need to explore multiple types of tasks and developmental stages.

Other types of displacement tasks have tested search performance following occluded movement. Transposition tasks test the ability to follow hidden objects in linear movement, where a reward is placed under one of many containers and locations are swapped while the platform remains stationary, and apes and prosimians have shown the capacity to successfully pass these occluded transposition tasks (Anderson, 2012; Barth & Call, 2006; Beran & Minahan, 2000; Call, 2003; Roojjakkers et al., 2009). Similarly, rotational displacement tasks test individuals on their ability to follow hidden objects in rotational movement, where a reward is hidden under one of two or three cups in an array, and then the platform is rotated circularly 180 degrees before search. Many species of great ape have exhibited a capacity to pass rotation tasks, but both humans and nonhuman primates struggle with tracking rotational movement without some external cue or landmark (Acredolo & Evans, 1980; Albiach-Serrano, 2010; Barth & Call, 2006; Beran & Minahan, 2000; Beran, Beran, Menzel, 2005; Bremner, 1978; Call, 2003; Collier-Baker, 2006; Haun et al., 2006; Okamoto-Barth & Call, 2008). The difficulty with rotational movement in particular may be due to its rarity in nature, which reveals how the type of displacement and ecological validity of a task can also impact results, and these results also show the ways in which individuals may compensate for this difficulty by incorporating allocentric information.

Piaget (1954) argued that a shift from egocentric to allocentric coding occurs around the fourth stage of object permanence, and that the construction of a referential environment with attention to object-to-object relationships permits the biggest improvements in object permanence. This introduces another important factor to investigate when exploring the interaction of cognitive developmental milestones. The development of allocentric spatial reasoning may interact with shifts in stage IV and VI object permanence tasks. The attention to object relationships also develops in tandem with attention to social relationships and means-ends behaviors, and we must evaluate performance across all of these domains to better understand how overlapping developmental milestones might interact in a nonhuman primate's early development.

Around the ages that human infants are between object permanence stage III and IV, they also begin exhibiting intentional means-ends behavior, and around 7 or 8 months they begin to solve simple problems that involve the deliberate completion of one intermediate action or behavior that will lead to an eventual goal (Diamond, 1985). Piaget (1953) argued that stage IV object permanence, where individuals begin recovering fully occluded objects, requires the ability to hold a goal in mind while completing another step, and that this sequential, goal-directed behavior must require at least a basic concept of causality. Researchers have long used the *support problem* task to investigate the early development of means-ends reasoning across species because it is one of the simplest tests of tool-use understanding (de Mondonca-Furtado & Ottoni, 2008; Hauser et al., 1999; Piaget, 1952; Range, Hentrup, & Viranyi, 2011; Spinozzi & Poti, 1989; Willatts, 1984, 1990; Yocom & Boysen, 2010).

In this task, a reward is placed on the end of a cloth, and while the reward itself is out of reach, the end of the cloth is within reach. The solution to this problem consists of simply pulling the cloth to bring the reward within reach. Humans under 9 months may grab or pull at the support, but this action is not necessarily goal-directed, and may only be a reaction to having an item within hand-reaching distance. Infants around this age are still largely focused on self-other relationships, where they will reach directly for a goal item and may even understand how their actions affect the goal item, but they will not intentionally use another item as an intermediate step to extend their reach to a final goal. When infants begin to fully acknowledge other-other relationships, they can finally understand that interacting with an unattached object or tool is a necessary intermediate step to achieve a final goal of attaining a reward located in a distant space outside of immediate hand-reaching distance (Kowaguchi et al., 2016).

By 12 months, when infants also successfully overcome the A-not-B object permanence error, they begin consistently pulling a cloth support because they understand that the action of pulling will achieve the goal of accessing the object. At this age infants also represent an understanding of causality by consistently refraining from pulling the cloth support when a reward is not in contact with it (Piaget, 1952). The interaction between the development of allocentric, other-other relationships, means-ends reasoning, and object permanence is an important area of focus in evaluating the components of early cognitive development.

Piaget hypothesized that infants should consistently pass means-ends and causality tasks as a prerequisite to achieving higher stages of object permanence, and one study (Matthews et al., 1996) explored the relative role of means-ends reasoning in object permanence development in humans infants using four different tasks: a modified A-not-B task where infants were required to retrieve a reward from one of two covered locations after a delay; a two-location, non-reaching A-not-B task where infants were required only to look at the correct location after a delay; a Barrier Detour task where infants had to retrieve a reward from one side of a transparent box; and a means-ends support problem task where infants were required to pull a cloth support to bring a reward within arm's reach. Older infants tolerated longer delays in the A-not-B task and performed better on the means-ends tasks, but there was little evidence to suggest that performance on the means-ends tasks necessarily influenced performance on the A-not-B tasks and vice versa. Performance on the means-ends tasks improved sharply in the first two months of testing and remained high while performance in the A-not-B tasks improved at a relatively constant rate over the duration of the study. This study was unable to capture a causal relationship between means-ends and object permanence early in human development, but with a small sample size of only 20 individuals ranging from 7 to 15 months, they were also unable to further explore the relationship between these abilities independent of age. Additional studies are required to understand whether nonhuman primates exhibit a similar interaction of developmental milestones that are proportional to development in humans.

Looking time paradigms have also potentially revealed an earlier capacity to use means-ends reasoning to identify and differentiate causal associations in human infants. In one looking time study, Baillargeon, DeVos, and Black (1992) showed that 6-month-old humans were able to differentiate between possible and impossible support problem scenarios. In the possible scenario, infants were shown that an object resting on a platform was successfully retrieved after the platform was pulled, and in the impossible scenario, the object was placed just next to and not touching the platform but was still retrieved after the platform was pulled. Overall, infants looked significantly longer at the impossible scenario over the possible scenario, suggesting that young infants may already possess knowledge to differentiate between physically possible and impossible means-ends sequences as young as 6 months.

These results appear to suggest that much younger infants are equipped to identify impossible object permanence and means-ends scenarios but looking time does not necessarily indicate that younger infants understand exactly *why* these scenarios are impossible and how to execute the same, correct sequences to achieve the same goal (Willatts, 1997; 1999). Infants at 6 months might expect that the movement of a support will move an attached object, but they do not necessarily know what action will bring the object within reach. Even if infants at this age do comprehend the necessary means to an end, they often do not meet the attentional demands of the sequence, and the act of reaching or pulling interferes with their capacity to keep the goal in mind (Bushnell, 1985; Willatts, 1984). Additionally, distant goals and associations are more difficult for young infants to identify and maintain attention to because they are outside of their immediate space (Freedman, 1992). Young infants may succeed in looking time tasks but fail on interactive tasks because they are unable to inhibit their overwhelming desire to reach directly for the reward, and consequently never identify or complete the intermediate step of reaching for the cloth (Baillargeon, 1993). In this regard, it is important to compare looking time and interactive tasks, incorporating multiple domains of object permanence and means-ends reasoning that involve object tracking, spatial relationships, and attention to distal information.

Nonhuman primates also show means-ends reasoning in problem solving and decision-making, but less is known about the development of these abilities. Macaque monkeys appear to identify and differentiate actions based on function, but many of these experiments rely on looking time tasks where participants look longer at an experimenter that is using inefficient or irrelevant actions to attain a goal (Rochat et al., 2008). Spinozzi and Poti (1989) tested a small sample of infant macaques, capuchins, and apes on a support problem task, where participants were given an opportunity to pull a cloth with a reward placed on top and an opportunity to pull a cloth with a reward placed just next to it, and all participants responded by pulling the cloth only when there was a reward in physical contact with it. Additional research in great apes, tamarins, and capuchins had similar results (Albiach-Serrano et al., 2015; Hauser, Kralik, and Botto-Mahan, 1999; Hauser et al., 2002; Weiss et al., 2007; Yocom & Boysen, 2010), though tamarins struggled to solve problems that involved minor changes to the relevant features of the cloth and were only able to improve over repeated exposures. Alternatively, capuchins exhibited an advanced capacity to generalize their knowledge to other variations of the problem. By comparing performance on a battery of tasks in rhesus macaques in their first two years, we can construct a more complete understanding of the early development of these cognitive achievements and interactions in nonhuman primates that exhibit varying degrees of experience with tool use and problem solving in the wild.

While considerable shifts in means-ends behavior and object permanence occur in the first two years, infant attention is also shifting. Eye gaze is a tool that is often used to interpret the perception and intention of another individual and developing attention to these cues is a fundamental aspect in social cognition and theory of mind. Human infants between 2 and 6 months begin responding to head turns and averted eyes, and around 10 to 12 month they exhibit a steep increase in the frequency of their gaze following (Butterworth, 1991; Scaife & Bruner, 1975; Shepherd, 2010). Around 12 months, when humans also begin to achieve stage V object permanence, they also begin following the gaze of another toward target objects and will share attention in visible space. Around 18 months, when humans achieve stage VI object permanence, infants begin following the gaze of another toward objects that are beyond their immediate view (Moll & Tomasello, 2004). This suggests that an improvement in gaze following is consistent with object permanence milestones, where the ability to follow gaze beyond one's immediate view requires the development of a mental representation of a shared goal even when it is out of sight. Geometrical gaze following also introduces successful generalization between allocentric and egocentric space, where attention to triadic interactions incorporates knowledge about self-to-object and other-to-object relationships that are central to spatial cognition as well as the development of object permanence and means-ends reasoning.

Most importantly, there are many subtle distinctions in the development of gaze following, and while humans improve significantly in gaze following in their first year, the ability to judge exactly what another is looking at may not arise until around three years of age (Doherty, Anderson, & Howieson, 2009). This suggests that gaze following has a more complex developmental time course that requires a closer investigation to understand how intimately it is connected with other developmental milestones. There are many developmental mechanisms that interact with the emergence of gaze following. For one, the joint attention abilities that emerge around 10 months in humans also appear to predict the timing of language acquisition (Brooks & Meltzoff, 2005, 2008; Mundy et al., 2007; Tomasello & Farrar, 1986), and poor joint attention skills can predict impairment from autism spectrum disorders (Charman, 2003; Nation & Penny, 2008; Klin et al., 2002). Considering this apparent interaction between gaze following and other developmental mechanisms, it is crucial to explore how this interaction differs across phylogeny.

Thus far, previous research has found that apes and monkeys also respond to head direction, habituate to misleading gaze cues throughout adolescence, and will follow gaze geometrically from eye cues in adulthood, but the onset and development of these abilities as well as the interaction with other cognitive mechanisms is understudied (Shepherd, 2010). Rosati and colleagues (2016) only recently pursued research in the development of gaze following in free-ranging rhesus macaques across the lifespan, and found that while infants will follow experimenter gaze, they are most likely to follow gaze in juvenility. Additionally, rhesus macaques showed trends that were comparable to humans, where older individuals were less likely to follow gaze than juveniles and where females were more likely to follow gaze than males. Given what we know about the complexity of gaze following development and its interaction with other developmental mechanisms, a more detailed comparison of early developmental milestones will help clarify the similarities and differences in the details of human and nonhuman cognitive development.

We know that apes and many species of old and new world monkeys demonstrate the ability to follow gaze geometrically and the ability to use attention cues from both conspecifics and human experimenters (Amici et al., 2009; Anderson et al., 1996; Anderson & Mitchell, 1999; Brauer et al., 2005; Burkart & Heschl, 2006; Itakura, 1996; Povinelli & Eddy, 1996). Additionally, primates in the wild have been known to regularly use gaze to gain information about food sources, social dominance, or threats (Chance, 1967; Emery et al., 1997; Menzel & Halperin, 1975; Povinelli & Eddy, 1996; van Schaik et al., 1983). Some individuals are even known to use gaze information to deceive others, by directing their gaze in the opposite direction of a food source to draw attention away from it (Whiten & Byrne, 1988). In rhesus macaques, many captive studies have shown that adults will follow the head turns and eye gaze of experimenters (Ferrari et al., 2000), and research in free-ranging individuals has illustrated their capacity to encode social stimuli and looking cues and apply them to interpretations of what others perceive (Flombaum & Santos, 2005).

As highly social animals, nonhuman primates also have a highly sophisticated understanding of another's point of view. However, these individuals still appear to fail at using gaze following to solve object-choice and hidden food tasks (Anderson, Montant, & Schmitt, 1996; Hare & Tomasello, 2004; Miklosi & Soproni, 2006; Ruiz et al., 2009), which presents an interesting divergence in early cognitive abilities between humans and nonhuman primates. By comparing performance on multiple search and gaze tasks, we can begin to understand where the development of gaze following interacts with the development of other cognitive mechanisms early in life.

In humans, we have observed an overlap in the emergence of object permanence, means-ends cognition, gaze following, allocentric reasoning, and representational thought in the first few years of life. These dramatic changes early in development appear to collectively facilitate a healthy sensorimotor development that lays the foundation for increasingly complex cognitive abilities that emerge when language and symbolic thought occur between 2 to 7 years of age, when consistent logic emerges between 7 to 12 years, and throughout adolescence and adulthood. While nonhuman primates do not undergo the same advanced stages of language and logic development as humans, there is still considerable evidence to support that nonhuman primates have a comparable early cognitive development and exhibit many of the same cognitive abilities. Many of the studies thus far have only tested nonhuman species on isolated tasks in either the first few months of infancy or well into adulthood.

In this chapter I compare cognitive performance from infancy to juvenility in a population of free-ranging rhesus macaques using multiple cognitive tasks: a gaze following task, support problem tasks assessing means-ends behavior and causal reasoning, and multiple search tasks evaluating stage V and VI object permanence. I also incorporate looking time and search tasks that focus on attention to spatial characteristics and mental representation to determine how these abilities interact with task performance. Using adaptations of methods regularly used to assess these abilities in both human and nonhuman animals (Herrmann et al., 2007), I address 1) when cognitive abilities emerge and develop in rhesus macaques in the first two years of life, 2) how cognitive abilities interact and reflect the cognitive development defined in humans, and 3) how performance on looking time tasks assessing spatial coding and mental representation correspond to performance on interactive tasks from 1 to 2 years.

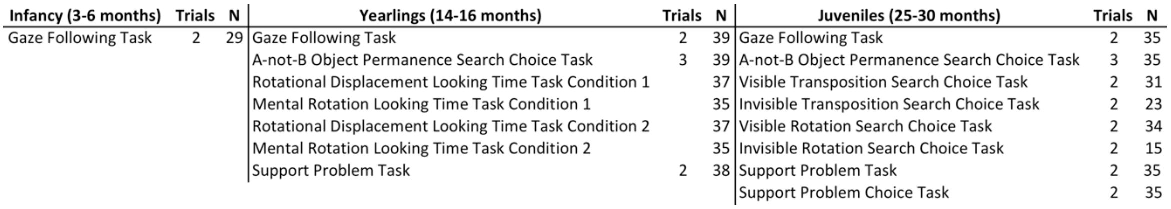
Methods

Participants, Design, and Data Analysis

These data were collected from the same sample of rhesus macaque monkeys evaluated in Chapter 2. The 51 focal individuals were born between July and September of 2013 and randomly selected from three separate groups in the free-ranging population of around 1,500 individuals and seven groups at the Caribbean Primate Research Center on the island of Cayo Santiago, Puerto Rico. Of these 51 individuals, 36 were successfully trapped for testing at 3-6 months of age (infants), 41 at 14-16 months of age (yearlings), and 35 at 25-30 months of age (juveniles). Of those trapped for testing, 4 individuals were only trapped as infants, 3 were only trapped as yearlings, 3 were only trapped as infants and yearlings, and 6 were only trapped as yearlings and juveniles. Only 29 individuals were trapped and tested in all three years, and 35 were trapped and tested as both yearlings and juveniles. Additionally, due to time constraints during testing, not all individuals received all of the tests and not all tested individuals participated. So, while participants were selected from the same pool of 51 individuals, there was variation in sample sizes when comparing within and across individuals, years, and tasks (see Table 3.1). Accordingly, comparisons of overall performance across years relied on proportions of tested and participating individuals, and comparisons of individual performance across years used listwise deletion to only represent those individuals that participated in all relevant tasks.

During trapping and testing, individuals were given 15 minutes to habituate to their 2’ by 2’ by 2’ squeeze cage before undergoing 15-30 minutes of cognitive testing while still in this cage. Due to the infrequency of trapping and the limited time for testing, participants were only exposed to these testing protocols once during each trapping period spaced approximately one year apart. Due to the infrequency and stress associated with trapping, these results may not be representative of all capabilities of rhesus macaques at these ages and may involve a higher frequency of reluctance to participate than cognitive batteries conducted in captive or laboratory facilities. However, the tasks are designed to capture spontaneous reactions and search behavior, and repeated exposures may only measure learned associations over time. Additionally, the tasks conducted were adapted to fit the expected level of participation, attention, and skill for each year. At infancy, individuals were trapped with their mother for the first time in their lives and were separated from their mothers for testing, so these individuals were only exposed to looking time and gaze following tasks and pilot studies for interactive tasks. As yearlings, individuals were primarily exposed to looking time tasks, but a simple A-not-B object permanence task and support problem task were incorporated. At juvenility, individuals were exposed to a more extensive battery of interactive search tasks.

For the duration of the testing period, subjects were recorded with a video camera mounted on a tripod. Every participant was exposed to the same order of task presentation (see Table 3.1), but variation in conditions for each task was randomized for each individual. At infancy (between 3-6 months), participants were first exposed to a *gaze following task* where they were evaluated based on whether or not they followed the head and eye turn of an experimenter. As yearlings (between 14-16 months), participants were given the same *gaze following task* followed by a simple *A-not-B object permanence search choice task* where they received several trials to successfully recover a reward between one of two hiding locations. That same year they were also exposed to two conditions for a *rotational displacement looking time task* and two conditions of a *mental rotation looking time task* (see Chapter 2). Next, individuals were exposed to a *support problem task* where they were evaluated based on whether or not they pulled a support to reach a distant reward. At juvenility (between 25-30 months), participants were first exposed to the same *gaze following task* and *A-not-B object permanence search choice task* followed by a *visible transposition search choice task*, *invisible transposition search task*, *visible rotation search choice task,* and an *invisible rotation search choice task* in which they received several trials to successfully recover a reward in one of two hiding locations after occluded movement. Participants were then exposed the task *support problem task* assessing whether or not they would pull a support to reach a distant reward and a *support problem choice task* assessing whether they would pull the strip in physical contact with a distant reward between two options.



Infancy (3-6 months)	Trials	N	Yearlings (14-16 months)	Trials	N	Juveniles (25-30 months)	Trials	N
Gaze Following Task	2	29	Gaze Following Task	2	39	Gaze Following Task	2	35
			A-not-B Object Permanence Search Choice Task	3	39	A-not-B Object Permanence Search Choice Task	3	35
			Rotational Displacement Looking Time Task Condition 1		37	Visible Transposition Search Choice Task	2	31
			Mental Rotation Looking Time Task Condition 1		35	Invisible Transposition Search Choice Task	2	23
			Rotational Displacement Looking Time Task Condition 2		37	Visible Rotation Search Choice Task	2	34
			Mental Rotation Looking Time Task Condition 2		35	Invisible Rotation Search Choice Task	2	15
			Support Problem Task	2	38	Support Problem Task	2	35
						Support Problem Choice Task	2	35

Table 3.1: **Order of task presentation for each year.** The minimum number of trials each individual received for a given task are indicated in the Trials column and the sample size for each task is indicated in the N column.

Each interactive task trial was baited with a fresh papaya cut into 1” by 1” by 1” pieces. At least 3 of these rewards were used for the A-not-B object permanence task, 4 for the visible and invisible transposition tasks, 4 for the visible and invisible rotation tasks, and at least 2 for the support problem tasks. Task order remained constant across individuals to allow for a more accurate comparison of individual differences in task performance, however, it is important to note that individuals that participated in all tasks may have accessed several rewards and may therefore have been less incentivized by the rewards at end of the cognitive battery.

Looking time tasks were assessed frame by frame (with 60 frames per second, and 600 frames per trial) by a naïve coder using QuickTime Player 7, and differences in trial times were analyzed using SPSS Statistics Software. A paired-samples t-test was used to compare trial and condition looking times across individuals, but a partial correlation was used to reveal a relationship between the continuous looking times for the different conditions. Participants were categorized into different groups based on the consistency of their looking time in each of the conditions and whether they increased or decreased their attention in response to the final test condition (see Chapter 2). Using these groupings, continuous measures of performance and looking time in other tasks were compared using an independent-samples t-test and binary measures of performance and looking time in other tasks was compared using chi squares.

Both the gaze following task and support problem task did not compare correct and incorrect choice, and performance could only be assessed based on varying degrees of participation. Two experimenters evaluated gaze following tasks and independently agreed on the number of times an individual appeared to follow experimenter gaze. Ambiguous trials were excluded. I used a paired-samples t-test to compare the overall frequency of gaze following across all individuals from year to year and a Pearson correlation to further support whether individuals exhibited consistency in their performance across years. I categorized individuals as following gaze if they appeared to follow the gaze of the experimenter in at least one of their trials, and I used a McNemar test to further compare the differences in the overall proportion of individuals that followed gaze from one year to the next and used a chi square to compare to successful and unsuccessful performance on other tasks. Similarly, in the support problem task, individuals were categorized as successfully exhibiting means-ends actions if they pulled the support to access a distant reward in at least one of their trials, but this task did not include an incorrect choice and therefore could only be used to represent degrees of participation based on the total number of trials in which individuals pulled a support.

For search and support problem tasks in which individuals exhibited unambiguous searching and pulling actions, videos were viewed and evaluated by one experimenter, and SPSS software was used to compare overall performance and individual differences in performance. In the search and support problem tasks that included a choice between two options, I used a binomial test to evaluate whether successful search across all trials was above chance (level 0.5). I also used a chi square to compare performance across tasks, where individuals were categorized as "passing" a choice task when they were successful in all of their trials and were categorized as "failing" if they made errors in at least one of their trials or did not attempt any search.

