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Natalie Pilgeram

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Individual variation in typically developing rhesus macaque infants (*Macaca mulatta*): The role of matrilineal social rank

By

Natalie R. Pilgeram
Doctor of Philosophy

Graduate Division of Psychology

Jocelyne Bachevalier, Ph.D.
Advisor

Patricia Bauer, Ph.D.
Committee Member

Warren Jones, Ph.D.
Committee Member

Donna Maney, Ph.D.
Committee Member

Mar Sanchez, Ph.D.
Committee Member

Accepted:

Kimberly Jacob Arriola, Ph.D., MPH
Dean of James T. Laney School of Graduate Studies

Date

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Natalie R. Pilgeram
M.A., Emory University, 2020

Advisor: Jocelyne Bachevalier, Ph.D.

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Abstract

Individual variation in typically developing rhesus macaque infants (*Macaca mulatta*): The role of matrilineal social rank

By Natalie R. Pilgeram

Newborn primates acquire vital information about the social world first and foremost through caregivers, relying on dynamic, species-typical exchanges of vocalizations, facial expressions, and shared gaze. Infant-caregiver interactions are facilitated by neonates' attentional preference for socially informative cues like conspecifics' eyes. In studies of this early-emerging visual preference, rhesus macaques (*Macaca mulatta*) are an indispensable model system due to the species' altricial birth, extended development, and complex social life. Rhesus macaques live in matriarchal groups structured around highly stable, linear dominance hierarchies. Ranking is transferred intergenerationally from dams to their offspring. For infants, the social environment is shaped from birth by their dams' social status, yet it is not clear to what extent rank explains interindividual variation in social development, or at what age(s) such differences emerge. The goals of this dissertation were to: (1) investigate the role of matrilineal rank in the social development of male rhesus macaques during the first year of life and (2) identify behavioral measures in early infancy that predict social competency in the juvenile stage. Development was tracked longitudinally from birth to 1 year of age in male infants born and reared at the Emory National Primate Research Center Field Station (Lawrenceville, GA). In Study I, maternal behavior and focal infants' interactions with groupmates were analyzed from 2 weeks of age through 1 year. The data showed effects of matrilineal rank on some maternal behaviors, but not on infants' interactions with groupmates. In Study II, eye-tracking data were collected over 14 sessions spanning the first 6 months of life, during which infants voluntarily viewed videoclips depicting a single conspecific or dam-infant interactions. The results suggested that by 4 to 5 months of age, low-ranking infants developed covert viewing strategies in order to monitor social cues while avoiding direct eye contact with conspecifics. In addition, rates of initiating social play at 1 year were positively predicted by saccades to dam-infant videos, but negatively predicted by both maternal cradling and rates of withdrawing at younger ages. Overall, this dissertation demonstrated the value of the rhesus macaque model for investigating the neurobiological processes supporting evolutionarily conserved social abilities among primates, as well as the disruption of these processes in atypically developing infants and children.

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GENERAL INTRODUCTION

Newborn primates acquire vital information about their world first and foremost through caregivers, relying on dynamic, species-typical exchanges of vocalizations, gestures, physical touch, facial expressions, and eye gaze. The latter two domains are the frequent focus of an expansive and growing body of research into the mechanisms of “social-visual attention.” This compound term - sometimes used interchangeably with “social-visual engagement” – has been broadly defined as “attention (orienting, focusing and disengagement of visual systems) in the context of social streams of information” (Salley & Colombo, 2016, p. 3), “a preference for social stimuli, such as faces, eyes, and body motions” (van Rijn et al., 2019, p. 565), or simply as “flexibly changing one’s behavior or attention in response to social information” (Wang, 2019, p. 1). In this dissertation, I discuss social-visual attention in the developmental context, as the attentional bias of infants towards socially informative visual “cues” like the eyes, mouth, and face of conspecifics. This early emerging preference scaffolds the maturation of increasingly complex social cognitive capacities, such as mutual/shared gaze, gaze following, and perspective taking (Emery, 2000; Klin et al., 2015; Wagner et al., 2013; Wang, 2019).