Because the A-not-B object permanence task requires the completion of all three trials (two with the reward in the 'A' location and one with the reward in the 'B' location) to determine whether individuals were making the A-not-B perseverance error, this task was evaluated in multiple ways. Individuals only qualified for stage V object permanence if they successfully located the reward in two consecutive trials when the reward was hidden in location 'A' followed by one trial when the reward was hidden in location 'B.' Individuals were otherwise categorized as qualifying for stage IV object permanence if they successfully located the reward in the same location in two consecutive trials but were unsuccessful in locating the reward when it was hidden in the opposite location. Individuals that did not complete all of their trials or exhibited inconsistent search behavior could not be definitely categorized, but their attempts to search for the reward after occlusion suggests at least basic object permanence, while individuals that did not attempt search in any trials fail to present evidence for object permanence above stage II. Participants were categorically ranked based on this participation and performance, and a Wilcoxon signed rank test was used to determine whether there was change or consistency in participation and performance across trials and years. A binomial test with chance level 0.5 was used to determine whether individuals overall were successful at above chance levels across all trials and therefore confirming at least basic object permanence.

Apparatus and Procedure

Gaze following Task. As infants (3-6 months), yearlings (14-16 months), and juveniles (25-30 months), individuals were tested on a simple gaze following task in which the experimenter first gains the attention of the participant and then uses both head and eyes to look up or to the side for ten seconds each. Each participant was exposed to both conditions and the order of presentation was randomized. Following data collection, two isolated coders watched a video of this interaction to determine whether the participants followed the gaze of the experimenter until an agreement was made. If subjects were thought to have looked in the direction of the experimenter in both conditions, they were categorized as consistent gaze followers.

A-not-B Object Permanence Search Task. As yearlings (14-16 months) and juveniles (25-30 months), individuals were tested on a simple A-not-B object permanence search task used to establish whether participants are capable of reasoning through and recalling the location of an occluded item even when the item is hidden in two different locations. In this task, the participant was shown a reward, and then the experimenter concealed the reward under one of two black cups (location A) that were both approximately 6 inches away from each other. The participant was then given the opportunity to search for the reward. Next, this step was repeated with the reward hidden under the cup in the same location (A). On the third trial, the reward was placed under the opposite cup, and after being revealed in its new location for 5 seconds (location B), the reward was concealed, and the participant was given an opportunity to search (Figure 3.1). Both cups were picked up and set down at the same time so as not to bias the participant to search under the cup that was most recently contacted, and the reward was concealed for a full 3 seconds before the participant was given the opportunity to search.

If participants are able to correctly identify the location of the reward in all three occluded locations, this suggests an understanding of stage V object permanence. Those that are able to correctly identify the location of the reward in the first two locations (A), but not in location B are exhibiting the "A-not-B error" or "perseverative error" associated with stage IV object permanence. These individuals still understand that objects continue to exist when they are occluded and will attempt to search for a fully obscured object, but they demonstrate an incomplete schema where they see the reward and remember where it *was* rather than where it *is*. Participants that do not show consistency in their search behavior and appear to search randomly in location A or B after occluded are considered capable of stage IV object permanence but may still be in a transition phase from stage III to IV object permanence. Individuals that do not search at all may only be capable of stage III object permanence or lower, but it is possible that these individuals are more reluctant to engage in highly interactive search tasks, which is why it is important to compare performance across multiple interactive tasks as well as looking time tasks.

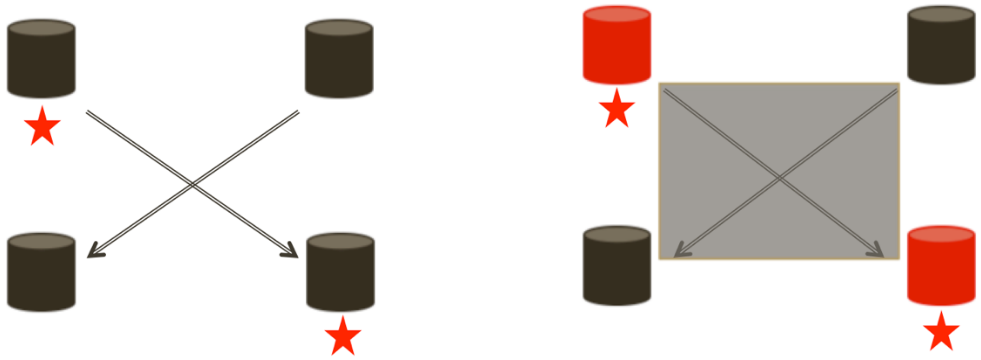
Figure 3.1: A-not-B object permanence search task presentation and participation. Participants were presented with the location of a reward under one of two hiding locations (A) approximately 6 inches apart before being given an opportunity to search for the reward (shown above). In the second trial, this was repeated again with the reward in the same location (A), and in the final trial, this was repeated with the reward under the opposite hiding location (B).

Invisible Displacement Search Tasks. At juvenility (25-30 months), more complex search tasks were incorporated to interpret varying degrees of attention to spatial relationships, tracking occluded movement, and mental representation. Participants were first tested on a visible transposition task where they were shown the location of a reward either on the left or the right for 5 seconds, and then the reward was concealed under one of two black cups that were both simultaneously placed in front of the participant approximately 6 inches apart. Next, the cups were switched in front of the participant so that the reward that was previously concealed under the cup on left was now hidden under the same cup but on the right or vice versa. Participants had full visual access to this switch, which only required that they recall and track the linear movement of the occluded reward. After observing this transposition, participants were given the opportunity to search for the reward, and this task was repeated at least one more time, randomizing the side on which the reward begins (Figure 3.2a).

Next, the original cups were replaced with visually distinct cups (one red and one black), and the transposition task was repeated, but this time the occluded movement took place behind a barrier, so participants would have to visualize the location of the reward under the distinct cup as well as the unseen transposition of that cup and identify the location of the reward using the featural cues of the cup. First, the participant was shown a reward on either the left or right, and then the reward was covered by one of the two visually distinct cups that were positioned approximately 6 inches apart. A barrier was then placed between the observer and the cups, and the cups were then switched so the reward was still hidden under the same color of cup, but on the opposite side. The barrier was then removed, and individuals were given the opportunity to search for the reward, and this task was at least one more time, randomizing the starting location of the reward (Figure 3.2b).

If participants correctly locate the reward in all trials of the visible transposition task, this would support a capacity to track occluded movement in linear displacement that is associated with stage V object permanence. If participants are able to correctly identify the location of the reward in all trials of the invisible transposition task, this suggests that they are attending to and recalling the location of the reward based on featural cues and are capable of mentally representing the occluded movement, which is associated with stage VI object permanence. If participants are unable to correctly identify the location of the reward or appear to search randomly, this would fail to support a capacity for higher order object permanence in rhesus macaques at 2 years of age when the development of this ability should occur as early as 4 to 5 months if rhesus macaques have a cognitive development that is proportional to humans.

If participants are successful in one task but unsuccessful in the other, this would support the accuracy of this assessment and illuminate where differences in development occur. Success in the visible task but failure in the invisible task would indicate that rhesus macaques at this age only exhibit stage V object permanence. If participants are successful in the invisible task but not in the visible task, this may suggest that attention to object features is influencing performance more than tracking and visualizing occluded movement, and this would reveal an interesting use of environmental cues to find a solution to a search task that does not necessarily require stage VI object permanence. Introducing additional tasks assessing participation and performance in different types of movement will help assess these results.



a) Visible transposition ***b) Invisible transposition***

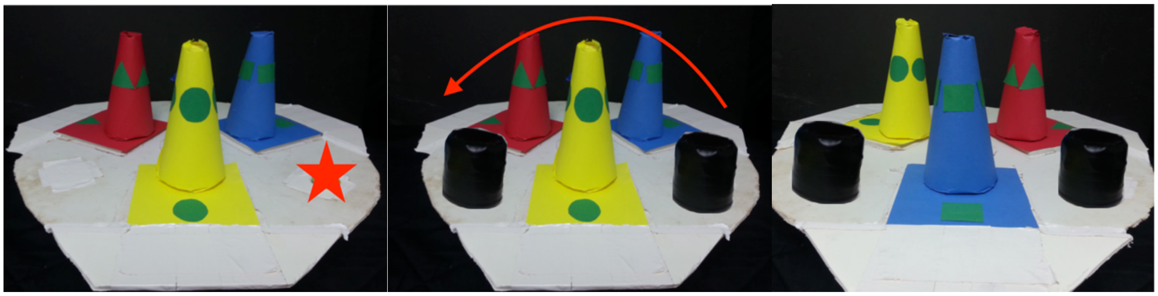
Figure 3.2: Transposition tasks. The star represents the hiding location of the reward. The cups at the top represent the starting presentation. The arrows represent the movement of the cups, with the gray box indicating occluded movement. The cups at the bottom represent the final presentation before search.

As juveniles (25-30 months), individuals were further tested on occluded rotational movement. In the visible rotation task, participants were first shown the location of a reward on the left or right side of the array, between two of three conical landmarks that were each a distinct color (yellow, red, or blue) and were covered in three distinct green shapes (a circle, triangle, or square). Previous research has indicated that rhesus macaques have detection thresholds for all colors that are similar to humans and only slightly higher chromatic sensitivity (Gagin et al., 2014), though colors were selected based on the largest possible differences in wavelength. The three locations between the landmarks were then covered by three different black cups, and the array was rotated 240 degrees to either the left or the right so that the reward was still hidden under the same cup and in the same location relative to the landmarks, but on the opposite side of the array relative to the observer (Figure 3.3). Participants had full visual access to the rotated movement, and only needed to track the rotational movement of the occluded reward before they were given the opportunity to search. This task was repeated at least one more time, randomizing the side on which the reward begins.

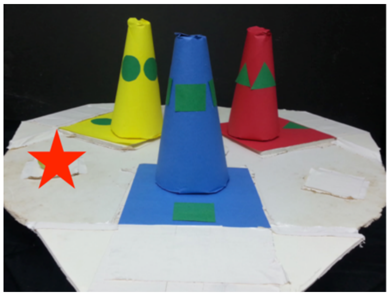
Following this task, participants were tested on an invisible rotation task in which they were first shown a reward between two of the three distinct landmarks in the array, and then all three locations between the landmarks was covered with black cups. At this point a barrier was raised between the observer and the array, and behind the barrier the array was rotated 120 degrees, so the reward was again located under the same cup and in the same location relative to the landmarks, but a different location relative to the observer. When the barrier was raised, participants were given the opportunity to search for the reward, and this task was repeated at least one more time, randomizing the starting location of the reward and the direction of array rotation.

If participants correctly locate the reward in all visible rotation trials, this support a capacity to track occluded movement in rotational displacement that is associated with stage V object permanence. If participants correctly identify the location of the reward in all trials of the invisible rotation, this suggests that they are attending to and recalling the location of the reward based on landmark cues and are capable of mentally representing occluded rotational movement associated with stage VI object permanence. If participants do not search or appear to search randomly, selecting the incorrect location in all or the majority of their trials, this would fail to support the capacity for stage VI object permanence in rhesus macaques at 2 years of age, despite the emergence of this ability in humans of a comparable age. Success in the transposition tasks but not the rotation tasks supports the complexity of rotational movement that is observed in both humans and nonhuman primates that may be due to the absence of rotational movement in nature. Additional tests would be necessary to determine how the perception of rotational movement contributes to early sensorimotor development in nonhuman primates.

If participants are successful in the visible rotation task but not the invisible rotation task, this would illuminate a capacity to track rotational movement and achieve stage V object permanence, but an inability to achieve stage VI object permanence. If participants are successful in the invisible rotation task but not in the visible task, this would present an interesting circumstance where participants are prompted to attend to landmark cues to recall object location only when the movement of the array is unseen. Additionally, if participants regularly search in the last location that they saw the reward relative to themselves, they may be prioritizing egocentric information, and if participants regularly search in the correct location relative to the landmarks in the array, they may be prioritizing allocentric information. If the consistency of this search behavior differs between the visible and invisible rotation task, we could learn a lot about how rhesus macaques change their spatial coding and search strategy according to the amount of movement they observed. Comparing these results to looking time tasks conducted as yearlings (14-16 months), we can better understand how looking time results correspond with search task performance and attempt to better interpret how young rhesus macaques respond to and encode occluded rotational movement and attempt to solve these tasks using egocentric or allocentric spatial information. This will also help to validate consistency in looking time and search task results across developmental stages and testing periods.



Starting Location **Hide and Rotate** **Present for Search**



Final location of reward after rotation

Figure 3.3: Rotational displacement search tasks. The star represents the location of the reward among the three landmarks before all three locations were covered with black cups, and the array was rotated 240 degrees so the reward was now hidden under the cup in the opposite location relative to the observer, but the same location relative to the landmarks in the array. This was repeated for an invisible displacement task where a barrier was placed between the observer and the array before rotation and removed after rotation and before search.

Support Problem Tasks. As yearlings (14-16 months) and juveniles (25-30 months), individuals were tested on a support problem task that assessed means-ends reasoning and attention to distant goals. Participants were first exposed to a reward placed at the end of a cloth strip that was approximately 1 foot long and given 30 seconds to pull the strip to access the reward. Next, a reward was placed at the end of a cloth strip that was 3 feet long, and participants were given 30 seconds to attempt to access this more distant reward (Figure 3.4).

This task is commonly used to assess means-ends behavior, testing whether individuals will attempt the intermediate step of pulling a proximate support to access a distant reward. If individuals consistently pull both strips to attain the reward, this would support the notion that participants are identifying and maintaining attention to goals in increasingly distant extrapersonal space. From this task alone, we cannot determine if the participants understand the full efficacy of their actions, but the fact that they pull the support even when the goal reward is well out of reach indicates that they can focus their attention on a distant goal and execute the necessary intermediate actions to achieve this previously inaccessible reward. If individuals consistently pull the 1-foot cloth but not the 3-foot cloth, this might suggest that individuals are only attempting to access the reward that is just out of reach and unintentionally move the cloth without intention, but do not even identify the more distant reward as an attainable goal.

If individuals did not pull either the 1-foot cloth or the 3-foot cloth, this fails to support that these individuals exhibit means-ends behavior associated with stage IV sensorimotor development in humans. Though, these individuals may simply lose interest or be more reluctant to participate, and only in introducing and comparing performance on other interactive tasks can we better understand this result. Comparing performance on this task to performance in the A-not-B object permanence task can identify whether the concurrent development of these abilities in rhesus macaques is analogous to the sensorimotor stages expressed in humans. Additionally, comparing performance on other tasks that involve object-to-object relationships and attention to distal cues in particular may help evaluate the cognitive mechanisms that are involved in the development of these abilities, and additional testing is needed to further determine whether rhesus macaques understand the causal relationship between the reward and the cloth strip.

Figure 3.4: **Support problem task presentation and participation.** Participants were presented with a reward placed on the end of a 1-ft long cloth strip followed by the reward placed on the end of a 3-ft long cloth strip. In both conditions, the cloth strip was within reach of the participant.

As juveniles (25-30 months), individuals were further tested on a support problem choice task where participants were simultaneously presented with two identical cloth strips approximately 1-foot long. One strip had a reward placed at the end and the other strip had a reward placed just next to its end but out of contact with the strip itself (see Figure 3.5). Participants had 30 seconds to choose which strip to pull to access a reward, and each individual received at least two trials, randomizing the side on which the reward made contact with the strip.

While the previous support problem task compared whether or not an individual would pull a support to reach a distant reward, this task introduces an incorrect option to determine whether individuals understand the functional causality of pulling a strip to access a distant reward. If participants consistently pull the strip in contact with the reward at levels above chance, this would suggest that individuals are indeed choosing based on the causal relationship between pulling the strip and accessing the reward. If participants appear to pull both supports randomly, this would support that individuals are not discriminating a causal relationship between their actions and the goal they are trying to reach and would fail to support that rhesus macaques at this age fully understand the causal connection between the pulling action and consequence.

If participants are successful in the previous means-ends support problem task but not in this causality support problem task, this may still suggest that individuals are able to identify a distant goal and attempt to reach for it, but they just do not understand the full function of their actions and the support relationship between the cloth and the reward. Unfortunately, we can gain little insight from those individuals that do not participate but may understand more about their cognitive processes upon comparing their participation across multiple tasks.

Figure 3.5: Support problem choice task presentation and participation. Participants were presented with two separate 1-ft long cloth strips, where a reward was placed at the end of one of the two strips and a reward was placed just next to the end of the other strip.

Rotational Displacement Looking Time Task. As yearlings (14-16 months), individuals were exposed to two conditions of a rotational displacement looking time task to assess if they primarily coded spatial information in an array of three visually distinct landmarks using allocentric or egocentric cues (see Chapter 2). Subjects were first shown a reward on the right or left between two of the three landmarks, the array was rotated 360 degrees back to its starting location, and looking time was recorded for 10 seconds before a barrier was placed between the observer at the array. When the barrier was removed, the array was rotated a full 360 degrees again, and looking time was recorded for another 10 seconds. Then the barrier was placed between observer and array again. In the *egocentric* condition, the array was rotated 120 degrees behind the barrier and the reward was moved so that the reward now appeared in the same location relative to the observer but a different location relative to the landmarks in the array, then the barrier was raised and looking time was recorded for 10 seconds. In the *allocentric* condition, the array and reward were rotated 120 degrees behind the barrier, so the reward now appeared in a different location relative to the observer but the same location relative to the landmarks in the array. Then the barrier was lifted, and participants were given 10 seconds to inspect the array.

This looking time task was designed to determine whether yearlings were differentiating between possible and impossible rotational movement and establish whether individuals were prioritizing egocentric or allocentric information when this rotational movement is invisible. Participants should decrease looking time from the first to the second identical trial, but an increase in looking time for the final test trial in one condition and a decrease in looking time for the other supports the possibility that individuals are reacting to a violation of expectation in one condition and an expected location in the other condition by prioritizing certain spatial information and making predictions based on either egocentric or allocentric information. By comparing this looking time task as yearlings to similar search tasks as juveniles will help to interpret relationships between looking time and search results and assess the development of these skills within and across individuals.

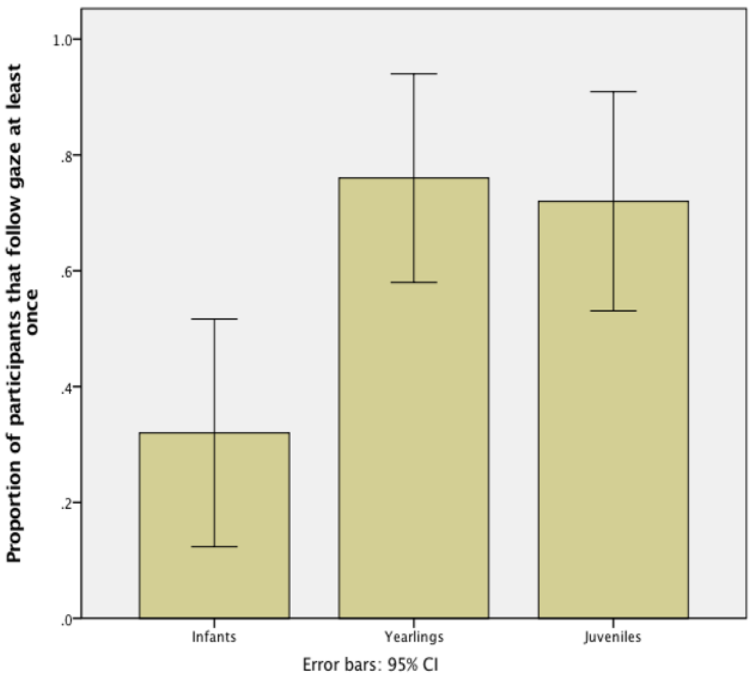


Figure 3.6: Gaze following task results. The proportion of participants that followed gaze at least once when tested at infancy (0.379, N = 29), as yearlings (0.789, N = 38), and as juveniles (0.714, N = 35).

Results

Gaze following

Of the 29 infants tested on gaze following at 3-6 months, 6 (20.7%) appeared to follow the gaze of the experimenter in one of the two trials, and 5 (17.2%) appeared to follow gaze in both trials. The following year, when 38 yearlings aged 14-16 months were tested on the same gaze following test, 23 (60.5%) individuals appeared to follow gaze in at least one of the two trials, while 7 (18.4%) followed gaze in both trials. Using a paired samples t-test, I identified a significant improvement in gaze following from infancy (m = 0.46 times, se = 0.14) to yearlings (m = 0.92 times, se = 0.14); t(25) = -2.483, p = 0.02, showing overall improvement. Using a McNemar test, there was also a significant difference in the proportion of individuals that followed gaze from infancy to their first year (p = 0.013; Figure 3.6). However, there was no obvious consistency among individuals between the two years, where gaze following was not significantly correlated (r = 0.077, p = 0.708). Though, 13 (50%) of the 26 participants tested in both years improved from infancy to yearling, while 7 followed gaze in both years, 5 followed gaze in neither year, and only 2 individuals appeared to decline in their willingness to follow gaze, representing either consistency or improvement across individuals.

The next year, 35 juveniles aged 25-30 months were tested on the gaze following task, and 20 (57.1%) appeared to follow the gaze of the experimenter in at least one trial, while 5 (14.3%) consistently followed gaze in all trials. There was no significant change in the overall frequency of gaze following when participants were tested as yearlings (m = 1.0, se = 0.11) and as juveniles (m = 0.82, se = 0.11); t(33) = 1.139, p = 0.263, and no significant difference in the proportion of individual that followed gaze from infancy to juvenility (p = 0.549; Figure 3.6). Again, gaze following as yearlings and juveniles was not significantly correlated (r = 0.150, p = 0.396), but 20 (58.8%) of the 34 individuals that participated in both years followed gaze in both years, 4 improved, 3 did not follow gaze in either year, and 7 appeared to decline from following gaze as yearlings to not following gaze as juveniles. These results indicate a significant shift in overall improvement from infancy through the first year, but it is possible that participants were less successful at gaze following in infancy due to the stress of being trapped and separated from their mothers for the first time rather than an effect of age.

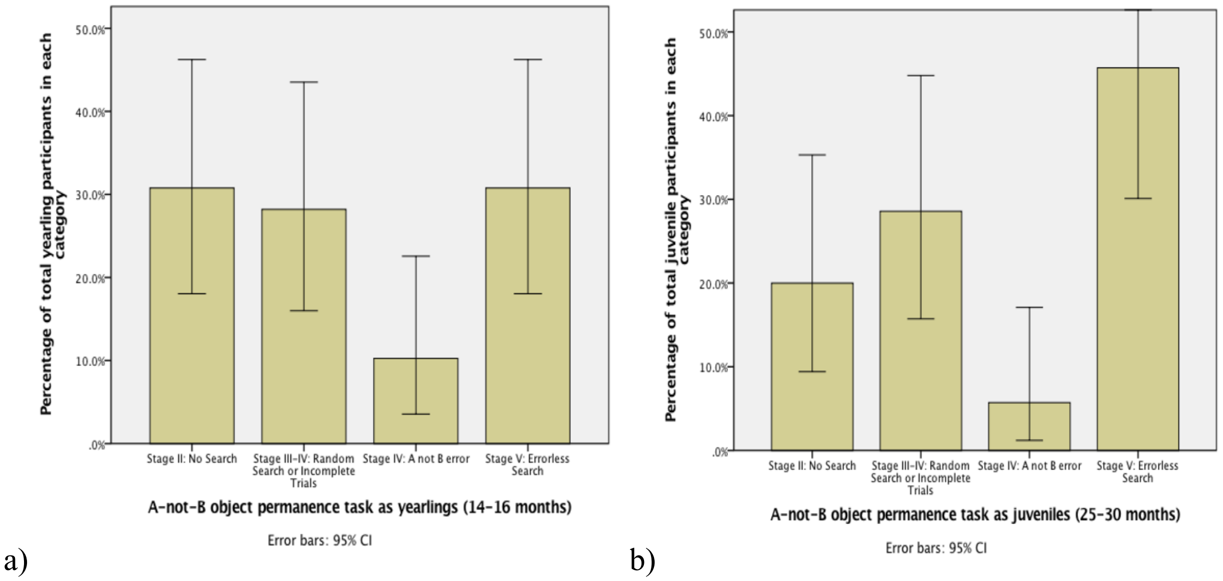


Figure 3.7: Distribution of object permanence stages. Percentage of participants that fell into the categories of stage II object permanence (no search), stage III-IV (random search or incomplete trials), stage IV (A not B error), and stage V (errorless search performance) out of a) 39 tested as yearlings (14-16 months) and b) 35 tested as juveniles (25-30 months).

A-not-B Object Permanence Search Task

39 individuals were tested on an A-not-B object permanence search task as yearlings (14-16 months), and 12 (30.8%) successfully located the reward in all trials without error, consistent with stage V object permanence, while 4 (10.3%) exhibited search behavior that was consistent with the perseverance (A-not-B) error associated with stage IV object permanence (Figure 3.7a). Among the others, 11 (28.2%) appeared to search randomly in both hiding locations or did not complete all of their trials, which may support stage III to IV object permanence, while 12 (30.8%) individuals did not search in any trials. Those that did not search may indicate object permanence ability at stage III or lower, but this is inconclusive, as we cannot know which individuals failed to search because of a reluctance to participate and which individuals failed to search due to another limitation. Only 18 (46.2%) of 39 individuals participated in all three trials, but 12 (66.7%) of those 18 correctly located the reward in all of those trials. Overall, participants

were successful in 50 (73.5%) of the 68 individual trials where search was attempted, which was significantly above chance (binomial test $p < 0.01$), and they exhibited comparable success when the reward was hidden in location A (72.5%) and location B (76.5%), supporting a general capacity for stage IV to V object permanence in these yearling rhesus macaques using an isolated A-not-B task and free-ranging individuals with no previous, repeated exposure to cognitive testing. Still, yearlings only attempted search in 50.7% (68 of 134) of their trial exposures, suggesting a general reluctance to participate, limitations in cognitive ability, or other possible shortcomings of task execution.

It is difficult to interpret the abilities of those that did not search at all, but 8 of the 12 that did not search in any of their trials did approach the testing apparatus and accept a visible reward. This suggests that these individuals may still have been willing participants and failed to search due to other limitations. I also found that overall participation improved slightly with each trial, where 17 (43.6%) of the 39 individuals tested attempted search in the first trial and 21 (53.8%) attempted search on the second trial, and performance also improved with each trial, where participants were successful in 47.1% of searches in the first trial and 90.5% of searches in the second trial. A Wilcoxon signed rank test showed that there was a significant improvement in participation and performance from the first to second trial ($Z = -2.117$, $p = 0.034$), where individuals were ranked from no search to unsuccessful search to successful search, but there was a significant decrease in performance between the second trial in which the reward was hidden in location ‘A’ and the test trial in which the reward was hidden in location ‘B’ ($Z = -2.46$, $p = 0.014$).

As juveniles (25-30 months), 35 individuals were tested on the A-not-B object permanence task, and 16 (45.7%) consistently passed all of their trials, suggesting stage V object permanence while only 2 (6%) exhibited the perseverance error consistent with stage IV object permanence. Alternatively, 10 (28.6%) appeared to search randomly or did not participate in all of their trials, which may suggest stage III to IV object permanence, and 7 (20%) did not search in any of their trials (Figure 3.7b). As juveniles, 24 (68.7%) of the 35 participated in all of their trials, in contrast with the 46.2% that participated in all of their trials the previous year, and 16 (66.7%) of those 24 individuals successfully located the reward in all of their search attempts, which is comparable to the 66.7% that successfully located the reward in all of their searches the previous year. A Wilcoxon signed rank test showed a significant improvement in search and performance in the first trial from yearling testing to juvenile testing ($Z = -2.329$, $p = 0.020$), but no significant improvement in the second trial from year to year ($Z = -0.513$, $p = 0.608$), showing an improvement in the first trial and comparable search behavior in the second trial where the reward was hidden in location 'A.' A Wilcoxon signed rank test also revealed a significant improvement in search behavior in the final test trial where the reward was hidden in location 'B' from the first to second year ($Z = -2.265$, $p = 0.023$).

Overall, participants were successful in 71 (79.8%) of all 89 trials in which search was attempted at juvenility, which was significantly above chance (binomial test $p < 0.01$), and participants exhibited comparable success when the reward was hidden in location A (79.4%) in the first two trials and location B (80.9%) in the final test trial. A Wilcoxon signed rank test showed that there was no significant difference in search behavior and success between the first and second trial in which the reward was hidden in location 'A' ($Z = -0.047$, $p = 0.963$), and no significant difference between the second trial and test trial when the reward was hidden in location 'B' ($Z = -1.155$, $p = 0.248$). Juveniles also attempted search in 89 (71.8%) of the 124 total trial exposures across all 35 individuals, which improved from the 50.7% in the previous year.

All 35 individuals that were tested as juveniles were also tested as yearlings, with 27 individuals participating as yearlings, 28 individuals participating as juveniles, and 21 individuals participating in both years. Using a student's t-test, I found no significant difference in the proportion of correct search choices across the 27 participating yearlings (m = 0.664, se = 0.078) and the 28 participating juveniles (m = 0.779, se = 0.061); t(53) = -1.15, p = 0.128 (Figure 3.8a). Running a paired samples t-test, I also found no significant difference in the proportion of correct search choices across the 21 individuals as yearlings (m = 0.687, se = 0.085) and as juveniles (m = 0.779, se = 0.070); t(20) = -0.956, p = 0.351 (Figure 3.8b). Though, 12 (34.3%) individuals achieved the same level of object permanence in both years and 12 (34.3%) improved in the stage of object permanence they achieved, while 11 (31.4%) appeared to decline in their performance or level of participation from one year to the next.

Results from these isolated A-not-B object permanence tasks as yearlings and juveniles support a general capacity for stage IV to V object permanence in the first year, with an improvement in participation from the first to second year. This supports the prediction that rhesus macaques will develop stage V object permanence around 1 year but presents variation in individual performance.

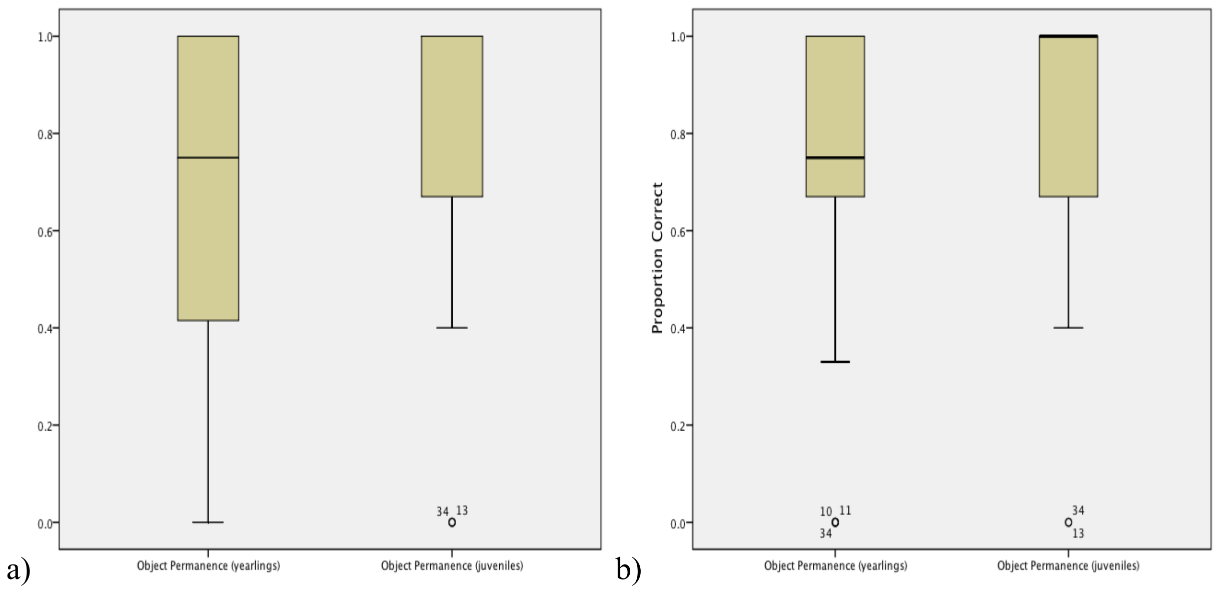


Figure 3.8: A-not-B object permanence task results. Proportion of correct choices across participating individuals as yearlings and juveniles using a) pairwise deletion to represent the 27 participating yearlings and 28 participating juveniles and b) listwise deletion to represent only the 21 individuals that participated in both years. Both years represent successful search at above chance (0.5 level binomial test, $p < 0.01$).

Invisible Displacement Search Tasks

As juveniles (25-30 months), 31 individuals were tested on a transposition search task where a reward was hidden under one of two cups. The two cups were then switched so the reward remained in the original cup and moved with that cup, and while the movement of the cups was fully visible to the participants the reward inside was not. Participants then had the opportunity to search for the reward. In this task, only 4 participants (12.9%) consistently selected the correct cup in all of their search attempts, and 5 (16.1%) consistently searched under the incorrect cup on the side where they last saw the reward in both of their search attempts. 6 individuals did not attempt search in any of their trials, while the remaining majority of 16 (51.6 %) appeared to search randomly in their trial exposures. On average, the 25 participating individuals were successful 47.2% (se = 6.4%) of the time (Figure 3.9). All 31 individuals were tested on 2-3 trials each, but there was variability in individual participation (m = 1.97 trials each, se = 0.31), which made it difficult to determine if individuals differed significantly in their rate of success. I compiled all 86 trials conducted across the 31 individuals tested and found that individuals participated in 61 (70.9%) of the 86 trials and were successful in 28 (45.9%) of those 61 search attempts, which did not differ significantly from chance (50% binomial test, p = 0.7). With these data, we cannot conclude that these juvenile rhesus macaques are solving occluded movement in linear transposition.

Following participation on the visible transposition task, 23 individuals were tested on an invisible transposition search task, where participants observed as a reward was now hidden under one of two color-coded cups, and a barrier was placed between the participant and cups so participants no longer had visual access to the movement of the cups. In this condition, participants were encouraged to visualize this movement and attend to cup features. In this task, 6 (26.1%) individuals searched correctly in all of their search attempts and 4 (17.4%) consistently search in the incorrect location, while 8 (34.8%) appeared to search randomly and 5 individuals did not attempt to search in any of their trials. On average, the 18 participating individuals were successful 52.2% (se = 9.4%) of the time (Figure 3.9). Each individual was tested on 2-3 trials each, but there was variability in participation (m = 1.78 trials, se = 0.23) that made it difficult to determine if individuals differed significantly in their rate of success. Overall, individuals attempted search in 41 (77.4%) of the 53 trials conducted and were only successful at locating the reward in 20 (48.8%) of the 41 search attempts, which did not differ significantly from chance (50% binomial test, p = 1). These results also fail to support that these juvenile rhesus macaques are solving a transposition task using cup features.

34 of the same individuals were then tested on a rotation search task in which a reward was now hidden under one of three cups positioned in a rotating array. The array was rotated so

participants had full visual access to this movement before they were given the opportunity to search for the reward between the two closest cups. 10 (29.4%) individuals successfully located the reward in all of their trials, 6 (17.6%) consistently searched in the incorrect location, 4 (11.8%) individuals appeared to search randomly, and 8 individuals did not attempt to search in any trials. On average, the 20 participating individuals were successful 59% (se = 10.1%) of the time (Figure 3.9). Each individual was tested on 2-3 trials, but there was variability in participation (m = 0.91 trials, se = 0.17) that made it difficult to determine if individuals differed significantly in their rate of success. Overall, I conducted 78 trials and found that individuals only participated in 31 (39.7%) of those 78 trials and were successful in 18 (58%) of those 31 search attempts, which was not significantly above chance (50% binomial test, p = 0.47). According to these results, we cannot conclude that these juveniles are solving occluded movement in rotation.

Next, only 15 individuals could be tested on an invisible rotation search task due to time constraints. In this task, a reward was hidden under one of the three cups among three distinct landmarks, but a barrier was placed between the participant and the array, so the rotation of the array was no longer visible to the participants. This encouraged visualization of the movement and the use of landmark cues to successfully locate the reward. Only 2 (13.3%) successfully located the reward in both of their trials and 4 (26.7%) consistently searched in the incorrect location. 6 individuals appeared to search randomly across their trials and 3 did not attempt search in any of their trials. On average, the 12 participating individuals were successful 40.8% (se = 11.4%) of the time (Figure 3.9). Each of the 15 individuals were tested on 2-3 trials each, but variability in participation (m = 2.33 trials, se = 0.44) made it difficult to determine if individuals differed significantly in their rate of success. Overall, individuals participated in 35

(71.4%) of the 49 trials conducted but were only successful in 14 (40%) of those 35 search attempts, which did not differ significantly from chance (50% binomial test, p = 0.31). Once again, this does not provide any evidence that these juvenile rhesus macaques are successfully tracking and solving occluded rotation search tasks using landmark cues.

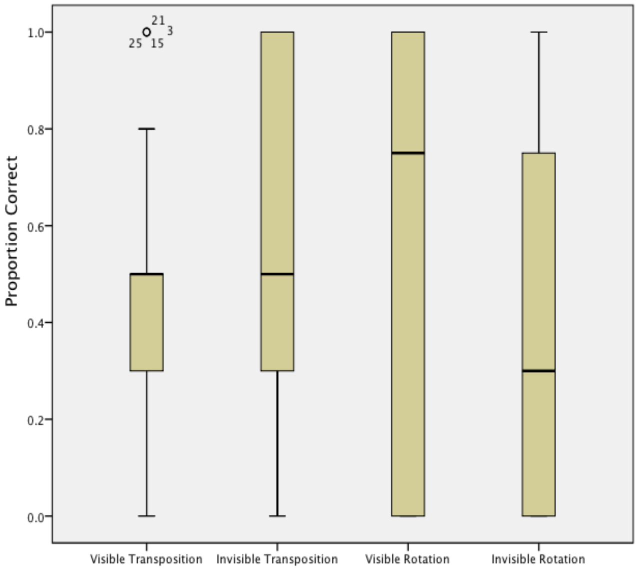


Figure 3.9: Invisible displacement tasks results. Proportion of correct choices across all participating individuals in the visible transposition (N = 25), invisible transposition (N = 18), visible rotation (N = 20), and invisible rotation (N= 12) tasks using pairwise deletion. Distribution represents search at chance (0.5 level binomial test, p > 0.05) for all tasks.

Support Problem Tasks

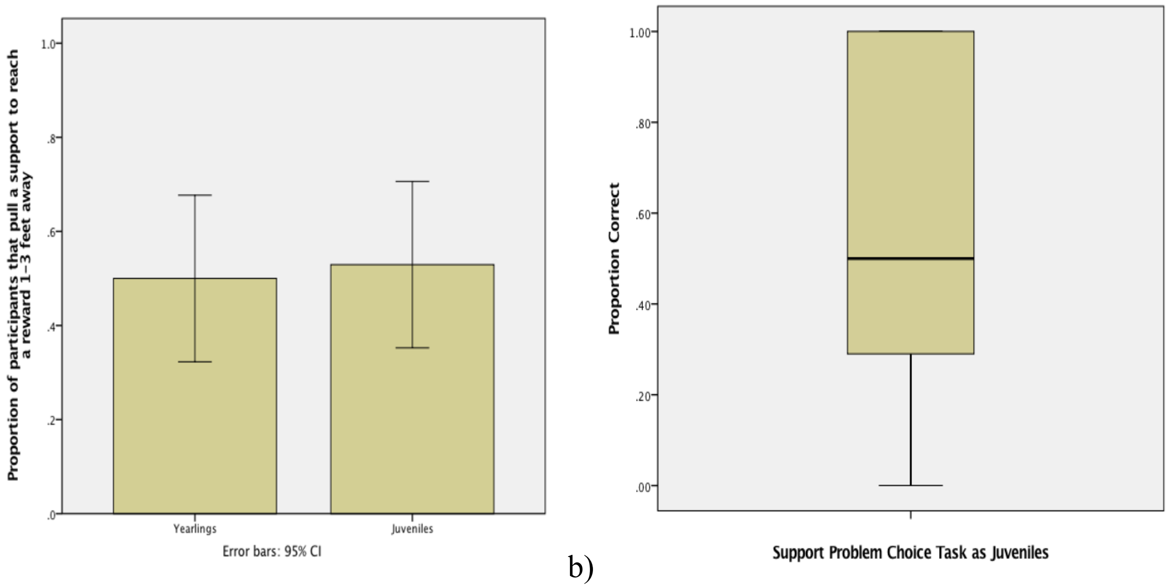
As yearlings (14-16 months), 38 individuals were tested on a support problem task, where subjects were given the opportunity to pull a 1-foot and a 3-foot long cloth strip to access a reward placed at the end of each strip. The majority of individuals (20 or 52.6%) approached and inspected the strip but did not attempt to pull the strip to access the reward in either condition, while 11 (28.9%) individuals pulled up to the 1-foot strip, and 7 (18.4%) pulled both the 1-foot and the 3-foot strip. Unfortunately, 8 of the 11 individuals that only pulled up to the 1-

foot strip were not given the opportunity to pull the 3-foot strip due to time constraints and presentation errors, which limits a comparison of performance by length of support.

As juveniles (25-30 months), 35 of the same individuals were tested on this same task. This time, 16 (45.7%) individuals inspected but did not pull either strip, 5 (14.3%) only pulled the 1-foot strip, and 14 (40%) pulled both the 1-foot and the 3-foot cloth. While I could not compare improvements in the tendency to pull a more distant 3-foot support to reach a reward from one year to the next, I did note that 26 (76.5%) of the 34 individuals that were tested in both years pulled the strip in at least one year, and 19 (73.1%) of these 26 individuals pulled up to the 3-foot long strip, which supports a general capacity to attend and respond to distal objects between 1 and 2 years.

Overall, there was little improvement from one year to the next, where 47.5% of yearlings pulled at least one support and 54.3% juveniles pulled at least one support (Figure 3.10a). 10 (29.4%) of the 34 individuals that were tested in both years pulled a support in both years and 9 (26.5%) did not pull a support in either year. Of the remaining individuals tested in both years, 8 (23.5%) pulled the support as juveniles but not as yearlings, and 7 (20.6%) pulled the support as yearlings but not as juveniles. The majority of participants either improved or remained the same, but it was difficult to interpret ability in this task when it was impossible to determine whether individuals that did not pull a support did so because of a cognitive limitation or because they chose not to participate.

As juveniles (25-30 months), I introduced a support problem choice task to determine whether individuals were choosing to pull a support based on its connection with a distant reward and the causal relationship between pulling the support and accessing the reward. In this task, participants were given an option to either pull a 1-foot strip with a reward at the end or pull a 1-foot strip with a reward placed next to but out of contact with the strip. I tested 35 individuals on 2-3 trials each, but variability in participation (m = 0.971 trials each, se = 0.23) made it difficult to evaluate performance. Only 15 individuals participated in their trials, and on average, these individuals were successful 57.13% of the time (se = 10.51%; Figure 3.10b). Across the 34 trials in which individuals participated, individuals were successful in 19 (55.9%) of trials, which did not differ significantly from chance (50% binomial test, p = 0.61). This low participation rate may be due to the difficulty of the task or because it came at the end of the cognitive battery when individuals were less incentivized to participate, but this task did not provide enough data to determine whether individuals were selecting the causally relevant strip at levels above chance.



a) b)

Figure 3.10: Support problem task results. a) The proportion of participants that pulled a support to reach a reward 1-3 feet away as yearlings (0.474) and as juveniles (0.543). Error bars represent 95% confidence interval. b) Proportion of correct choices in the support problem choice task across 15 participating juveniles (m = 0.571, se = 0.105).