In this introduction to the dissertation, I first provide an overview of three theoretical frameworks through which to investigate social-visual attention, and early social development more generally: (1) niche construction, (2) endophenotypes, and (3) developmental continuity and early prediction. I then introduce the non-human primate (NHP) model used in the studies that constitute this dissertation, and review its practical advantages, before describing how matrilineal dominance ranking in NHPs can be studied as a window into early developmental processes. Finally, I summarize the overall aims of the research and briefly describe Study One and Study Two in turn.

ATYPICAL SOCIAL DEVELOPMENT: ECOLOGICAL & CLINICAL PERSPECTIVES

Ontogenetic Niche Construction

"Niche construction" is a theoretical framework borrowed from ecology and evolutionary biology; applied to developmental science, this approach emphasizes that offspring are raised by caregivers within surroundings constrained by the wider environment, in particular the social environment (Fairbanks, 1996; Flynn et al., 2013; Karmiloff-Smith, 1998). In this view, young animals move through early life in a "niche" that is shaped profoundly by the social context, resulting in the *construction* of alternative pathways of development. The developmental, or ontogenetic, niche construction framework as applied to an NHP model will be covered in a later section. This framework is also instructive in conceptualizing atypical development in human children. Indeed, niche construction has consilience with transactional models of development that emphasize the child's ability to flexibly engage with and adapt to atypical environments (Constantino et al., 2021). Autism[1], for example, has been understood as the downstream result of niche construction, as early disruptions to social-visual attention push infants to adapt to an atypical sensory world (Johnson, 2017; Klin & Jones, 2018; Shultz et al., 2015, 2018). In other words, autism is an adaptive and "perfectly ordered developmental response in the face of an unusual starting state" (Johnson, 2017, p. 6).

Developmental Endophenotypes

Disruptions to social-visual attentional processes are frequently observed in conjunction with serious perinatal challenges; infants with congenital heart disease, infants born prematurely, and infants with low birth weights are all at increased risk for later impairments in speech and social functioning (de

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[1] Throughout this dissertation, I have made efforts to respect the preferences of autistic self-advocates and professionals, as stated in the online terminology guide created in 2023 by a multinational workgroup within CAPTAP, the Community Against Prejudice Towards Autistic People (see also Bottema-Beutel et al., 2020). Following CAPTAP's guidelines, I use identity-first language (i.e., "autistic child" rather than "child with autism") and avoid diagnostic terminology such as "Autism Spectrum Disorder" except when necessary for the sake of clarity and/or precision.

Schuymer et al., 2012; Dudova et al., 2014; King & Bearman, 2011; Kuban et al., 2016; Larsson et al., 2005; Losh et al., 2012; Marino et al., 2015; Pritchard et al., 2016). The mechanism underlying atypical social development in vulnerable neonates is not fully understood. It has been suggested that critical caregiver interactions are disrupted in these infants due to parental stress, extended periods of time spent in intensive care units, and/or congenital abnormalities in visual attention. The deprivation of social inputs then results in accumulating and long-term consequences for neurodevelopment (de Schuymer et al., 2012; Field, 1977; Klin & Jones, 2018).

In the case of Autism Spectrum Disorder (ASD), a more circumscribed diagnosis characterized by difficulties with normative social interactions and language (A.P.A., 2013), disruption to social-visual engagement is a candidate *endophenotype* - that is, a measurable factor that represents a portion of the causal pathway for a particular condition (Cannon & Keller, 2006; Constantino, 2018; Gould & Gottesman, 2006; Klin et al., 2015). In Cannon and Keller's "watershed" model (2006), endophenotypes are the many intermediate "tributaries" linking "upstream" biological factors (e.g., specific alleles) to the "downstream" disorder. Among a list of proposed criteria (see Cannon & Keller, 2006; Gould & Gottesman, 2006), endophenotypes should be heritable, found along a continuum (or "spectrum") in the general population, and observed at higher rates in family members of diagnosed individuals. Autism is not a pathology; however, we do know that individual differences in social-visual attention are heritable and are often observed in the close family members of children diagnosed with ASD (Constantino et al., 2017; Wagner et al., 2018).

Disruption to social-visual engagement during early infancy is perhaps "*necessary* but not *sufficient*" (Constantino, 2018, p. 21) for the genesis of autism, functioning as just one of many potential developmental endophenotypes (reviewed by Constantino, 2011). Klin and Jones have hypothesized that "the (vastly heterogenous) nature of autism is nevertheless well-captured by a syndromewide entity…not because of commonalities across the hundreds of initial causes (the so called 'autisms') but because of commonalities in what these causes disrupt: infant-caregiver reciprocal social engagement, the universal platform for survival that is also co-opted as a platform for social and communication brain-behavior development" (2018, p. 5).

Continuity, Discontinuity, & Early Prediction

Continuing advancements in neonatal medicine are likely to increase the proportion of high-risk infants that will survive adverse perinatal events. It is therefore increasingly important to identify factors that support development of the attentional processes necessary for accessing the social information provided by caregivers. Identifying divergence from typical social development in humans is a subjective process that currently relies on in-person assessment by a specialized clinician. In the case of ASD, the earliest age at which reliable diagnosis is possible is 18 months (Johnson & Myers, 2007). In practice, the median age of diagnosis in the United States is 49 months, extending to as late as 59 months, or nearly five years of age, in certain states (Maenner et al., 2023). A central aim of autism research is to facilitate early diagnosis and thus the timely provision of behavioral therapies and support services, in particular by identifying objective behavioral markers in infants that predict the later emergence of autistic traits (e.g., see Jones et al., 2023a, 2023b; Shic et al., 2022).

In pursuing the goal of identifying early developmental markers, researchers assume a clinically meaningful relationship between early development and late development, such that it is possible, with reasonable accuracy, to predict at very early ages the developmental outcomes observed at later ages. Studies of atypically developing infants do provide some evidence of continuity between early and late social development. Jones and Klin (2013), for example, found a robust correlation between the degree of early decline in eye fixation and the level of social disability at two years of age. Evidence for continuity has also been found in the context of typical development via prospective studies aimed at quantifying individual, nonclinical differences (see, e.g., Morales et al., 2000a, 2000b; Schietecatte et al., 2012; Wagner et al., 2013). The extent to which interindividual variability in social functioning is trait-like, stable across time, and predictable remains, however, a pressing question in the field of developmental psychology.

A NON-HUMAN PRIMATE MODEL OF SOCIAL DEVELOPMENT

In order to study atypical developmental trajectories, it is essential that we begin from a detailed, accurate understanding of how *typical* development progresses. NHP models have proven to be a powerful tool in this effort. In particular, rhesus macaques (*Macaca mulatta*) are indispensable as a model system due to their rich and complex social life, altricial birth, and extended development with distinctive stages of infancy and juvenescence (reviewed by Machado & Bachevalier, 2003). Modelling the earliest periods of development in macaques offers the practical advantage of an accelerated timeline, as 1 week for a newborn macaque is roughly equivalent to 1 month in the life of a human infant (Boothe et al., 1985). The four to one ratio in developmental progression means that projects involving longitudinal data collection can be completed in a quarter of the time that would be required for a study with human participants. Working with NHPs also makes dense longitudinal sampling of developmental data more feasible, since it avoids the logistical challenges of requesting that participating caregivers bring their infant into the lab or clinic on multiple, closely spaced dates. Finally, human infants are brought up in environments that are staggeringly variable in housing quality, intensity and variety of sensory inputs, nutrition, availability of healthcare, exposure to environmental toxins, age and gender of primary caregiver(s), educational resources, language(s) spoken, etc. An additional benefit of NHP models in general is the ability to remove confounding factors and control the wider context in which development unfolds (Feldman, 2015).

In 2019, the National Institute of Mental Health (NIMH) issued a notice containing guidelines for the use of nonhuman animal model in basic or pre-clinical neurobehavioral research. The authors recommended that animal models be used "*for* addressing neurobiological questions rather than [as] models *of* specific mental illnesses" (NIMH, 2019, emphasis added). In line with these recommendations, the rhesus macaque model introduced here was intended to reflect core developmental processes that are evolutionarily conserved among primates (see Machado & Bachevalier, 2003). Though some aspects of early social-visual engagement are species-unique, humans and macaques alike exhibit experience-dependent individual differences in attention (Kano et al., 2018). Much like human children, young macaques engage in frequent play and interact closely with caregivers. An attentional bias towards direct gaze in conspecific faces emerges in early infancy and peaks at around two months (roughly analogous to eight months for a human infant)(Muschinski et al., 2016). This early bias for direct gaze likely facilitates instantiation of shared gaze and mother-infant interactions more generally (Ferrari et al., 2009). Beginning at two to three weeks after birth, macaque females bond with their infants through dynamic exchanges of eye contact (mutual gaze) and exaggerated lipsmacking (a species-typical affiliative behavior). Dams may lick and groom the area around her infant's eyes, or even manually grasp and tilt its head upwards in order to initiate mutual gaze. Mother-infant interactions of this type continue through around two months of age but are especially frequent and robust in the infant's first few weeks. The suite of behaviors has been compared to the "motherese" shared between human infants and their caregivers, which is similarly characterized by close physical contact, mutual gaze, and exaggerated facial expressions (Ferrari et al., 2009).