TEST	Age	Testing Sample Size	Participating Sample Size	Total Trials	Trial Participation	Trial Success	Proportion Participation	Proportion Success	BINOMIAL TEST (0.5 LEVEL) P VALUE
Object Permanence	Yearlings	39	27	134	68	50	**0.51**	**0.74**	$**p < 0.01$
Object Permanence	Juveniles	35	28	124	89	71	**0.72**	**0.80**	$**p < 0.01$
Visible Transposition	Juveniles	31	25	86	61	28	**0.71**	**0.46**	$p = 0.7$
Invisible Transposition	Juveniles	23	18	53	41	20	**0.77**	**0.49**	$p = 1$
Visible Rotation	Juveniles	34	20	78	31	18	**0.40**	**0.58**	$p = 0.47$
Invisible Rotation	Juveniles	15	12	49	35	14	**0.71**	**0.40**	$p = 0.31$
Support Problem Choice	Juveniles	35	15	66	34	19	**0.52**	**0.56**	$p = 0.61$

Table 3.2: Cognitive tasks with correct and incorrect choice. Reports the proportion of trials in which individuals participated and the proportion of participating trials in which individuals were successful, binomial test p value is reported for chance level 0.5.

Overlap in gaze following and search and support problem task performance

There was no significant relationship between gaze following and A-not-B object permanence performance as yearlings ($\chi^2 = 1.458$, $p = 0.227$; $p > 0.05$ Fisher's exact test). Though, only 1 (12.5%) of the 8 individuals that did not follow experimenter gaze passed the A-not-B object permanence task without error, while 3 (42.9%) of the 7 that consistently followed gaze in all trials passed the A-not-B task without error. There was also no significant relationship between gaze following and performance on the support problem task as yearlings ($\chi^2 = 2.533$, $p = 0.115$), but again, only 2 (25%) of the 8 individuals that did not follow gaze pulled a support, while 5 (71.4%) of the 7 that consistently followed gaze also passed the support problem task. These relationships are statistically insignificant, but they do show that gaze following consistently favors success on other tasks. As juveniles, there was no relationship between gaze following and object permanence ($\chi^2 = 0.184$, $p = 0.668$; $p > 0.05$ Fisher's exact test) or gaze following and performance on the support problem task ($\chi^2 = 0.184$, $p = 0.184$, $p = 0.668$; $p > 0.05$ Fisher's exact test). As juveniles, the rate of gaze following was comparable whether participants failed or passed these cognitive tests.

Overlap in object permanence and support problem task performance

As yearlings (14-16 months), there was a significant relationship between the performance on the support problem task and the A-not-B object permanence task ($\chi^2 = 8.111$, $p = 0.01$; $p < 0.05$ Fisher's exact test), where individuals that passed the A-not-B object permanence task without error were more likely to pull a strip to reach a distant reward and vice versa, while those that did not pull the strip more commonly made errors or failed to search in the object permanence task. When individuals that did not search at all in the A-not-B task were eliminated from analysis, this relationship disappeared ($\chi^2 = 1.155$, $p = 0.283$, $p > 0.05$ Fisher's exact test), suggesting that this result may have been a function of participation, where a lack of participation in one task corresponds to a lack of participation in the other. When individuals were tested as juveniles (25-30 months), there was no significant correlation in performance between the object permanence and means-ends task ($\chi^2 = 0.60$, $p = 0.439$) regardless of participation.

However, all 6 individuals that consistently pulled the correct strip in all of their support problem choice tasks as juveniles passed the A-not-B object permanence task as both yearlings and as juveniles ($\chi^2 = 13.079$, $p = 0.0003$; $p < 0.05$ Fisher's exact test), and only 1 of the 9 individuals that made errors in the support problem choice task passed the A-not-B object permanence as a yearling and 3 of the 9 individuals passed the A-not-B task as juveniles. This supports a possible relationship between object permanence performance and causal reasoning from one to two years.

Spatial coding in rotational displacement as yearlings and performance on gaze following, object permanence, and support problem tasks over two years

As yearlings, 14 participants were categorized as "allocentric coders" and 10 individuals were categorized as "egocentric" coders based on looking time in a rotational displacement task. In most looking time tasks, an increase in observer looking time from habituation to test trial is interpreted as a violation of expectation, when a view is inconsistent with predictions and prompts greater investigation. In this task, each individual was exposed to an "allocentric" scenario in which an edible reward appeared in an array among three visually distinct landmarks that were then rotated 120 degrees behind a barrier, and when the barrier was lifted the reward appeared in the same location relative to the landmarks in the array, but a different location relative to the observer. Each individual was also exposed to an "egocentric" scenario, in which the array was rotated 120 degrees behind a barrier, but the reward was not rotated with the array, and when the barrier was lifted, the reward appeared in the same location relative to the observer but a different location relative to the landmarks. There were no significant differences in overall looking time between these conditions, but there was consistency within individuals, where the majority of individuals increased looking time in one condition and decreased looking time in the other, independent of the order in which they saw the conditions (see Chapter 2). This suggested that individuals may be consistently identifying one condition as "possible" and the other condition as "impossible" according to a certain spatial coding strategy. Individuals that increase their looking at the allocentric condition and decrease their looking in the egocentric condition may be encoding and predicting the location of a reward based on its relation to self and were therefore categorized as "egocentric" coders, while an increase in looking in the egocentric condition and a decrease in looking in the allocentric condition suggests that individuals may be encoding and predicting the location of the reward based on its relation to landmarks and substrate and were therefore categorized as “allocentric” coders.

Overall, there were no significant relationships between spatial coding and cognitive task performance, but there was still a trend where “allocentric” coders consistently outperformed “egocentric” coders. There was no significant relationship between spatial coding preference and gaze following ($\chi^2 = 0.062$, $p = 0.803$) as yearlings, but 13 (92.9%) the 14 “allocentric” coders followed experimenter gaze at least once, with 4 of these individuals appearing to follow gaze in both trials, while no “egocentric” coders followed gaze in both of their trials. Due to the ambiguity in interpreting gaze following tasks, additional gaze following trials may be required to reveal a significant relationship between gaze following and spatial attention. There was also no significant relationship between spatial coding preference and performance on the A-not-B object permanence task as yearlings ($\chi^2 = 0.697$, $p = 0.404$), but the majority (9 or 64.3%) of the 14 “allocentric” coders participated in the A-not-B object permanence task, and 5 (55.6%) of those 9 successfully passed without error, while only 1 (10%) of the 10 “egocentric” coders passed the A-not-B task without error. Additionally, there was no significant relationship between coding preference and performance on the support problem task as yearlings ($\chi^2 = 2.178$, $p = 0.099$), but 9 (69.2%) of the 13 “allocentric” coders tested pulled a strip to reach a distant reward while only 2 (20%) of the 10 “egocentric” coders pulled the support.

Even more interesting, the categorization of “allocentric” or “egocentric” that was determined from looking time tasks as yearlings appeared to interact with performance on cognitive tests that were conducted in both infancy and juvenility. There was a significant relationship between spatial coding and performance on the support problem task as juveniles ($\chi^2 = 8.025$, $p = 0.0046$), where “allocentric” coders were more likely to pull a support than “egocentric” coders. Additionally, there was a trend where “allocentric” coders were also more likely to follow experimenter gaze at infancy ($\chi^2 = 3.348$, p = 0.067), and no “egocentric” coders ever appeared to follow experimenter gaze more than once. At juvenility, there was no significant relationship between spatial coding and gaze following ($\chi^2 = 0.527$, p = 0.696), but again, no “egocentric” coders appeared to follow gaze more than once. There was no significant relationship between coding preference and performance on the A-not-B task at juvenility ($\chi^2 = 0.4443$, p = 0.5051), but a higher proportion of “allocentric” coders participated in and successfully passed this task.

I also considered how looking time in the egocentric and allocentric conditions might independently interact with performance on cognitive tasks. When exposed to the allocentric condition, 26 individuals appeared to habituate to the first two identical trials, and 10 of those individuals continued to lose interest in the test trial while 16 individuals increased their looking in response to the allocentric test trial. When exposed to the egocentric condition, 30 individuals exhibited successful habituation to the first two trials, and 8 individuals continued to lose interest in the test trial, while 22 individuals increased their looking in the egocentric test trial. Using this approach, I revealed that participants that increased their looking time in the allocentric condition as yearlings also more consistently failed, searched randomly, or did not fully participate in the object permanence task as yearlings ($\chi^2 = 4.399$, p = 0.036) and were less likely to the pull the strip in the support problem task, while those that lost interest in the allocentric condition more often pulled the support ($\chi^2 = 4.996$, p = 0.025). Individuals that increased their looking time in the allocentric condition as yearlings were also less likely to pull the cloth in the support problem task as juveniles, while those that decreased their looking time were more likely to pull the support ($\chi^2 = 4.112$, p = 0.043), but there was no significant relationship between looking time in the allocentric condition and performance on the object permanence task as juveniles ($\chi^2 = 0.75$, p = 0.387).

There was no significant relationship between looking time in the egocentric condition and performance on the A-not-B object permanence task as yearlings ($\chi^2 = 0.016$, p = 0.901) or as juveniles ($\chi^2 = 0.222$, p = 0.638), and there was no significant relationship between looking time in the egocentric condition and performance on the support problem task as yearlings ($\chi^2 = 0.240$, p = 0.624). Though, individuals that increased their looking in the egocentric condition pulled the support at a higher proportion than those that decreased their looking, and this relationship was significant at juvenility ($\chi^2 = 4.299$, p = 0.038). These results support a relationship between spatial coding and cognitive performance, where reaction to the allocentric condition is the best predictor of performance.

Rotational displacement looking time as yearlings and performance on invisible displacements as juveniles

When comparing individuals that were categorized as “allocentric” or “egocentric” spatial coders as yearlings, I found no significant difference in their frequency of success on the visible transposition task ($\chi^2 = 1.4782$, p = 0.2241), but there was a trend for “allocentric” coders to more frequently succeed in the invisible transposition task than “egocentric” coders ($\chi^2 = 3.2401$, p = 0.0719), providing some validation that an increased looking response in the egocentric condition and a decrease in looking at the allocentric condition is consistent with success in occluded movement and attention to object features. When comparing each condition individually, I found no significant effect of looking in the allocentric condition on invisible transposition task performance ($\chi^2 = 0.8936$, p = 0.3445), though individuals who increased their looking in the allocentric condition failed the majority of their invisible transposition trials (8 out of 14 or 57.1%) while those that decreased their looking time succeeded in the majority of their trials (10 out of 14 or 71.4%). Alternatively, when I compared performance based on response to the egocentric condition, I found a significant relationship where individuals that increased their looking in the egocentric condition were more successful in the invisible transposition task ($\chi^2 = 4.6089$, $p = 0.0318$), supporting that individuals that reacted to the egocentric condition as a violation of their expectation might be better at tracking occluded movement at least one year later.

The rotation search tasks conducted at juvenility were almost identical to the rotational displacement looking time tasks received as yearlings, providing ideal conditions to compare looking time and search task performance. However, participation in these tasks was low, and only 9 "allocentric" coders and 4 "egocentric" coders participated in the visible rotation task, and only 3 "allocentric" coders and 1 "egocentric" coder participated in the invisible rotation task. There were no significant differences in performance by looking time for the egocentric or allocentric conditions, which is inconclusive but may reveal an interesting difference in how individuals react in a looking time paradigm compared to how they behave when given the opportunity to search. The fact that "allocentric" coders do not clearly outperform "egocentric" coders in an identical search task may also indicate an error in how looking time results were interpreted. Nevertheless, sample sizes were too small to make any definitive conclusions, and it is necessary to conduct repeated measures at multiple developmental time points to determine if and when rhesus macaques are capable of solving these transpositions and rotation tasks and what cues they use in the process.

Discussion

This ambitious cognitive battery sought to measure and compare performance in object permanence, means-ends reasoning, spatial attention, mental representation, and joint attention in a population of free-ranging rhesus macaques for the first time. Each individual was tested in isolation once in infancy between 3 to 6 months, once as a yearling between 14 to 16 months, and once in juvenility between 25 and 30 months, and there was no precedent for how willing individuals would be to participate or how accurately the tests would represent their abilities. While there was a great deal of variability in participation and performance, these methods did appear to successfully capture interesting details of emergence and overlap in cognitive development.

I predicted that the emergence of object permanence, gaze following, and means-ends abilities would develop similar to humans and be present in infancy and improve over the first year. In infancy, only 37.93% of the 29 tested individuals appeared to follow experimenter gaze at least once, and this improved to 78.95% of the 38 individuals that were tested as yearlings and was maintained over testing in juvenility, suggesting improvement and proficiency over the first year. Additionally, the fact that younger infants less frequently followed experimenter gaze supports a shift in the gaze following ability in the first few months, when rhesus macaques are known to undergo many cognitive and motor developmental transitions. Unfortunately, I did not introduce additional search, problem solving, and looking time tasks until the end of their first year, which meant that I could not compare overlapping abilities around 3 to 6 months of age.

When I first introduced an A-not-B object permanence task when individuals were between 14 and 16 months, only 30.8% were completely error free in their A-not-B object permanence task, which improved to 45.7% in their second year. Though, there was no difference in success across participating individuals, suggesting that individuals only improved in their rate of participation, but did not exhibit a significant improvement in performance between their first and second year. Overall, participants exhibited successful stage IV to V object permanence at object chance in both years.

As juveniles, participants were exposed to more complex invisible displacement tasks in an effort to evaluate a transition into stage VI object permanence. Unfortunately, few individuals attempted search in these tasks, which may have been due to their difficulty or because they came at the end of the cognitive battery when individuals were less attentive and incentivized. Accordingly, I only evaluated performance in those individuals that attempted search, and found that on average individuals were only successful in 47.2% (N = 25, se = 6.4%) of their visible transposition tasks, 52.2% (N = 18, se = 9.4%) of their invisible transposition tasks, 59% (N = 20, se = 10.1%) of their visible rotation tasks, and 40.8% (N = 12, se = 11.4%) of their invisible rotation tasks, which did not significantly differ from chance. These null results fail to support the notion that participants were solving these particular invisible displacements and do not provide evidence for stage VI object permanence at 2 years of age. More time for repeated trials and more opportunity to control for delays between hiding and searching could reveal more accurate results. Of course, this is a limitation of working in a free-ranging population, which offers a more natural alternative to working with individuals raised in captive environments at the cost of less time and flexibility in testing conditions. Despite considerable room for improvement, these results still notably provide evidence of successful participation and performance in a battery of cognitive tests in young free-ranging individuals with no previous training or exposure, which introduces reliable, spontaneous methods for future cognitive testing in wild and free-ranging populations.

When the same individuals were tested on a simple support problem task as yearlings and juveniles, a comparable number of individuals attempted to pull a support to access a distant reward when they were yearlings (47.4%) and when they juveniles (54.3%), which does not indicate that an overwhelming majority consistently pulled a support as yearlings or juveniles, but these proportions are difficult to interpret as this task only compares whether an individual will participate and pull a support and not whether they can successfully pull a causally relevant support given a correct and incorrect choice. When I introduced a choice task at juvenility, only 15 individuals participated, and they were only successful 57.1% (se = 10.5%) of the time. This fails to support that individuals were fully competent in their means-ends reasoning and identification of causal relationships at juvenility, which may also indicate that participants in the support problem task were reaching for the reward without any recognition of the efficacy of their actions. However, it is important to note that this does not necessarily indicate a complete lack of capacity for means-ends abilities at this age. Rhesus macaques are not known for their use of tools, and the act of searching that is used in object permanence tasks is more ecologically salient than pulling a support to reach a reward. The fact that 27 (71.1%) of the 38 individuals tested pulled a support in one or both years indicates that regardless of their comprehension of causality, these young rhesus macaques can attend to distant goals and initiate intermediate, goal-directed actions to attempt to access those goals. A more ecologically relevant test of means-ends reasoning might better evaluate the emergence of these abilities at a younger age, when individuals are beginning to exhibit many other complex cognitive abilities. These results could also be improved with more time for repeated exposures.

While these data provide inconclusive results in gaze following, object permanence, and means-ends reasoning early in rhesus macaque development, we do see that many individuals participate in and solve these tasks. This provides an opportunity to compare the emergence of abilities across and within individuals as well as the relationship between these abilities. The tendency to follow gaze was not significantly correlated with performance in object permanence or support problem tasks, but individuals that clearly followed gaze in all of their trials also appeared to do better on these tasks as yearlings. Though, these results are inconclusive due to the difficulty in interpreting subtleties in gaze following. Participants were only evaluated based on two gaze following trials a year, and gaze following cues can be difficult to detect. Like the support problem task, the gaze following task does not provide a comparison between a correct and incorrect option, and it is therefore difficult to interpret whether an individual is not following gaze because they lack the capacity or because they are simply distracted. Still, this introduces an interesting relationship between attentiveness to one's environment and performance on additional tasks. At juvenility, there was no relationship at all between gaze following and performance on other tasks, which may also indicate that the role of gaze following is more apparent at an earlier, developmental stage. Supplemental testing in repeated gaze following tasks with correct and incorrect options can better reveal the role of gaze following and attention in cognitive transitions. I also found a significant relationship between performance on the A-not-B object permanence task and the support problem task as yearlings and a significant relationship between the A-not-B object permanence task and the support problem *choice* task at juvenility, which supports the prediction that a capacity for means-ends reasoning may indeed be related to more advanced stages of object permanence early in rhesus macaque development.

Finally, I compare whether attention to spatial relationships in the first year interacts with performance across cognitive tasks. I found that individuals the appeared to attend to allocentric information to identify an “egocentric” scenario as a violation of expectation and an “allocentric” scenario as consistent with expectation also performed better at object permanence and means-ends tasks up to a year after the spatial coding looking time task was conducted. Participants that were designated “allocentric coders” as yearlings were more likely to pull the strip in the support task and successfully recover the reward in the invisible transposition task as juveniles, and there was a trend where individuals that followed experimenter gaze as infants were also more often designated “allocentric coders.” These relationships provide some validation for the interpretation of looking time measures that support the prediction that the emergence and capacity of allocentric reasoning is positively correlated with cognitive performance in early development.

These novel methods produced significant results that were consistent with predictions, but they could certainly be improved in many ways. For one, the looking time tasks were only presented at one year due to time and testing restrictions, which eliminated a comparison of looking time across years. Additionally, the looking time tasks would have benefitted from additional controls and preference conditions that would more accurately evaluate baseline attention and discrimination between the two conditions. Cognitive testing took place between 3-6 months, 14-16 months, and 25-30 months because these were the only ages at which individuals could be trapped for isolated cognitive testing, but this battery would certainly benefit from more frequent and consistent testing in early development to more accurately measure the gradual emergence of these cognitive milestones and the relationships between them. Despite the limitations inherent in this testing protocol, these procedures do present reliable spontaneous measures that could not be achieved if individuals received regular testing.

Overall, these results support a relationship between cognitive abilities in rhesus macaques over their first two years, which also provides evidence that rhesus monkeys and humans undergo a similar sequence of early cognitive development. Though, the rate of acquisition may not be proportional, as rhesus macaques may still show improvement on object permanence and spatial attention into juvenility. Humans also undergo a very different rate of motor development, in which they transition from sitting to standing to crawling to walking in tandem with many of these cognitive milestones, including the emergence of language and symbolic thought. In contrast, macaques go through several stages of weaning, but are proficiently locomotive soon after birth and do not develop language. It is possible that this divergence in early experiences and developmental milestones lay the foundation for divergence in the development of cognitive abilities. In the following chapter, I will address how early experiences and environmental factors can influence the emergence of cognitive abilities in the lives of young rhesus macaques.

Chapter 4

The role of motor experience and the maternal-infant dynamic on cognitive development in rhesus macaques in their first year

Abstract

In humans, the onset of self-propelled, independent locomotion appears to facilitate many shifts in spatial cognition. Regardless of age, locomotor infants consistently outperform prelocomotor infants in multiple tasks, and major milestones in object permanence and means-ends reasoning correspond to notable shifts in motor development. Rhesus macaques exhibit comparable transitions in cognitive development, but an earlier onset and a different sequence of locomotion development, which begs the question of whether rhesus macaques exhibit any relationship between motor and cognitive development early in life.

Maternal weaning behaviors can also mediate motor experience and cognitive development, where the duration, frequency, and onset of maternal abuse and rejection can impact infant both independence as well as an infant's long-term stress physiology. To investigate the strongest impacts on rhesus macaque cognitive development, I address 1) how activity and maternal-infant dynamics change and interact over the first year, and 2) how these shifts in independent activity and maternal-infant interaction correspond with notable shifts in cognitive performance and participation over the first two years.

Individuals that were designated as "allocentric" spatial coders based on their looking time at 14 to 16 months exhibited less independent movement and less frequent instances of breaking contact, reestablishing contact, and leaving the proximity of their

mothers in the first year than “egocentric” spatial coders. This is counter to the prediction that more frequent independent locomotion will improve attention to allocentric spatial relationships. Though, “allocentric” coders also experienced significantly less maternal abuse and rejection than “egocentric” coders in their first year, which indicates that there may be an interaction with the early socioemotional environment that is independent of the influence of motor experience.

Individuals that pulled a support to reach a distant reward in a means-ends task and individuals that attempted search in the A-not-B task in the first year experienced significantly less maternal abuse and rejection in their first few months than those that did not participate at all, which further supports an interaction between premature weaning behaviors and response to novel environments a year later. Further, those that consistently passed the A-not-B task and qualified for stage V object permanence in their first year of exposure did exhibit more independent locomotion and social play than those that searched randomly, but no difference in early maternal abuse and rejection.

Together, these results support a dynamic interaction between early maternal abuse and rejection, independent movement, and spatial cognition, where maternal weaning and independence appears to correspond with an “egocentric” attention, and where early maternal weaning can negatively impact participation in tasks, while independent movement and play may still impact successful performance in a search task.

Introduction

Without question, independent mobility exposes infants to a great deal of new information about their environment, but it is unclear how motor development facilitates shifts in cognitive development (McNamara, 2008). Previous research has provided evidence that locomotor status interacts with the way infants process visual input and solve spatial search tasks, but the mechanisms underlying changes in search patterns are not fully understood. By studying the interaction of early locomotion experience and cognitive development in nonhuman animal subjects, we can understand the range of factors that may be involved in this early developmental period and clarify the strength of their impact on cognitive development.

One of the most robust findings on the influence of locomotion experience is the emergence of a wariness of heights. Human infants with locomotor experience show significantly greater cardiac acceleration than prelocomotor infants when they are lowered into the deep side of a visual cliff (Bertenthal & Campos, 1990; Campos, Bertenthal, Kermoian, 1992). Additionally, only individuals with *active* locomotor experience appear to develop an avoidance of heights, while those who are carried or pushed in a stroller but have no control over their motion do not (Hein, Held, Gower, 1970; Held & Hein, 1963). Furthermore, infants that have not yet developed the ability to crawl or walk on their own and are given motorized control over their mobility also develop an increased wariness of heights (Dahl et al., 2013), indicating that this is not a shift that corresponds to age or other cognitive factors, but a shift that is cultivated by self-propelled locomotion experience. Additionally, this research shows that a wariness of heights does not need to develop following a series of falls that condition infants to be fearful. Independent locomotion itself changes how individuals perceive and react to optic flow and facilitates the development of visual proprioception, which is an individual's sense of the relative position of their body and the effort required to move it.

Optic flow is the pattern of apparent motion of objects in a visual scene caused by the relative motion between an observer and that scene (Mahbub et al., 2011). When an individual is locomoting independently, they must be able to successfully differentiate between central and peripheral optic flow, and increased locomotor experience shifts their exposure and attention to optic flow in order to control posture and spatial perception in mobile situations. As in earlier findings, individuals with more locomotor experience exhibit greater responsiveness to peripheral optic flow and exhibit more postural stability over a dynamically changing base support than prelocomotor individuals (Higgins, Campos, Kermoian 1996; Uchiyama et al., 2008; Witherington, Campos, Kermoian, 1995).

Once vision and movement are coordinated, infants are able to construct more accurate perception of depth and distance. The visual system of prelocomotor infants is only skilled at distance perception within a limited range of 1 to 2 meters from themselves, but locomotor experience can help calibrate distance information beyond this limit by introducing a dynamic perspective and demanding attention to previously ignored distal information (Berti & Frassinetti, 2000). Moving over large distances allows infants to build three-dimensional representations of space and objects in their environment, and they can consequently make more accurate judgments of depth and distance based on motion parallax. In contrast, prelocomotor infants possess only a static, monocular perspective and consistently determine distance exclusively by object size relative to themselves (Thomas & Crow, 1988). Self-movement supports shifts in attention from near to far space and from self-centered to more environment-centered perspectives, but it is difficult to determine precisely how motor development facilitates cognitive development after the onset of locomotion, when individuals experience so many changes across multiple domains.

Functional locomotion is intimately connected with spatial cognition as one must continuously orient themselves to an external environment, encoding past and future routes and destinations, and recalling where objects are located or hidden (Clearfield, 2004; McKenzie, 1990). One pivotal milestone in cognitive development that is linked with locomotion experience is the acquisition of *object permanence*. Understanding this concept shows that an infant can reason about objects and people as having a separate, permanent existence that can be mentally represented even when the objects is out of view. This exemplifies a major transition in an infant's understanding of spatial relations. Research using looking time paradigms has shown that human infants as young as 3.5 months of age have a rudimentary understanding of object permanence (Baillargeon & DeVos, 1991). However, human infants do not manually search for a fully hidden object until around 9 months of age and undergo many dramatic improvements in object permanence abilities over the first two years (Piaget, 1954).

Early transitions in object permanence have been tested using an A-not-B task in which infants retrieve an object hidden at one of two locations (location A), and then must locate the object when it hidden in the other of the two locations (location B). The infant sees the object move to its new location, but infants around 9 - 12 months or younger still frequently make the error of looking in the first hiding spot (location A).

This phenomenon distinguishes stage IV and stage V object permanence, where individuals with stage IV object permanence consistently make this “perseverance error,” while individuals with stage V object permanence do not. The transition from random search behavior and perseverance errors to consistent success in the A-not-B task may occur because of an improvement in spatial memory or inhibitory control with age, but it also corresponds with improvements in hand-eye coordination, increased curiosity and attention to novelty, improved means-ends logic and intentional behaviors, and notable shifts in motor development (Piaget, 1954).

To investigate whether these shifts in motor development actually interact with shifts in object permanence, researchers showed that infants with hands-and-knees and walker-assisted locomotor experience outperformed prelocomotor infants on search tasks independent of their age (Horobin & Acredolo 1986; Kermoian & Campos 1988; Smith et al., 1999). Additional studies have also shown improved spatial search scores based on the quality and length of independent locomotion, where hands-and-knees crawlers also outperform belly crawlers. This suggests that the type and quality of locomotion experience after onset may continue to influence an individual’s ability to track and recall the movement of hidden objects in an array. Additionally, infants who were delayed in locomotion by two to four months also exhibited developmental delays in the A-not-B task and improved dramatically as a function of their locomotor experience (Campos et al. 2009; Tao & Dong, 1997), further supporting an intimate relationship between locomotor experience after onset and shifts in spatial cognition development.

Piaget (1954) was also the first to propose that infants that more commonly make the A-not-B perseverance error may be doing so because they are encoding the position of the objects egocentrically (relative to their self) rather than allocentrically (relative to other stable environmental features), which has been connected with locomotor experience. As stated, stationary, prelocomotor infants maintain an egocentric perspective of space, and as they begin to locomote, they can build a more dynamic, allocentric perspective. The egocentric spatial coding system can be initially more efficient when avoiding or reaching for objects in near space, but allocentric representations allow an individual to recognize objects and scenes relative to each other and make more accurate identification of a space from multiple perspectives and distances (Campos et al, 2000). As individuals gain locomotor experience, they may continue to apply both egocentric and allocentric strategies to their environment based on context (Bremner 1978; Burgess, 2004, 2006; Milner & Goodale, 2008), but allocentric representation only emerges with exposure to multiple perspectives and is crucial for more complex search tasks.

Complex allocentric and egocentric referencing has been tested by introducing landmark cues to spatial search tasks and observing how they affect successful recollection and navigation in a changing environment. Researchers introduced position constancy tests to evaluate an individual’s ability to update their perspective and find an object or location following a shift in their spatial relation to that object or location. Bai & Bertenthal (1992) found that prelocomotor infants had more difficulty recalling the location of an object when they were moved to a different vantage point than locomotor infants. When researchers introduced a different type of displacement search task where the array rotated relative to the observer rather than moving the observer relative to the array, even locomotor infants began to fail at this task (Barth & Call, 2006; Okamoto-Barth & Call, 2008). Only with visual access to the displacement and landmarks in the array, did locomotor infants improve (Bremner, 1978; Lasky et al., 1980; Okamoto-Barth & Call, 2008), and the capacity to apply landmark cues was strongly correlated with an individual's age (Acredolo & Evans, 1980; Crowther, Lew, Whitaker, 2000; Lew, Bremner, Lefkovitch, 2000). Still, more research is necessary to determine whether shifts in spatial reorientation and attention was affected by the locomotor status achieved at a given age. Some research has also suggested that infants are capable of using simple allocentric spatial coding strategies prior to the onset of independent locomotion, but these more complex applications in spatial search tasks only emerge later in development (Acredolo, 1978, 1995; Bremner, 1993; Bremner & Bryant, 1997; Lepecq, 1990; Piaget, 1954).

Locomotor experience also influences how and why an individual directs their attention, which may influence spatial coding and the improvements seen in search tasks over time. Locomotion demands attentiveness to distal events and spatial relationships, and infants with locomotor experience more commonly direct their attention to objects, people, and motion in distant space than prelocomotor infants that tend to look at nothing in particular (Freedman, 1992; Gustafson 1984), though there have been no significant distinctions based on the quality of locomotor experience after onset. Locomotor infants also maintain a longer attention span in general than prelocomotor infants (Acredolo, Adams, Goodwyn, 1984; Acredolo, 1985; Horobin & Acredolo, 1986).

As stated, prelocomotor infants do not engage in goal-directed movement and behavior, and therefore have little need to maintain a specific focus of attention. Locomotion is an inherently goal-oriented activity, where individuals must achieve intermediate actions to reach a destination (Diamond, 1991). Accordingly, the onset of locomotion also cultivates more efficient detection and discrimination of relevant information and means-ends reasoning (Smith et al., 1999; Thelen et al., 2001). Additionally, locomotor infants are not only more successful than prelocomotor infants in search tasks, they also exhibit a greater tolerance for delays in hiding and recovering an object regardless of age, which is also crucial aspect of means-ends behaviors that require that one maintain a goal as they attend to intermediate actions (Herbert et al., 2007; Tao & Dong, 1997).

Furthermore, locomotion experience not only interacts with current cognitive development, it may also impact future development. Oudgenoeg-Paz et al. (2014) found that the amount of spatial exploration in infancy predicted the spatial memory of children four to six year later. The impact of locomotion onset and experience is indisputable, though we still do not know how these developmental milestones interact in a species with a comparable early cognitive development to humans, but a different locomotive development, where infants are fully mobile within the first few days of birth and only exhibit quadrupedal locomotion rather than a range from crawling to walking bipedally.

In the first 5 months, human infants are completely prone and reliant on their caregivers and are not even capable of lifting their head until around 1.5 months (Adolph, 2013). Around 2 months, infants begin using their arms for support and by 4 to 5 months they can roll over on their own. It is not until 6 months that infants are able to sit up without support and not until 8 to 10 months that they begin crawling. Around 9 to 12 months, they can pull themselves up, stand with the aid of a support, and use a support to move around a space, and by 15 months infants finally establish locomotive agency. Even still, it is not until 2 years that humans can run and jump, 3 years before they can balance and catch a projectile, 4 years before they can climb, and 5 years before they have the motor coordination to swim. With such a long period of gross motor development and variation in the onset, quality, and duration of these motor milestones, humans are an ideal species in which to compare the cognitive abilities of prelocomotor and locomotor stages. However, we cannot establish a relationship between motor and cognitive development using humans alone, and we must compare these relationships in multiple species to understand how multiple factors may impact interactions in early development. Humans diverge from most other primate species in their bipedal locomotion, in their cognitive repertoire that includes complex problem solving, mental representation, and language and learning, and in both qualitative and quantitative differences in populations based on cultural identity.

Rhesus macaques live approximately 25 years in contrast to the 80-year average lifespan of humans. They develop more quickly and begin searching for occluded objects around 2 to 4 months age (Antinucci, 1990), while most human infants begin showing this ability around 8 months of age (Piaget, 1954). Adult rhesus macaques are known to successfully track objects through movements, disappearances, and different angles of approach, and exhibit the same sequence of object permanence development as humans, including successful stage V object permanence where individuals do not make the A-not-B perseverance error, and potentially stage VI where they can solve invisible displacements (Call, 2000; De Blois & Novak, 1994; De Blois, Novak & Bond, 1998; Dore & Dumas, 1987; Dumas & Brunet, 1994; Mathieu et al., 1976; Natale et al., 1986; Natale & Antinucci, 1989; Parker, 1977; Redshaw, 1978; Schino et al., 1990; Wise, Wise, & Zimmerman, 1974; Wood et al, 1980). Rhesus macaques exhibit means-ends reasoning and have been observed pulling a support to access a distant reward even without any experience with tool use in the wild (Rochat et al., 2008; Spinozzi & Poti, 1989). While rhesus macaques exhibit a fairly analogous, accelerated cognitive development to humans, they are fully locomotive only a few days after birth, which introduces an opportunity to explore how motor experience continues to interact with cognitive development after the onset of locomotion. This also provides an opportunity to explore other factors that might manage cognitive development so that we can construct a more complete understanding of the dynamic systems interacting early in development.

Rhesus macaque infants can be fully locomotive shortly after birth, but they still exhibit a period of maternal attachment where they spend the majority of their time in contact with their mother and display variation in their amount of independent locomotion and exploration (Ainsworth et al., 1979, 2014; Bowlby 1969). In their first few months, infants largely spend their time resting with their mother, suckling, and clinging to her as she travels. This early in development, maternal caregivers are most invested in providing their infant with enough milk and protection to ensure their survivability (Lee, 1984; Lee, Majluf, & Gordon, 1991; Maestripieri, 2002). In the first few weeks, infants begin to regularly break contact with and return to their mothers as they explore for short distances, while mothers more often attempt to keep infants close. However, there is variation in the frequency of maternal protective behaviors like restraint and retrieval and in the frequency and severity of abusive or rejecting behaviors, and this can influence how much an infant is permitted or encouraged to explore and locomote independently (Fairbanks & McGuire 1988; Fairbanks, 2003; Lyons & Parker, 2007), but it can also have lasting consequences for an individuals' physiological development which can result in cognitive impairment and greater anxiety when exploring novel environments (Lyons & Parker, 2007).

When rhesus macaques are between 6 to 9 months, their mothers resume cycling and mating and reduce their maternal investment in a process referred to as weaning (Berman, Rasmussen, Suomi, 1993; Hinde & Spencer-Booth, 1971). Parent-offspring conflict theory (Trivers, 1974) dictates that as infants grow older, they will demand more parental resources than their parent is willing to offer, and during weaning conflict, mothers will more frequently encourage the autonomy of their infant with abuse and rejection (Maestripieri, 1994, 1995). These maternal behaviors can successfully encourage independent movement, travel, exploration, and play, but they can also vary in their frequency and intensity, and higher rates of abuse and rejection can elevate infant glucocorticoid concentrations that measure stress (Mandalaywala et al., 2014). Premature or excessive maternal maltreatment can also reduce the amount that an infant attempts to return to their mother and can increase their anxiety in novel situations (Aber & Allen, 1987). In severe circumstances, maternal abuse and rejection can result in cognitive or emotional deficits (Glaser, 2000; Kaufmen et al., 2000; Maestripieri, 2006; McEwen, 2001; Newport et al., 2002).

The maternal-infant dynamic is an important point of focus as it can have both a considerable impact on an individual's early locomotive experience as well as their cognitive and socioemotional development, and it is important to consider how these factors are related in the early development of rhesus macaques. First, we must identify important shifts in activity, independent locomotion, and maternal behavior, and then we can determine how differences in early experiences interact with attention to spatial information, means-ends activities, and object permanence performance in the first year. The free-ranging population of rhesus macaques on Cayo Santiago is the ideal research site for this particular study as free-ranging animals exhibit a broader spectrum of behaviors than what is observed in a laboratory setting (Dunbar & Badam, 1998), but still provides an accessible format for conducting isolated cognitive testing.

According to previous research in humans, independent movement rather than overall movement should influence an individuals' performance on search and reasoning tasks, and more frequent exploration to and from a secure base should facilitate a greater attention to environmental, allocentric relationships. I also predict that maternal abuse and rejection will have a positive correlation with infant separations, and that this may interfere with cognitive performance such that highly abused and rejected individuals will exhibit more stressed and anxious phenotypes in the context of novel environments and testing scenarios.

Methods

Participants

These data were collected from the same sample of rhesus macaque monkeys evaluated in Chapter 2 and Chapter 3. The 51 focal individuals were born between July and September in 2013 and were randomly selected from three of seven distinct groups on the island of Cayo Santiago, Puerto Rico populated by approximately 1,500 free-ranging individuals. Of these 51 individuals, 36 were successfully trapped for testing in their infancy at 3 to 6 months of age, 41 were trapped for testing as yearlings at 14 to 16 months of age, and 35 were trapped for testing as juveniles at 25 to 30 months of age.

Four individuals were only trapped as infants, three were only trapped as yearlings, three were only trapped as yearlings and juveniles, and six were only trapped as yearlings and juveniles, so only 29 individuals were trapped and tested at all three periods. Additionally, of the 51 original individuals, 8 did not survive to their first year, and two others had mothers that died in their first 1 to 2 years. Accordingly, individuals without surviving mothers were not included in analyses of maternal interaction, and due to time constraints, video coding and behavioral data evaluation was prioritized for those individuals that were trapped and tested at multiple time points, which accounts for the variation in sample sizes across analyses.

Individual rank was determined based on a database maintained by the Caribbean Primate Research Center that observes and analyzes the outcomes of dyadic agonistic interactions between individuals. According to this database, females and matrilines within each social group were organized into an equal distribution of low, moderate, and high-ranking individuals and participants were assigned a ranking based on their status relative to other individuals within their group. Group R is an alpha group on the island made up of approximately 325 individuals, and the relative rank of 67 females from this group was used to determine the ranking of 15 participants from group R, which included 6 high-ranking individuals, 6 moderate-ranked individuals, and 3 low-ranking individuals. Group KK is made up of approximately 175 individuals, and the relative ranking of 37 females from this group was used to determine the rank of 18 participants from group KK, which included 7 high-ranked individuals, 6 moderate-ranked individuals, and 5 low-ranked individuals. Group S is made of up 150 individuals, and the relative ranking of 33 females from this group was used to determine the rank of 4 participants from group S, which included 2 moderate-ranked individuals and 2 low-ranked individuals.

Behavioral Data Collection

When individuals were in their first three months, they were observed between 7:00 and 14:30 twice per week for 30-minute periods using a handheld video camera. Weekly behavioral data collection was weighted to include both morning behaviors (collected between 7:00 and 12:00) and afternoon behaviors (collected between 12:00 and 14:30), and 12 hours of video footage were collected over 12 weeks for each individual. Videos were randomly coded by five trained observers using continuous focal-animal sampling (Altmann, 1974) in Microsoft Excel with automatic time-stamp function. Observers only began interpreting behaviors once inter-observer reliability reached Cohen's $k = 0.90$ in agreement on individual occurrences of behaviors (Caro et al., 1979). Those data were then converted into mean hourly frequencies (event behaviors) and mean hourly durations (state behaviors) using Microsoft Excel. The dataset for the first three months included 552 hours of video across 46 individuals, and key state behaviors were analyzed for 37 of those individuals and key event behaviors were analyzed for 44 of those individuals.

Between March and November of 2014, 43 individuals were followed approximately once per week for 30-minutes, amounting to 13.2 hours of behavioral data per individual (sd = 0.589). Behaviors were collected using handheld Psion Workabout event recorders loaded with "Behavior" software (Syscan International., Montreal, Quebec) and later cleaned, coded, and analyzed in Microsoft Excel. To ensure an accurate distribution of behaviors, half of the data for each individual were collected in the morning (7:00 to 12:00) and half were collected in the afternoon (12:00 to 14:30). Because the first half of the year (March to June) took place during the mating season and the second half of the year (July to November) took place during the birthing season, behavioral data was separated by season to parse out any impact on behavioral development. During the mating season from March to June, 8.24 hours of data (sd = 0.5) were collected for each individual, and during the birthing season from July to November, 4.95 hours of data (sd = 0.62) were collected for each individual.

To investigate the influence of maternal-infant dynamic, I collected behavioral data on the duration, frequency, and quality of time spent between mother and infant. This included the duration that individuals spent in physical contact with their mother as well as the duration that individuals spent in proximity of their mother, which was defined as being within eye sight or within approximately 5 meters of each other. The frequency that mother and infant broke contact, left proximity, reestablished contact, and reestablished proximity was recorded as well as which of the two initiated the separation or reunion. The frequency that mothers directed abuse and rejection at their offspring was also recorded, where abuse was defined as any overtly aggressive bite, hit, drag, throw, sit on, or improper handling of the infant, and rejection was defined as any non-aggressive movement that prevented that infant's access to contact or suckling, which included blocking the infant with an arm or leg and pushing or pulling away.

To investigate activity levels, I recorded the frequency and duration of movement that took place riding dorsally on another individual, riding ventrally on another individual, traveling independently but next to another individual, traveling alone, exploring, and playing alone or with others. Exploration was defining as aimless wandering and investigation of the environment and others. Independent movement and locomotion was defined as all instances of movement that was self-propelled, which included traveling next two another, traveling alone, exploring, or playing. Other state behaviors of resting, grooming, suckling, and foraging were also recorded, and event behaviors of self-directed scratching, vocalizations, and other various social behaviors were also recorded but not used in these analyses.

Cognitive Data Collection

During trapping and testing, individuals were given 15 minutes to habituate to isolation in their 2’ by 2’ by 2’ cage before undergoing 15 to 30 minutes of cognitive testing in select looking time and interactive tasks that were adapted from a Primate Cognition Test Battery (Herrmann et al., 2007; Schmitt et al., 2012). When participants were yearlings between 14 to 16 months, they were tested on a spatial coding looking time task, and as both yearlings and juveniles at 25 to 30 months, they were also tested on a support problem task that evaluated attention to distal information and means-ends reasoning and an A-not-B object permanence task that evaluated multiple stages of object permanence development (see Chapter 3). All tasks were baited with fresh papaya cut into 1” by 1” by 1” pieces.

Spatial Coding Looking Time Task. The spatial coding looking time task involved two conditions of three, 10-second trials, which included two consecutive habituation trials followed by a test trial with a change in display. Looking time in each trial was recorded frame by frame (60 frames = 1 second) by a naïve coder using QuickTime

Player 7. Participants were categorized into two groups based on the consistency of their looking time in an *allocentric* condition, where a reward appeared in the same location relative to three visually distinct objects in an array after rotation but a different location relative to the observer, and an *egocentric* condition, where a reward appeared between different objects within the array but the same location relative to the observer (see Chapter 2). Of the 37 individuals that were exposed to both the egocentric and allocentric condition, 14 increased their looking at the egocentric test trial and decreased their looking in the allocentric test trial regardless of the order in which they were exposed to each condition, and 3 others increased their attention to the egocentric test trial by 130 to 260 frames (60 frames = 1 second) more than they increased their attention to the allocentric test trial. These individuals were categorized as "allocentric," as they appeared to react to the "egocentric" condition as a violation of their expectation and respond to the "allocentric" condition as consistent with their expectation, which may indicate a greater attention to spatial relationships when evaluating the reward's location.

Alternatively, 10 individuals increased their looking at the allocentric test trial and decreased their looking in the egocentric test trial regardless of the order of exposure, while 2 others increased their attention to the allocentric test trial by 150 to 220 frames more than they increased their attention to the egocentric test trial. These individuals were categorized as "egocentric" based on a reaction to the allocentric condition that was consistent with a violation of expectation and a reaction to the egocentric condition that was consistent with their expectation, indicating a possible prioritization of egocentric information. This novel approach to evaluating looking times and spatial coding strategies was further supported by comparisons that showed that "egocentric" individuals took longer to process rotated images than “allocentric” individuals and that “allocentric” individuals outperformed “egocentric” individuals on A-not-B object permanence tasks and means-ends support problem tasks (see Chapter 3).

Support Problem Task. In the support problem task, a reward was placed at the end of cloth strips that were 1- and 3-feet long, and participants were given an opportunity to pull the cloth strip to retrieve the reward that was otherwise out of reach. In this task, 18 of the 38 individuals tested in their first year pulled a cloth strip and successfully retrieved the reward and 19 of the 35 individuals tested in their second year successfully retrieved the reward. Individuals that pulled the reward showed that they could attend to distal information and apply intermediate means-ends behaviors to access an otherwise inaccessible reward.

I categorized participants as high- and low-performing based on their participation in this task over two years of testing. The low-performing group was made up of 9 individuals that did not attempt to pull the support in either year of testing, while the high-performing group was made up of 10 individuals that pulled the support in both years of testing. I also compared the group of 20 individuals that did not pull the support in their first year of exposure to the task to the group of 18 individuals that did pull the support in their first year in order to evaluate interactions that may occur in the first year alone.

A-not-B Object Permanence Task. In the A-not-B object permanence search task, participants were shown the location of a reward before it was concealed under one of two hiding locations (location ‘A’) and given the opportunity to search. This process was repeated with the reward hidden under the same hiding location (‘A’) for the second trial, but in the third trial the reward was hidden under the opposite hiding location (location 'B'). Individuals that successfully located the reward in all trials qualified for stage V object permanence. When tested at 14 to 16 months, 12 of the 39 individuals tested qualified for stage V object permanence, and when tested at 25 to 30 months, 18 of the 35 individuals tested qualified for stage V object permanence (See Chapter 3).

Participants were separated into high- and low-performing groups based on their consistent performance over both years of testing. The low-performing group was made up of 12 individuals that did not show evidence of exceeding stage III to IV object permanence when tested in their first two years, which included 5 individuals that did not search in either year of testing, 5 individuals that did not search in one year of testing and searched randomly in the other, and 2 individuals that always appeared to search randomly. High scoring individuals were made up of 12 participants that consistently scored higher than stage IV object permanence in both years of testing. This included 10 individuals that were successful in all of their trials over both years of testing and 2 individuals that exhibited the stage IV A-not-B error in one year but were successful in all of trials in the other year of testing.

I also compared three groups with varying performance on the A-not-B object permanence task when they were first exposed to the task in their first year. This included 12 individuals that did not attempt any search, 10 individuals that appeared to search randomly and therefore did not exceed stage III to IV object permanence, and 12 individuals that searched correctly and qualified for stage V object permanence.

Data Analysis

One-way ANOVAs were used to evaluate differences in age, activity, and maternal interaction between independent groups of "allocentric" versus "egocentric" spatial attention as well as high- versus low-performing individuals in the support problem and A-not-B object permanence task at 1 and 2 years of age. Chi-square tests were used to determine differences in the distribution of sex, rank, and siblings between groups, and Pearson correlations were used to determine relationships between the occurrence of behaviors early in development. A Student's two-tailed t-test was also used to compare changes in behavior over time.

Results

Early experience and activity in the first year

Proximity and Contact. In their first three months, infants spent 100% of their time in proximity of mom, and 85.2% of their time in contact with mom, ranging from 67% to 97% (sd = 6.3%), and they did not begin spending more than 25% of their time out of contact with their mother until they were around 6.22 weeks old (sd = 2.52). When individuals reached between 6 to 9 months of age, their time spent in proximity of mom decreased to 80.8% on average, ranging from 13% to 100% (sd = 16.95%), and their time spent in contact with mom decreased to 38% (range: 6% to 83%, sd = 15%), which differed significantly from the first three months; t(36) = -21.42, $p < 0.00001$. Between 10 and 13 months, individuals spent 61.8% of their time in proximity of their mother, ranging from 0% to 90% (sd = 18.8%), and only spent 17.9% of their time in physical contact with mom, ranging from 0% to 46% (sd = 10.9%), which also differed significantly from the previous four months; $t(42) = -8.69$, $p < 0.00001$.

Breaking Contact and Proximity. In the first three months, mothers and infants broke contact around 8.05 times per hour (sd = 2.80) and 9.9 times for every hour they spent in contact with each other (sd = 3.74). At 6 to 9 months, mother and infant broke contact with each other around 7.07 times per hour (sd = 2.46), but they increased to 20.36 instances of breaking contact for every hour they spent in contact (sd = 7.78). By 10 to 13 months, yearlings and their mothers broke contact 4.01 times per hour (sd = 2.5) and increased to breaking contact 25.95 times per hour of contact (sd = 12.32). Between 6 and 9 months of age, mother and infant also left the proximity of each other 1.43 times per hour on average (sd = 0.68) and 1.89 times for every hour they spent in proximity (sd = 1.02). From 10 to 13 months, mother and offspring left proximity of each other 2.18 times per hour (sd = 0.84) and 3.89 times for every hour of proximity (sd = 1.78).

Initiating Separation and Reunion. When mother and infant broke contact in the first three months, infants were responsible for initiating the separation in 88.27% of cases (sd = 7.93%) and reestablished contact in 72.5% of reunions (sd = 10.63%), showing frequent infant-initiated exploration. At 6 to 9 months, Infants initiated breaks in contact in 57.14% of the instances of separation (sd = 11.18%) and initiated departure from their mother's proximity in 59.23% of cases (sd = 19.78%), while they reestablished contact in 87.91% of reunions (sd = 9.22%) and reestablished proximity in 76.38% of cases (sd = 18.37%). At this point, we see the influence of weaning on a higher proportion of mother-initiated separations and infant-initiated reunions. At 10 to 13 months, individuals broke contact with mom in 51.9% (sd = 16.7%) of separations and reestablished contact in 76.5% (sd = 19.1%) of cases and were responsible for leaving proximity in 60% of cases (sd = 18.1%) and reestablished proximity in 69.4% of cases (sd = 20.5%).

		Age (months)		Statistical Difference
Behavior	**0-3**	**6-9**	**10-13**	
Percentage of Total Time				
Proximity to Mom	*M* = 100% *SD* = 0%	*M* = 80.79% *SD* = 16.95%	*M* = 61.8% *SD* = 18.8%	*t (36) = -21.42, *p* < 0.00001
Contact with Mom	*M* = 85.2%* *SD* = 6.3%	*M* = 37.6%*/** *SD* = 15.23%	*M* = 17.9%** *SD* = 10.9%	**t (42) = -8.69, *p* < 0.00001
Frequency of Breaks in Proximity				
per Hour	N/A	*M* = 1.43 *SD* = 0.68	*M* = 2.18 *SD* = 0.84	
per Hour of Proximity	N/A	*M* = 1.89 *SD* = 1.02	*M* = 3.89 *SD* = 1.78	
Frequency of Breaks in Contact				
per Hour	*M* = 8.05 *SD* = 2.80	*M* = 7.07 *SD* = 2.46	*M* = 4.01 *SD* = 2.50	
per Hour of Contact	*M* = 9.90 *SD* = 3.74	*M* = 20.36 *SD* = 7.78	*M* = 25.95 *SD* = 12.32	
Percentage of Breaks in Proximity				
Infant-Initiated Departure	N/A	*M* = 59.23% *SD* = 19.78%	*M* = 60.00% *SD* = 18.10%	
Infant-Initiated Proximity	N/A	*M* = 76.38% *SD* = 18.37%	*M* = 69.40% *SD* = 20.50%	
Percentage of Breaks in Contact				
Infant-Initiated Separation	*M* = 88.27% *SD* = 7.93%	*M* = 57.14% *SD* = 11.80%	*M* = 51.90% *SD* = 16.70%	
Infant-Initiated Reunion	*M* = 72.50% *SD* = 10.63%	*M* = 87.91% *SD* = 9.22%	*M* = 76.50% *SD* = 19.10%	

Table 4.1: Maternal-infant dynamic in the first year.

Maternal Abuse and Rejection. From 0 to 3 months of age, infants averaged 2.02 instances of maternal abuse and rejection per hour (range: 0 to 9.67, sd = 2.46) and 2.67 (sd = 3.18) times per hour of contact. The frequency of abuse and rejection in the first three months was not significantly correlated with the frequency that mother and infant broke contact (r = 0.292, n = 41, p = 0.064), and there was no significant relationship with the frequency that the infant initiated separation from mom (r = 0.121, p = 0.490) or reestablished contact (r = 0.215, p = 0.177), but there was a significant relationship with the amount that mom initiated separation (r = 0.732, $p < 0.00001$) and contact (r = 0.346, p = 0.027).

At 6 to 9 months, mothers exhibited 3.12 (sd = 2.36) instances of abuse and rejection per hour on average and a higher rate per hour of contact (m = 8.70 times per hour of contact, sd = 5.81) than over the first three months (m = 2.67, sd = 3.18); t(35) = 6.70, $p < 0.001$. Between 6 and 9 months, there was a significant relationship between the frequency of abuse and rejection per hour and the frequency that mother and infant separated (r = 0.52, n = 40, p = 0.0006), and there were significant relationships with the amount that infants initiated separation each hour (r = 0.409, p = 0.009), the amount infants initiated reunions (r = 0.535, p = 0.0004), and the amount that mom initiated separation each hour (r = 0.544, p = 0.0003), but there was no relationship with the amount that mothers initiated reunions each hour.

At 10 to 13 months, yearlings experienced 1.02 (sd = 1.33) instances of maternal abuse and rejection per hour and 4.94 (sd = 4.5) per hour that mother and offspring spent in contact, which was significantly lower than the previous 4 months; t(38) = -3.282, p = 0.001. At these ages, a trend persisted where individuals that received higher rates of abuse and rejection also exhibited higher rates of separation ($r = 0.734$, $n = 41$, $p < 0.00001$), infant-initiated separation ($r = 0.477$, $p = 0.002$), infant-initiated reunions ($r = 0.791$, $p < 0.00001$), and mother-initiated separations ($r = 0.810$, $p < 0.00001$), but not mother-initiated reunions ($r = 0.157$, $p = 0.327$).

The strength of the relationship between maternal abuse and rejection, mother-initiated separation, and infant-initiated reunions between 10 to 13 months illustrates the weaning process as a response to a yearling's more frequent displays of attachment and a mother's efforts to move away from the infant.

		Age (months)		**Statistical Difference**
	0 - 3	**6 - 9**	**10 - 13**	
Instances of Maternal Abuse and Rejection per Hour;	$M = 2.02$ $SD = 2.46$	$M = 3.12$ $SD = 5.81$	$M = 1.02$ $SD = 1.33$	$** \ t(35) = 6.70$ $p < 0.001$
per Hour of Contact	$M = 2.67**$ $SD = 3.18$	$M = 8.70**/***$ $SD = 5.81$	$M = 4.94***$ $SD = 4.50$	$*** t(38) = -3.28$ $p = 0.001$
Correlation with Maternal Abuse and Rejection				
Separations per Hour	$r = 0.292$ $p = 0.064$	$r = 0.52$ $p = 0.0006*$	$r = 0.734$ $p < 0.00001*$	
Infant-Initiated Separations per Hour	$r = 0.111$ $p = 0.490$	$r = 0.409$ $p = 0.009*$	$r = 0.477$ $p = 0.002*$	
Infant-Initiated Reunions per Hour	$r = 0.215$ $p = 0.177$	$r = 0.535$ $p = 0.0004*$	$r = 0.791$ $p < 0.00001*$	
Mother-Initiated Separations per Hour	$r = 0.732$ $p < 0.0001*$	$r = 0.544$ $p = 0.0003*$	$r = 0.810$ $p < 0.00001*$	
Mother-Initiated Reunions per Hour	$r = 0.346$ $p = 0.027*$	$r = 0.233$ $p = 0.15$	$r = 0.157$ $p = 0.327$	

Table 4.2: Maternal abuse and rejection and relationship mother-infant dynamic in the first year.

Movement and Activity. Between 0 and 3 months of age infants spent 29.8% of their time in movement, ranging from 20.8% to 39.4% (sd = 5.2%), which included riding dorsally and ventrally on mom while she traveled, traveling next to mom, traveling independently, exploring independently, and playing either alone or with others, but only 56.4% (sd = 12.4%) of that movement was self-propelled and independent from mom. The majority of the infant's time (m = 61.3%, sd = 6.6%) was spent resting, suckling, and grooming with mom, while all remaining time was spent participating in rare or unknown behaviors.

After 6 months, infants spent around 22.63% of their time in movement (sd = 4.17%), and 90.72% (sd = 13.11%) of that movement occurred independent of mom. At this age, only 32.4% (sd = 10.9%) of time was spent resting and grooming with others. More time was spent to foraging on vegetation, chow, or soil (m = 26.67%, sd = 5.6%) rather than suckling, and remaining time was spent in rare or unknown behaviors. When infants were between 6 and 9 months of age, their mothers began mating and becoming pregnant with new infants, and 33 of the 46 focal mothers gave birth to new siblings when our focal infants reached 10 to 13 months of age and considered yearlings.

The influence of new siblings on activity and the mother-infant dynamic

Yearlings with new siblings spent significantly less time in contact with their mothers (m = 25.46%, sd = 12.82%) compared to those without new siblings (m = 14.63%, sd = 8.38%) (F(1, 41) = 11.11, p = 0.002), but they did not exhibit any significant differences in the percentage of time they spent in proximity of mom. Yearlings with new siblings also broke and made contact with mom less often (m = 3.3, sd = 1.8) than yearlings without siblings (m = 5.5, sd = 3.3); F(1,40) = 8.06, p = 0.007, but there was no significant difference after controlling for their lower proportion of maternal contact; F(1, 38) = 1.55, p = 0.22. Though, yearlings with siblings showed a higher rate of leaving the proximity of mom (m = 2.59 times per hour in proximity of mom, sd = 1.30) compared to those without siblings (m = 1.63, sd = 0.82); F (1, 39) = 5.622, p = 0.023, and before siblings were born, there were no significant differences between the amount of time infants spent with a mom that was pregnant (m = 36.5%, sd = 13.44%) versus a mom that did not give birth that season (m = 40.15%, sd = 19.1%); F (1, 41) = 0.516, p = 0.476).

However, yearlings without new siblings suffered from a higher rate of abuse and rejection (m = 2 times per hour, sd = 1.91) relative to those with new siblings (m = 0.54 times per hour, sd = 0.56); F(1, 40) = 14.623, p = 0.0005), and received a higher rate of maternal aggression (m = 7.36 times per hour of contact, sd = 5.94) than those with new siblings (m = 3.68, sd = 3.34) even after controlling for the amount of time spent in contact with mom; F(1, 38) = 6.283, p = 0.017). There was also no difference in maternal abuse and rejection between yearlings with new siblings (m = 11.94, sd = 12.64) and yearlings without new siblings (m = 10.24, sd = 14.22) prior to the birthing season (F (1, 39) = 0.14, p = 0.707).

The influence of infant sex on activity and the mother-infant dynamic

In the first few months, males also received significantly higher rates of abuse and rejection per hour (m = 2.94, sd = 3.06) than females (m = 1.36, sd = 1.73); F(1, 39) = 4.359, p = 0.046, and males experienced significantly higher rates of maternal abuse and rejection per hour of contact (m = 3.93, sd = 3.81) compared to females (m = 1.66, sd = 2.13); F (1, 34) = 5.022, p = 0.03. However, this sex difference did not exist between 6 and 9 months; F(1, 38) = 0.03, p = 0.87, or from 10 to 13 months; F(1, 37) = 0.003, p = 0.96. At 0 to 3 months there was also no apparent sex difference in the amount of time infants spent in contact with their mother; F(1, 34) = 1.53, p = 0.22, or in the frequency that they broke or made contact with their mother; F(1, 34) = 0.44, p = 0.51. Though, females were more likely to initiate separation from mom (m = 90.91% of instances of separation, sd = 5.97%) compare to males (m = 86%, sd = 9.58%); F(1, 38) = 3.93, p = 0.05, and from 6 to 9 months of age, females spent significantly more time in proximity of their mother (m = 86.41%, sd = 7.25%) compared to males (m = 74.37%, sd = 21.85%); F(1, 40) = 5.942, p = 0.019, though this difference did not exist between 10 to 13 months of age; F (1, 39) = 0.379, p = 0.542.

The influence of maternal age on activity and the mother-infant dynamic

There were also notable weak to moderate relationships between the age of the mother and mother-infant dynamics and infant activity levels. When infants were between 0 and 3 months, there were inverse relationships between maternal age and the amount of time mother and infant spent in contact with other (r = -0.365, n = 37, p = 0.03), the rate the mom initiated contact with the infant (r = -0.447, n = 43, p = 0.002), the rate that mom restrained and retrieved the infant (r = -0.332, n = 44, p = 0.03), the amount that mom and infant traveled (r = -0.359, n = 32, p = 0.04), and the amount that mom carried the infant during travel (r = -0.401, n = 32, p = 0.02). As a result, there was also a positive relationship between maternal age and the proportion of total travel that infants did independently (r = 0.411, n = 32, p = 0.02) and a positive relationship between maternal age and the frequency that infants interacted with others (r = 0.369, n = 32, p = 0.04).

After 6 months, the negative relationship between maternal age and the frequency of overall travel persisted (r = -0.387, n = 41, p = 0.01), and there was a negative relationship between maternal age and the frequency that mother and infant climbed trees (r = -0.531, n = 41, p < 0.001), but no relationship between maternal age and the amount of time that infants spent in proximity or contact with their mother. From 10 to 13 months, maternal age was also negatively correlated with the frequency of infant-initiated contact with mom (r = -0.327, n = 42, p = 0.03) and the frequency that mom reestablished proximity after separation (r = -0.323, n = 41, p = 0.04). Additionally, there was an inverse relationship between maternal age and the frequency of maternal abuse and rejection per hour (r = -0.392, n = 40, p = 0.01) between 10 and 13 months, but this relationship did not exist between 0 to 9 months of age.

The influence of maternal rank on activity and the mother-infant dynamic

From 6 to 13 months, high-ranking individuals also exhibited a lower rate of travel (m = 16.57 times per hour, sd = 2.59) compared to mid-ranking (m = 17.03, sd = 2.50) and low-ranking (m = 20.11, sd = 3.23) individuals; F(2, 34) = 5.40, p = 0.009, and high-ranking infants also exhibited lower rates of independent movement; F(2, 34) = 4.30, p = 0.02, but there was no difference in the duration of movement and travel by rank; F(2, 34) = 0.75, p = 0.48. Differences in the frequency of movement but not in duration is likely due to a higher frequency of displacement in low ranking individuals.

From 10 to 13 months, yearlings of high-ranking individuals also experienced the least amount of abuse and rejection (m = 2.61 times per hour in contact, sd = 1.93), while low-ranking individuals experienced the most (m = 7.37 times per hour in contact, sd = 5.093), and mid-ranking individuals experienced a moderate amount (m = 5.4 times per hour in contact, sd = 4.93); F(2, 32) = 3.44, p = 0.04.

When considering the impact of maternal-infant dynamics and activity on the development of social and physical cognition, we must be aware of these trends where maternal contact is also negatively associated with maternal age in the first three months and higher in individuals without siblings from 10 to 13 months, and where the duration and frequency of travel can also be associated with the age and rank of mothers. Additionally, the frequency of maternal abuse and rejection can be higher in male infants between 0 to 3 months and more frequent in low-ranking yearlings with younger moms and no new siblings between 10 and 13 months. Though, sample sizes were too small to control for all factors, I confirmed a equal distribution of rank, sex, age, and siblings before each comparison.

Comparing early development of "allocentric" and "egocentric" coders

When individuals were between 14 and 16 months, they were shown a looking time task that captured whether individuals were differentiating between two rotational displacement scenarios using allocentric or egocentric spatial coding strategies. Between the groups designated "allocentric" and "egocentric" coders at 14 to 16 months, there was no difference in the proportion with siblings born in their first year ($\chi^2 = 0.34$, p = 0.56), no difference in the sex ratios of each group ($\chi^2 = 0.08$, p = 0.77), no difference in the maternal age for each group; F(1, 27) = 0.003, p = 0.96), and no difference in the distribution of low, medium, and high ranked individuals ($\chi^2 = 1.77$, p = 0.41).

There was a positive correlation between the percentage of time that infants remained in contact with mom in the first three months and their change in looking time from habituation to test trial in the egocentric condition (r = 0.426, n = 34, p = 0.01), which may suggest a possible interaction between early experience and evaluation of the egocentric condition as “expected” or “unexpected.” However, there was no difference in the overall percentage of contact with mom between “allocentric” coders (m = 88.1%, sd = 6.81%) and “egocentric” coders (m = 85.25%, sd = 4.29%); F(1, 24) = 1.53, p = 0.23, and no significant difference in the frequency of separation between “allocentric” (m = 7.33 times per hour, sd = 3.25) and “egocentric” coders (m = 9.33 times per hour, sd = 2.34); F(1, 27) = 3.33, p = 0.08.

There was also no difference in the percentage of movement that was independent between “allocentric” (m = 52.6%, sd = 16.5%) and “egocentric” coders (m = 56.6%, sd = 5.9%); F(1, 20) = 0.53, p = 0.47, and no significant differences in the amount of maternal abuse and rejection behaviors that infants received in the first three months between “allocentric” (m = 1.99 times per hour, sd = 2.20) and “egocentric” (m = 3.10 times per hour, sd = 3.42) coders; F(1, 27), p = 0.29 (see Table 4.3).

0 – 3 months Behaviors	“Egocentric” (n = 12)	“Allocentric” (n = 17)	Statistical Difference
Maternal Contact	*M* = 85.25% *SD* = 6.81%	*M* = 88.1% *SD* = 6.81%	F (1, 24) = 1.53 *p* = 0.23
Separations per Hour	*M* = 9.33 *SD* = 2.34	*M* = 7.33 *SD* = 3.25	F (1, 27) = 3.33 *p* = 0.08
Infant-initiated Separations per Hour	*M* = 8.19 *SD* = 2.42	*M* = 5.60 *SD* = 2.94	F (1, 27) = 2.69 *p* = 0.11
Reunions that are Infant-initiated	*M* = 71.3% *SD* = 10.1%	*M* = 72.8% *SD* = 7.9%	F (1, 27) = 0.18 *p* = 0.67
Movement that is Independent	*M* = 56.6% *SD* = 5.8%	*M* = 52.6% *SD* = 16.5%	F (1, 20) = 0.53 *p* = 0.47
Abuse and Rejection per Hour	*M* = 3.10 *SD* = 3.42	*M* = 1.99 *SD* = 2.20	F (1, 27) = 1.14 *p* = 0.29

Table 4.3: Spatial attention and early experience at 0 to 3 months. Comparing the frequency and duration of experiences and behaviors at 0 to 3 months between individuals designated as “egocentric” and “allocentric” coders in their first year.

Once infants reached 6 to 9 months of age, they exhibited a wider range of maternal interaction and independent locomotion. At this age, there were still no significant differences in the amount of time that “egocentric” and “allocentric” coders spent in contact with their mother; F(1, 27) = 0.008, p = 0.93, or in proximity of their mother; F(1, 27) = 0.06, p = 0.81, but “egocentric” individuals initiated contact with mom in a significantly higher proportion of reunions (m = 92.4%, sd = 4.2%) compared to “allocentric” coders (m = 82.5%, sd = 10.2%); F(1, 27) = 10.12, p = 0.004, and “egocentric” coders left the proximity of mom in a significantly higher proportion of separations (m = 69.8%, sd = 11.2%) compared to “allocentric” coders (m = 50%, sd = 18.3%); F(1, 27) = 11.11, p = 0.003. Though, there were no significant differences in the total frequency of separations per hour; F(1, 27) = 0.52, p = 0.48, and there was no significant difference in the total frequency that mother and infant left proximity per hour; F(1, 27) = 0.20, p = 0.66. At this age, “egocentric” coders also exhibited a higher proportion of movement that was done independently (m = 91.9%, sd = 6.7%) compared to “allocentric” coders (m = 82.71%, sd = 14.3%); F(1, 27) = 4.28, p = 0.048. There was also a significant difference in the frequency of maternal abuse and rejection, where “egocentric” coders experienced higher rates per hour of contact with mom (m = 11.78, sd = 6.34) than “allocentric” coders (m = 6.02, sd = 3.34); F(1, 26) = 9.61, p = 0.005, and had higher rates of abuse and rejection overall (m = 4.62 times per hour, sd = 2.89) than “allocentric” coders (m = 2.23, sd = 1.52); F(1, 26) = 8.03, p = 0.009 (see Table 4.4).

6 - 9 month behaviors	**"Egocentric" (n = 12)**	**"Allocentric" (n = 17)**	**Statistical Difference**
Maternal Contact	*M* = 38.4% *SD* = 9.8%	*M* = 38.9% *SD* = 9.8%	F (1, 27) = 0.008 *p* = 0.93
Maternal Proximity	*M* = 81.3% *SD* = 12.4%	*M* = 82.7% *SD* = 15.9%	F (1, 27) = 0.06 *p* = 0.81
Separations per Hour	*M* = 7.63 *SD* = 2.47	*M* = 6.99 *SD* = 1.27	F (1, 27) = 0.51 *p* = 0.48
Proximity Departures per Hour	*M* = 1.44 *SD* = 0.55	*M* = 1.34 *SD* = 0.63	F (1, 27) = 0.20 *p* = 0.66
Reunions that are Infant-initiated	*M* = 92.4% *SD* = 4.2%	*M* = 82.5% *SD* = 10.2%	F (1, 27) = 10.12 *p* = 0.004**
Departures from Proximity that are Infant-initiated	*M* = 69.8% *SD* = 11.2%	*M* = 50.0% *SD* = 18.3%	F (1, 27) = 11.11 *p* = 0.003**
Movement that is Independent	*M* = 91.9% *SD* = 6.7%	*M* = 82.7% *SD* = 14.3%	F (1, 27) = 4.28 *p* = 0.048*
Abuse and Rejection per Hour	*M* = 4.62 *SD* = 2.89	*M* = 2.23 *SD* = 1.52	F (1, 26) = 8.03 *p* = 0.009**
Abuse and Rejection per Hour of Contact	*M* = 11.78 *SD* = 6.34	*M* = 6.02 *SD* = 3.34	F (1, 26) = 9.61 *p* = 0.005**

Table 4.4: Spatial attention and early experience at 6 to 9 months. Comparing the frequency and duration of experiences and behaviors at 6 to 9 months between individuals designated as "egocentric" and "allocentric" coders in their first year.

At 10 to 13 months, when mothers began giving birth to new siblings, "egocentric" coders exhibited significantly higher rates of breaking contact (m = 2.67 times per hour, sd = 1.09) compared to "allocentric" coders (m = 1.58 times per hour, sd = 1.09); F(1, 27) = 7.09, p = 0.01. "Egocentric" coders also initiated a higher percentage of departures from proximity of mom (m = 69.6% of all departures, sd = 15.5%) than "allocentric" coders (m = 56.5% of all departures, sd = 18.03%); F(1, 27) = 4.127, p = 0.05. Though, between these ages there were no significant differences in the proportion of time that yearlings spent contact with their mother; F(1, 27) = 0.04, p = 0.84, and the proportion of time that yearlings spent in proximity of their mother; F(1, 27) = 1.02, p = 0.32), and there was no significant difference in the amount of abuse and rejection experienced by "egocentric" coders (m = 5.49 times per hour of contact, sd = 4.27) and "allocentric" coders (m = 4.83, sd = 3.52); F(1, 26) = 0.20, p = 0.66 (see Table 4.5).

10 - 13 month behaviors	"Egocentric" (n = 12)	"Allocentric" (n = 17)	Statistical Difference
Maternal Contact	*M* = 19.92% *SD* = 7.15%	*M* = 19.12% *SD* = 85.41%	F (1, 27) = 0.04 *p* = 0.84
Maternal Proximity	*M* = 66.75% *SD* = 10.4%	*M* = 60.82% *SD* = 18.25%	F (1, 27) = 1.02 *p* = 0.32
Separations per hour	*M* = 4.71 *SD* = 1.14	*M* = 3.62 *SD* = 2.74	F (1, 27) = 1.65 *p* = 0.21
Proximity Departures per Hour	*M* = 2.18 *SD* = 1.08	*M* = 2.17 *SD* = 0.68	F (1, 27) = 0 *p* = 1.0
Infant-initiated separations per hour	*M* = 2.67 *SD* = 1.09	*M* = 1.58 *SD* = 1.09	F (1, 27) = 7.09 *p* = 0.01**
Departures from proximity that are infant-initiated	*M* = 69.58% *SD* = 15.5%	*M* = 56.5% *SD* = 18.03%	F (1, 27) = 4.13 *p* = 0.05*
Abuse and rejection per hour of contact	*M* = 5.49 *SD* = 4.27	*M* = 4.83 *SD* = 3.52	F (1, 26) = 0.20 *p* = 0.66

Table 4.5: Spatial attention and early experience at 10 to 13 months. Comparing the frequency and duration of experiences and behaviors at 10 to 13 months between individuals designated as "egocentric" and "allocentric" coders in their first year

When this spatial coding looking task was conducted at 14 to 16 months, participants exhibited a change in looking time in response to the egocentric test trial that was significantly higher than their change in looking between habituation trials, which was not present for the allocentric condition (see Chapter 2). These results confirm attention to change only in the egocentric condition, which was the impossible rotational displacement scenario where the reward did not appear to move with the landmarks in the array and instead appeared in the same location relative to the observer but between different objects, while there was no significant change in attention to the allocentric condition that was consistent with rotational displacement. Accordingly, it is important to investigate looking time in the egocentric condition alone. Using these methods, we find that participants that increased their attention to the egocentric condition also exhibited lower rates of infant-initiated separation in their first year from birth to 13 month; F(1, 35) = 4.94, p = 0.03, lower rates of infant-initiated reunions; F(1, 35) = 5.76, p = 0.02, and less overall independent movement in the first year; F(1, 35) = 4.84, p = 0.03, but no overall difference in their rate of maternal rejection in the first year; F(1, 35) = 0.81, p = 0.38 (see Table 4.6). These results offer a complex interaction between spatial attention in the first year, which consistently exposes a lower rate of movement away from mom among those that appear to identify the egocentric condition as a violation of their expectation.

0 – 13 months	Decreased looking at "Egocentric" (n = 14)	Increased looking at "Egocentric" (n = 23)	Statistical Difference
Infant-initiated Separation per Hour	*M* = 5.79 *SD* = 1.36	*M* = 4.74 *SD* = 1.41	F (1, 35) = 4.94 *p* = 0.03*
Infant-initiated Reunions per Hour	*M* = 6.35 *SD* = 1.48	*M* = 5.07 *SD* = 1.62	F (1, 35) = 5.76 *p* = 0.02*
Independent Movement	*M* = 18.64% *SD* = 5.18%	*M* = 14.52% *SD* = 5.72%	F (1, 35) = 4.84 *p* = 0.03*
Abuse and Rejection per Hour	*M* = 2.57 *SD* = 1.60	*M* = 2.08 *SD* = 1.59	F (1, 35) = 0.81 *p* = 0.38

Table 4.6: Looking time response to the egocentric condition and early experience from birth to 13 months. Comparing the frequency and duration of experiences and behaviors in the first year between individuals that decreased their attention from habituation to test trial (n = 24) and those that increased attention from habituation to test trial (n = 23) when exposed to an "egocentric" condition between 14 to 16 months.

Each of the aforementioned comparisons were selected based on potentially distinct impacts on spatial attention in order to differentiate whether duration, frequency, or the quality of movement and experience had the strongest interaction with performance. However, because multiple comparisons were made across multiple time points, I used Bonferroni corrections to consider significance only when the p value was less than or equal to 0.005 to avoid type I error. At this alpha level, the only significant differences between "egocentric" and "allocentric" individuals were in their frequency of infant-initiated reunions (p = 0.004), infant-initiated departures (p = 0.003), and the rate of maternal abuse and rejection per hour of contact (p = 0.005) between 6 to 9 months. Maternal abuse and infant contact and separation are highly correlated at this age, which suggests that attachment during the weaning period is interacting with spatial attention in some way but does not confirm a relationship between independent movement and spatial coding strategies.

Correlation between early experience and the support problem from 1 to 2 years

To compare factors of mother-infant dynamic and locomotive experience on cognitive development in the first year, participants were separated into high- and low-performing groups in the support problem task that was conducted when individuals were between 14 to 16 months and 25 to 30 months. The low-performing group was made up of 9 individuals that did not pull the support to reach a distant reward both when they were tested at 14 to 16 months and when they were tested at 25 to 30 months, and the high-performing group was made up of 10 individuals that pulled the support in both years. There were no significant differences in the sex ratio of each group ($\chi^2 = 1.27$, p = 0.26), no difference in the distribution of rank ($\chi^2 = 2.2$, p = 0.33), no difference in the proportion with siblings born in their first year ($\chi^2 = 0.95$, p = 0.33), and no difference in the age of their mothers; F(1, 17) = 0.04, p = 0.84.

In their first three months, low-performing individuals spent more time resting (m = 7.62 hours, sd = 0.93) than high-performing individuals (m = 6.61 hours, sd = 0.50); F (1, 12) = 6.41, p = 0.03, and there was a trend where high-performing individuals also exhibited higher overall duration of movement in their first 3 months (m = 4.10 hours, sd = 0.59) than low-performing individuals (m = 3.40, sd = 0.83); F(1, 12) = 3.33, p = 0.09, and a higher overall duration of independent movement (m = 2.63 hours, sd = 0.79) than low-performing individuals (m = 1.87 hours, sd = 0.61); F(1, 12) = 4.09, p = 0.066. From 6 to 13 months, high-performing individuals also exhibited a trend towards a higher frequency of social play (m = 4.67 times per hour, sd = 2.02) than low-performing individuals (m = 3.18, sd = 1.15); F(1, 17) = 3.75, p = 0.07, but they did not exhibit any differences in frequency of overall movement; F(1, 17) = 0.10, p = 0.76 (see Table 4.7).

	Low-performing Support Problem (n = 9)	**High-performing Support Problem (n = 10)**	**Statistical Difference**
0 – 3 months			
Resting	*M* = 7.62 hours *SD* = 0.93	*M* = 6.61 hours *SD* = 0.5	F (1, 12) = 6.41 *p* = 0.03*
Movement	*M* = 3.40 hours 0.83	*M* = 4.10 hours *SD* = 0.59	F (1, 12) = 3.33 *p* = 0.09
Independent Movement	*M* = 1.87 hours *SD* = 0.61	*M* = 2.63 hours *SD* = 0.79	F (1, 12) = 4.09 *p* = 0.07
6 – 13 months			
Movement per Hour	*M* = 17.49 *SD* = 3.39	*M* = 17.96 *SD* = 3.06	F (1, 17) = 0.10 *p* = 0.76
Social Play per Hour	*M* = 3.18 *SD* = 0.1.15	*M* =4.67 *SD* = 2.02	F (1, 17) = 3.75 *p* = 0.07

Table 4.7: Support problem participation over 1 to 2 years and early experience. Comparing behavior and early experience between individuals that are "low-performing" in the support problem task (consistently not pulling the support to reach a distant reward in both years of testing) and "high-performing" in the support problem task (consistently pulling the support in both years of testing).

I also found that those that pulled the support during their first exposure to the task at 14 to 16 months had a significantly lower frequency of abuse and rejection overall in the first 3 months (m = 1.11 times per hour, sd = 1.15) compared to those that did not pull the support (m = 3.28, sd = 3.05); F(1, 36) = 8.08, p = 0.007. There was also a trend where those that pulled the support spent less time in contact with their mothers in the first 3 months (m = 83.3% of their time, sd = 6.1%) compared to those that did not pull the support (m = 87.3%, sd = 6.3%); F(1, 33) = 3.73, p = 0.06, and at 10 to 13 months, individuals that pulled the support in the first year spent significantly less time in contact with mom (m = 14.17%, sd = 9.41%) than those that did not pull the support (m = 20.95%, sd = 10.4%); F(1, 36) = 4.41, p = 0.04 (see Table 4.8). Though, it is difficult to determine whether these early experiences are contributing to means-ends reasoning capacity since the support problem task does not differentiate between failing the task and choosing not to participate, but all individuals that were tested did approach the apparatus.

Comparisons were selected based on their potentially distinct impacts on task performance, but I used Bonferroni corrections to consider significance only when the p value was less than 0.01. This revealed a significant difference only in the rate of maternal abuse and rejection in the first three months between individuals that participated and those that did not participate in the support problem in their first year of exposure (p = 0.007). Once again, this supports a relationship between an early onset of weaning behaviors and participation in novel tasks rather than a clear relationship between motor experience and performance in rhesus macaques at this age.

	Do Not Pull Support at 14-16 months (n = 20)	**Pull Support at 14-16 months (n = 18)**	
0 – 3 months			
Abuse and Rejection per Hour	*M* = 3.28 *SD* = 3.05	*M* = 1.11 *SD* = 1.15	F (1, 36) = 8.08 *p* = 0.007**
Contact	*M* = 87.33% *SD* = 56.3%	*M* = 83.3% *SD* = 6.1%	F (1, 33) = 3.73 *p* = 0.06
10 – 13 months			
Contact	*M* = 20.95% *SD* = 10.4%	*M* = 14.17% *SD* = 9.41%	F (1, 36) = 4.41 *p* = 0.04*

Table 4.8: Support problem participation in the first year and early experience. Comparing behavior and early experience between individuals that did not pull the support in their first year of support problem testing and those that did.

Correlation between early experience and object permanence from 1 to 2 years

Participants were also separated into high- and low-performing groups in the A-not-B object permanence task based on their cumulative performance at 14 to 16 months and 25 to 30 months. The low-performing group was made up of the 12 individuals that did not show evidence of exceeding stage III to IV object permanence when tested in either year. This included 5 individuals that did not search in either year of testing, 5 individuals that did not search in one year of testing and searched randomly in the other, and 2 individuals that always appeared to search randomly. High scoring individuals were made up of 12 participants that consistently scored higher than stage IV object permanence in both years of testing. This included 10 individuals that successfully located the reward in all of their trials over both years of testing and 2 individuals that exhibited the stage IV A-not-B error in one year but success in all trials the following year. There was no difference in the sex ratio of each group ($\chi^2 = 0$, p = 1), no difference in the distribution of rank ($\chi^2 = 1.17$, p = 0.56), no difference in the distribution of mom's age (F(1, 22) = 0.004, p = 0.95), and no difference in whether a sibling was born in their first year ($\chi^2 = 0.18$, p = 0.67).

Low-performing individuals spent more time in contact with their mother between 6 to 9 months (m = 39.8%, sd = 16.0%) than high-performing individuals (m = 29.4%, sd = 11.9%); F(1, 22) = 3.21, p = 0.087 and exhibited a lower overall percentage of time in movement (m = 21.8%, sd = 3.2%) than high-performing individuals (m = 24.5%, sd = 3.9%); F(1, 22) = 3.52, p = 0.07. Low-performing individuals also exhibited significantly less time engaging in independent movement (m = 13.3 times per hour, sd = 2.7; m = 19.4% of time, sd = 5.0%) than high-performing individuals (m = 16.2 times per hour, sd

= 3.6; m = 23.6% of time, sd = 4.8%); F(1, 21) = 4.98, p = 0.037 and F(1, 22) = 4.29, p = 0.05 (see Table 4.9).

	Low-performing Object Permanence (n = 12)	**High-performing Object Permanence (n = 12)**	**Statistical Difference**
6 – 9 months			
Contact	*M* = 39.8% *SD* = 16.0%	*M* = 29.4% *SD* = 11.9%	F (1, 22) = 3.21 *p* = 0.09
Movement	*M* = 21.8% *SD* = 3.2%	*M* = 24.5% *SD* = 3.9%	F (1, 22) = 3.52 *p* = 0.07
Independent Movement	*M* = 19.4% *SD* = 5.0%	*M* = 23.6% *SD* = 4.8%	F (1, 22) = 4.29 *p* = 0.05*
Independent Movement per Hour	*M* = 13.3 *SD* = 2.7	*M* = 16.2 *SD* = 3.6	F (1, 21) = 4.98 *p* = 0.04*

Table 4.9: Object permanence participation over 1 to 2 years and early experience. Comparing behavior and early experience between individuals that are “low-performing” in the object permanence task (consistent no search, failed search, or random search in both years of testing) and “high-performing” in the object permanence task (consistent search and success in both years of testing)

I then compared groups based on their performance when they were first exposed to the A-not-B object permanence task at 14 to 16 months. Here, I found that individuals that did not attempt to search for the reward experienced significantly higher rates of maternal abuse and rejection in the first three months (m = 3.72 times per hour, sd = 3.37) compared to those that attempted search regardless of their performance (m = 1.52 times per hour, sd = 1.78); F(1, 37) = 7.10, p = 0.01, which further supports that intense, premature maternal weaning behavior can negatively impact willingness to participate in novel tasks a year later. Additionally, there was no difference in rates of abuse and rejection between those that appeared to search randomly (m = 1.52 times per hour, sd = 1.64) and those that were successful (m = 1.60 times per hour, sd = 2.08); F(1, 20) = 0.01,

$p = 0.92$, which suggests that early maternal abuse and rejection is only interacting with participation rather than performance (see Table 4.10).

To further examine what might be influencing participation and performance on this search task, I compared the 12 individuals that did not search at all in their first year to the 10 individuals that appeared to search randomly in their trials and to 12 individuals that searched correctly in all of their trials and qualified for stage V object permanence. From 0 to 3 months, individuals that qualified for stage V object permanence in their first year trended towards more independent movement ($m = 59.2\%$ of all movement, $sd = 10.7\%$) than those that randomly ($m = 47.9\%$, $sd = 13.9\%$); $F(1, 17) = 3.99$, $p = 0.062$, while there was no difference compared to those that did not attempt search in this task ($m = 60.9\%$ of all movement, $sd = 7.2\%$); $F(1, 16) = 0.14$, $p = 0.71$. Individuals that qualified for stage V object permanence in the first year also trended towards spending less time riding dorsally or ventrally on their mothers in the first few months ($m = 1.47$ hours, $sd = 0.31$) compared to those that exhibited random search behavior ($m = 1.81$ hours, $sd = 0.43$); $F(1, 17) = 4.07$, $p = 0.06$, while there was no significant difference compared to those that did not search ($m = 1.31$ hours, $sd = 0.39$); $F(1, 16) = 0.86$, $p = 0.37$.

Those that qualified for stage V object permanence in their first year also participated in a significantly higher rate of social play from 6 to 13 months ($m = 3.83\%$ of the time, $sd = 2.0\%$) compared to those that searched randomly (2.1% of the time, $sd = 1.4\%$); $F(1, 20) = 5.239$, $p = 0.033$, while there was no difference in rates of social play compared to those that did not search at all ($m = 2.8\%$, 1.3%); $F(1, 22) = 2.42$, $p = 0.13$. There were also trends where individuals exhibiting stage V object permanence in their first year spent more time moving and traveling independently (m = 22.6% of their time, sd = 5.3%) than those that searched randomly (m = 18.3%, sd = 5.0%); F(1, 20) = 3.80, p = 0.065, and they spent less time riding on mom when traveling (m = 1.0%, sd = 1.8%) than those that searched randomly (m = 2.8%, sd = 2.4%); F(1, 22) = 4.13, p = 0.056. Again, there was no significant difference in independent movement when compared to individuals that did not search (m = 20.6%, sd = 3.2%); F(1, 22) = 1.26, p = 0.27, and no significant difference in time spent traveling on mom when compared to those that did not search (m = 1.5%, sd = 2.1%); F(1, 22) = 0.398, p = 0.54 (see Table 4.10).

	No Search 14-16 months (n = 12)	**Search 14-16 months (n = 27)**	**Statistical Difference**
0 – 3 months			
Abuse and Rejection per hour	*M* = 3.72 *SD* = 3.37	*M* = 1.52 *SD* = 1.78	F (1, 37) = 7.10 *p* = 0.01**
	Random Search 14-16 months (n = 10) **No Search 14-16 months (n = 12)**	**Stage V: No Error Object Permanence 14-16 months (n = 12)**	
0 – 3 months			
Abuse and Rejection per hour	*M* = 1.52 *SD* = 1.64	*M* = 1.60 *SD* = 2.08	F (1, 20) = 0.01 *p* = 0.92
	M = 3.72 *SD* = 3.37		F (1, 22) = 3.43 *p* = 0.077
Travel on Mom	*M* = 1.81 hours *SD* = 0.43	*M* = 1.47 hours *SD* = 0.31	F (1, 17) = 4.07 *p* = 0.06
	M = 1.31 hours *SD* = 0.39		F (1, 16) = 0.86 *p* = 0.37
Percentage of Movement that is Independent	*M* = 47.9% *SD* = 13.9%	*M* = 59.2% *SD* = 10.7%	F (1, 17) = 3.99 *p* = 0.062
	M = 60.9% *SD* = 7.2%		F (1, 16) = 0.14 *p* = 0.71

Table 4.10: Object permanence at 1 year and early experience. Comparing early experience between individuals that did not search in their first year of object permanence testing and those that did; and comparing those that passed stage V object permanence, those that appeared to search randomly, and those that did not search in any of their trials in their first year of object permanence testing.

	Random Search 14-16 months (n = 10) **No Search 14-16 months (n = 12)**	**Stage V: No Error Object Permanence 14-16 months (n = 12)**	
6 – 13 months			
Travel on Mom	*M* = 2.8% *SD* = 2.4%	*M* = 1.0% *SD* = 1.8%	F (1, 22) = 4.13 *p* = 0.056
	M = 1.5% *SD* = 2.1%		F (1, 22) = 0.40 *p* = 0.54
Independent Movement Overall	*M* = 18.3% *SD* = 5.0%	*M* = 22.6% *SD* = 5.3%	F (1, 20) = 3.80 *p* = 0.065
	M = 20.6% *SD* = 3.2%		F (1, 22) = 1.26 *p* = 0.27
Social Play	*M* = 2.1% *SD* = 1.4%	*M* = 3.83% *SD* = 2.0%	F (1, 20) = 5.24 *p* = 0.033*
	M = 2.8% *SD* = 1.3%		F (1, 22) = 2.42 *p* = 0.13

Table 4.10 CONT'D: Object permanence at 1 year and early experience. Comparing early experience between individuals that did not search in their first year of object permanence testing and those that did; and comparing those that passed stage V object permanence, those that appeared to search randomly, and those that did not search in any of their trials in their first year of object permanence testing.

Again, while these comparisons were deliberately separated out to capture differences in the impacts of frequency, duration, and quality of early experience at different time points within a small sample size, I used Bonferroni corrections to account for the multiple comparisons made and only considered significance for p values less than 0.01. At this alpha level, there was only a significant difference in the rate of maternal abuse and rejection in the first three months between those that participated and those that did not participate in the search task in their first year of exposure (p = 0.01). Taken with the previous results, this further supports that the intensity and onset of weaning behaviors may have a lasting effect on an individual's participation in multiple cognitive tasks, but do not indicate any clear influence on performance among participating individuals.

After Bonferroni corrections, there were no significant differences in locomotion and play between successful and unsuccessful searchers in the object permanence task, but even without significance, there were consistently much larger differences between successful and unsuccessful searchers in these domains than between successful searchers and those that did not attempt search at all. Non-searchers only differed in their rate of maternal abuse and rejection, while successful and unsuccessful searchers did not. These results indicate that early motor experience and enrichment may still be interacting with cognitive development in rhesus macaques, and additional testing is required to further uncover the nature of this relationship.

Discussion

In humans, the onset of locomotion can directly facilitate the development of spatial perception and shifts in motor development are highly correlated with improvements in spatial search performance, means-ends reasoning, and attention to allocentric spatial properties. However, it is difficult to investigate the interaction between motor and cognitive development in species that do not exhibit the same gradual transitions from immobility to crawling to walking over several months. Still, it is possible that the quality of early motor experience can still impact cognitive development in a dynamic system. While rhesus macaques are fairly mobile from birth, there is still a lot of variation in the onset, frequency, and duration of their exploration in an environment, which is also mediated by maternal weaning behaviors. Accordingly, it is important to carefully investigate how the maternal-infant dynamic and early exploration have distinct impacts on an individual's performance and participation in cognitive tasks over the first two years.

I found that infants spend the overwhelming majority of their time in proximity and contact with their mothers in their first three months and only began regularly exploring away from their mothers around 6 weeks. Over the course of their first year, they consistently decreased their time in proximity and contact with their mothers and gradually increased the frequency that they made and broke contact. When infants reached 6 months, their mothers resumed mating, which marked a period of more intense weaning behaviors, and the frequency of mother-initiated separations and infant-initiated separations and reunions were tightly correlated with the amount of maternal abuse and rejection experienced at that time. Early maternal abuse and rejection clearly encouraged the amount that mother and infant broke contact and correlated with infant independence, but this does not fully capture the socioemotional impact of early and intense abuse and rejection.

If independent locomotion and exploration improves attention to allocentric spatial relationships in rhesus macaques, I would expect to see consistent correlations between highly independent behaviors and allocentric attention in the spatial coding looking time task conducted with participants were between 14 and 16 months. However, I found the exact opposite. "Egocentric" individuals were consistently showing more separations and reunions than "allocentric" individuals and spent a greater proportion of their movement on their own. Though, they did not necessarily experience more enriching movement overall, and after correcting for multiple comparisons, I revealed that “egocentric” individuals differed from “allocentric” individuals most in the frequency of the maternal weaning behaviors they experienced. From 6 to 9 months when weaning was at its peak, “egocentric” coders experienced significantly higher rates of maternal abuse and rejection per hour than “allocentric” coders and therefore broke and made contact with their mothers more. This revealed an interesting relationship between the nature of the weaning process and spatial attention that was not predicted and requires additional testing to clarify how weaning experiences might interact with cognitive development and possibly facilitate an egocentrically oriented attention.

It is possible that we are not accurately interpreting the looking time results that were used to evaluate spatial coding abilities, but because these conditions only differ in the relative location of the objects in the array, we know that the consistency in looking independent of the order of exposure must be due to some attention to spatial relationships. Still, these results do not expose any relationships between allocentric attention and a more enriching and dynamic early environment.

To further investigate how early experiences might interact with cognitive development in rhesus macaques, I compared high- and low-performing individuals in support problem and object permanence tasks based on their success over two years of testing. While I found that low-performing individuals in the support problem task rested more in their first few months and high performing individuals exhibited more independent movement, these results were inconclusive due to their inconsistency across multiple measures of independence and across different time points. After controlling for multiple comparisons, I found no significant differences in the motor development or early environment of high- and low-performing individuals, though I did reveal significant differences between those that participated and those that did not participate in these tasks during their first exposure. Individuals that did not participate in the support problem task and in the object permanence task in their first year experienced significantly higher rates of maternal abuse and rejection in the first three months than those that did participate. These results further support a meaningful relationship between the nature of the maternal-infant dynamic and participation in cognitive tasks one to two years later, and they support the prediction that intense and premature maternal abuse and rejection will impact an individual's attachment and anxiety in novel spaces later in life. However, they do not clarify how early experiences might facilitate the development of allocentric reasoning, means-ends reasoning, and object permanence.

I then compared the early experiences and behaviors of those that participated in the object permanence task in their first year of exposure and found no significant difference in the amount of early maternal abuse and rejection experienced between consistently successful searchers and unsuccessful searchers. This indicated that early maternal weaning behaviors were not necessarily impacting proficiency at this task. Instead, successful and unsuccessful searchers differed most in their movement, travel, and play, where successful searchers exhibited consistently higher rates of independent locomotion and play than unsuccessful searchers while non-searchers did not differ in these domains. These comparisons were not significant after Bonferroni correction, but they consistently supported the prediction that the quality of early interactions with an environment will influence performance in search tasks more than participation, while stressful encounters early in life are more likely to impact participation in novel testing scenarios.

Even without the same gradual motor development as humans, early independent movement, exploration, and play may still improve cognitive development in rhesus macaques, and additional testing is required to further understand the nature of this relationship. Additionally, we reveal competing costs and benefits of early maternal weaning behaviors, where an early onset of maternal abuse and rejection can encourage infant independence but negatively impact an infant's engagement with the environment. Considering the divergence in motor development between humans and rhesus macaques, we must further explore how the interaction between maternal-infant dynamics and infant locomotion facilitates rhesus cognition differently than in humans when interactions with caregivers and the physical environment are differently weighted. How might individuals with highly abusive mothers and high rates of independent locomotion compare to those with low rates of abuse and high rates of locomotion, high rates of abuse and low rates of locomotion, or low rates of abuse and low rates of locomotion? Additionally, maternal behaviors can take many qualitatively different forms, where mothers can be both highly abusive and highly protective. These details of early experience can be addressed with larger sample sizes and more consistent cognitive testing in the field and in the laboratory.

With these measures alone, it is difficult to determine whether certain individuals are just more precocious, but with additional testing we can begin to uncover causal relationships between early experience and cognition and determine how the early environment is formative on a mechanistic level. Though, these methods do contribute to a unique longitudinal database in which to explore emergent shifts in development and offer a comprehensive comparison between cognitive abilities and early behaviors in a nonhuman, free-ranging species for the first time.

Chapter 5

Conclusions

Research in humans has revealed a dynamic system of early development, where shifts in motor development interact with shifts in cognitive development, and where milestones in object permanence, spatial representation, means-ends reasoning, mental representation, inhibition, and attention repeatedly overlap early in life. These multimodal experiences self-organize to produce cohesive patterns in an individual's mind and biology, and small variations in the components of this dynamic system can lead to large differences in behavior. From birth to juvenility, humans exhibit a dramatic change from immobility to bipedal locomotion that coincides with many dramatic advancements in behavior and cognition, and over such a long developmental period, many factors can contribute to the emergence of universal milestones and dictate individual differences in ability. Still, the consistency of these dynamic systems has not been studied in a species of nonhuman primate with a similar developmental trajectory but some divergence in their motor and cognitive development.

I addressed three central questions: 1) do rhesus macaques exhibit a consistent spatial coding system when attending to small-scale visuospatial tasks in rotation?, 2) is there an interaction between spatial coding, object permanence, means-ends behavior, and gaze following early in development?, and 3) what interactions exist between early experiences and cognitive development? Each component contributes to a better understanding of the dynamic systems involved in spatial cognitive development in a nonhuman primate.

Spatial coding in small-scale visuospatial rotation tasks

To first address emergent spatial coding systems in rhesus macaques at one year, I introduced individuals to two conditions of a small-scale visuospatial task that only differed in whether a reward appeared in a location that was consistent with an exclusively egocentric spatial attention or in a location that was consistent with allocentric spatial relationships. In humans, the shift from egocentric to allocentric perspectives emerges with locomotor onset, and the use of allocentric spatial properties improves over the first few years with exploration and language acquisition. Yearling rhesus macaques have been independently locomoting and exploring their environment for over a year and should exhibit some capacity to attend to allocentric relationships. Accordingly, I predicted an overall capacity to identify and differentiate impossible and possible rotational displacement scenarios by attending to the relative positioning of objects in an array.

Participants responded to change in both conditions, however, they did not appear do differentiate between the two conditions in the same way. Instead, individuals exhibited consistent differences in their reaction to each condition. Some responded to the egocentric condition as a possible violation of their expectation but lost interest in the allocentric condition, while others responded to the allocentric condition as a violation of their expectation but lost interest in the egocentric condition, and these patterns in looking time were independent of their order of exposure. Looking time tasks are difficult to interpret since there are many reasons why an individual might increase or decrease their attention to a stimulus, and these methods are often used to compare averages in large population samples. However, looking time may be inconsistent across a population due to individual variation and it is important to further investigate how consistency in looking time might capture individual categories of expectation.

Accordingly, at least 14 individuals could be categorized as prioritizing allocentric information and at least 10 individuals could be categorized as prioritizing egocentric information. Rather than observing a clear shift from egocentric to allocentric attention, these results support a more dynamic system where small differences in development have resulted in individual differences in spatial processing and attention.

I further tested their attention to another small-scale visuospatial task comparing a rotated and altered image and found no significant differences in their attention to either condition overall. However, individuals that were categorized as prioritizing egocentric information in the other visuospatial task spent more time investigating the rotated image than those that appeared to prioritize allocentric information, which provided some evidence that spatial coding may interact with the speed of processing a rotated image, even when yearling rhesus macaques do not exhibit evidence for mental rotation and representation abilities overall. Though, spatial attention did not appear to interact with their ability to differentiate between rotated images.

Cognitive interactions across early development

I tested the same subjects on a more thorough cognitive battery and found that gaze following abilities appeared to improve the most in the first year of life and participation in an A-not-B object permanence task also improved from the first to second year of testing, but with comparable performance in both years. Unfortunately, I did not introduce an object permanence task in the first few months, so I was unable to capture any dramatic transitions in this domain. Though, in both years of testing, participants successfully recovered the reward at above chance levels, confirming achievement of object permanence as high as stage V. However, I found no evidence of stage VI object permanence overall when individuals were tested on more complex invisible displacements after the second year. Still, individuals exhibited internal consistency or improvement in the A-not-B task from one year to the next, which illustrates a successful introduction of spontaneous search tasks in a free-ranging animal that is infrequently tested in an isolated environment.

Only half of those tested attempted to pull a support to access a distant reward in their first and second year, but the majority pulled the support at least once in either year. This suggests a capacity to attend to distal information and enact intermediate steps to achieve a distant goal, but when individuals were tested on a support problem task that compared a choice between a causally relevant and irrelevant support, participants overall did not choose the causally relevant support at levels above chance. This indicates that while individuals did exhibit means-ends behaviors to achieve a distant goal, they did not necessarily understand the efficacy of their actions. Though, both this task and the invisible displacement tasks had such low participation at the end of the cognitive battery that these results are inconclusive. Additionally, because rhesus macaques do not exhibit any natural tool use behaviors, the conditions of this task may not have been sufficiently salient to capture causal reasoning in young rhesus macaques and could be improved with more ecologically relevant methods.

I further investigated how these cognitive abilities might overlap in a dynamic system to produce variation in proficiency, and I found a positive relationship between successful search in the A-not-B task and the act of pulling a support to reach a distant reward in both years of testing. This emphasizes a possible relationship between object permanence and means-ends behaviors in the development of rhesus macaques from infancy to juvenility. Moreover, there was a significant relationship between attention to allocentric information at one year and performance on the support problem task and an invisible displacement task the following year, which also supports the prediction that attention to spatial relationships will positively interact with object permanence ability and means-ends behaviors early in rhesus macaque development. There were also trends where consistent gaze following coincided with more successful search and pull behaviors, but the absence of any significant correlations may indicate a notable divergence in human and nonhuman developmental systems, where joint attention does not have the same strength of influence and interaction early in development. Though, it is important to note the difficulty in measuring subtle gaze following behaviors.

Dynamic relationship between experience and cognitive development

To determine what interactions in early experience might inform these individual differences in cognitive performance, I compared the early environments of individuals with different degrees of task mastery and attention. In humans, social and motor milestones are intimately connected with shifts in spatial attention, object permanence, and means-ends reasoning, and while rhesus macaques exhibit similar shifts in cognition, they do not exhibit the same progression of gross motor development.

Over the first year, infants steadily increased their time away from their mother, and therefore exhibited a steady increase in their independent movement overall. Though, rates of separation and independence were highly correlated with rates of maternal abuse and rejection. This introduces conflicting costs and benefits of the weaning process, which can have both positive or deleterious effects on infant cognitive development. There were also noticeable differences in the frequency of maternal abuse and rejection in mothers of different ages and rank, between infant sexes, and depending on whether a sibling was born in the first year, but there were no apparent differences in cognitive abilities within these categories.

I found that contrary to predictions, individuals categorized as “allocentric” in the first year actually exhibited lower average rates of independent movement and lower rates of making and breaking contact with their mother than those that appeared to prioritize “egocentric” information. Though, after Bonferroni correction, these groups only differed significantly in their rates of maternal abuse and rejection and bouts of separation and reunion during the weaning process at 6 to 9 months, which indicates an interesting interaction between weaning dynamics and spatial that was not predicted and requires additional testing.

I compared high- and low-performing individuals in the support problem and object permanence tasks across both years of testing and found some evidence for more independence and activity in high-performing individuals, but there was little consistency across measures and time points, and these differences were insignificant after correcting for multiple comparisons. Though, individuals that did not participate in their tasks during the first year of exposure continued to exhibit significantly higher rates of maternal abuse and rejection in their first three months than those that did participate in their tasks. These results are consistent with the prediction that severe, early onset of maternal aggression may increase anxiety and reluctance in the novel environments which impacts cognitive task participation, but there was no clear indication that early maternal abuse and rejection impacted cognitive performance.

When I compared consistently successful and random searchers in the object permanence task in the first year, successful searchers did not differ from random searchers in their rates of early maternal abuse and rejection. Instead, they exhibited higher rates of independent movement and play than random, unsuccessful searchers and did not differ from those that did not participate. These relationships were not significant after correcting for multiple comparisons, but they reveal a possible interaction between early enrichment and performance that is distinct from the impact of early maternal abuse and rejection.

General Conclusions

Overall, these results support dynamic systems in rhesus macaque development over the first year that generate individual differences and interactions in behavior and cognition. Variation in how individuals process spatial information appears to interact with variation in their object permanence and support problem abilities as well as variation in their maternal-infant dynamics. In particular, maternal abuse and rejection appears to negatively impact attention and participation in a cognitive battery with some evidence that motor experience and positive social interactions in the first year may contribute to more successful search performance even after the onset of locomotion.

Rhesus macaques differ from humans in the relative timing of their major cognitive and motor milestones and in their eventual cognitive repertoire, but they exhibit many of the same relationships throughout early development. Perhaps most importantly, these results provide validation for novel methods used to interpret individual differences in looking time, and they introduce a spontaneous cognitive battery conducted in a population of young, free-ranging rhesus macaques with no prior exposure and only one opportunity for isolated testing each year that produced meaningful results. These innovative approaches successfully elicited participation and captured consistency in performance, and these methods will remain invaluable to future research on the study of development in complex, higher order cognitive skills in wild and free-ranging environments.

Future directions

While these methods generated significant and intriguing results, they could be improved upon in many ways. Refining presentation techniques and constructing more visually distinct stimuli may better capture significant differences in interactions and looking time, and repeated exposures would better establish consistency and change over time and as a function of experience. Presenting simultaneous choices could also better measure preference and performance and introducing more controls would more reliably confirm our interpretations. While these studies did not reveal a capacity for causal reasoning and invisible displacements in this group of rhesus macaques, more time for testing would hopefully improve participation in these tasks to more accurately capture overall and individual proficiency.

Understanding the processes by which motor development facilitates and interacts with psychological change and spatial-cognitive development can provide insight into alternative developmental pathways that might assist individuals with delays or impairments in motor and cognitive milestones, and additional research can better reveal causal relationships between these variables and show how shifts in neural networking, physiology, and genetics interact within this dynamic system. Frontal lobe development interacts with sensorimotor and cognitive development and environmental experiences can shape neuronal networks and neural developments, and we can only improve our understanding of these systems by incorporating data on simultaneous changes in the brain. Additional measures of physiological development can also capture how the maternal-infant dynamic might specifically influence an individual's attention and participation in a cognitive battery, and further investigation into the epigenetic interactions between early experience and genetic, physiological, biological, and cognitive development can reveal the depth to which these dynamic systems shape the individual.

Emergence

Development is a dynamic process with ongoing reciprocity between perception, action, and cognition. Locomotion might generate experiences that trigger developmental shifts in cognition, but it does not have a singular effect. Development is a process by which we describe regularities and consistencies in nature, but these rules are not deterministic. Systems of being are far greater than the sum of their rules and relationships, and through our curiosity and exploration, we continue to generate novelty which paves infinite new futures.

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