Also shared between humans and macaques are significant features of neural structure and neurodevelopment. Macaques rely on vision as their primary sensory system, making social-visual attention a central factor in their development (Boothe et al., 1985; Machado & Bachevalier, 2003). Importantly, the rhesus macaque model reflects *prelinguistic* developmental processes in human infants. Despite the accelerated pace of development in rhesus macaques, there are striking parallels between macaque and human infants in patterns of social-visual attention across time. These patterns likely indicate an evolutionarily conserved transition in primate neurodevelopment from subcortical to cortical visual processing (Muschinski et al., 2016; Parr et al., 2016; Wang et al., 2020; see also Distler et al., 1996; Johnson, 2005; Morton & Johnson, 1991).

MATERNAL RANK “INHERITANCE” & NICHE CONSTRUCTION

The same set of guidelines released by the NIMH in 2019 stated, “Appropriately designed behavioral studies will consider…multiple interacting processes…that contribute to measures, and will identify and control for nonspecific mediators to enable unbiased interpretation of results…” In studies of rhesus macaques, one such nonspecific, interacting variable is individual social ranking. Rhesus macaques live in matriarchal social groups structured around highly stable, linear hierarchies. As will be discussed in greater detail throughout this dissertation, social status is transmitted intergenerationally from females to their offspring; matrilineal rank is thus a significant source of variation in the external rearing environment (Altmann, 1962; Bernstein, 1976; Bernstein & Williams, 1983). In order to effectively leverage this model system, it is critical that we have a thorough understanding of how and to what extent the ranking of their mother impacts typically developing rhesus macaques.

In a number of gregarious mammals including rhesus macaques, the intergenerational transference of social status has been termed “maternal rank inheritance” (Holekamp & Smale, 1991). Is social rank truly “inherited,” though? Wooddell et al. (2017) found that rank acquisition among infant rhesus macaques was predicted by the richness of individuals’ early social environment, as well as familiarity with their physical surroundings, but *not* by individual characteristics like age or weight. Studies of gene regulation in NHPs provide further insight. For example, Tung et al. (2012) separated adult female rhesus macaques into new social groups, introducing individual females sequentially in order to experimentally manipulate their relative rankings, then collected samples of immune cells. Gene expression levels predicted dominance rankings with 80% accuracy; even more compellingly, resampling at later timepoints allowed for accurately predicting shifts in ranking based on gene expression data alone. Importantly, there was no evidence of a distinct, functional “rank gene” or set of genes. Overall, the analysis showed that shifts in dominance status drive plastic shifts in gene expression, whereas there was little evidence of the reverse (see also Sanz et al., 2020). Additionally, if genetic factors do influence the development of rank-related social behaviors, we might expect infants to inherit status even in the total absence of the mother. This has so far *not* been the case in studies of nursery-reared macaques (Bastian et al., 2003; Paukner et al., 2017). It is likely that rhesus macaques acquire their social status over time via interactions with conspecifics and observational learning. Early in life, for example, dominance relations are “acted out” during social play with infant peers (Hinde & Spencer-Booth, 1967).

The behavioral and physiological phenotype associated with subordinate rank therefore seems to be an excellent example of ontogenetic niche construction. For infant rhesus macaques, maternal social ranking is an important variable shaping the developmental niche, if not the most important variable. Related developmental outcomes may then be best understood as functional adaptations to the social environment (Fairbanks, 1996; Flynn et al., 2013; Maestripieri, 2001), and the subordinate phenotype more broadly is more so a matter of evolutionary tradeoffs and “Darwinian fitness” than physiological health or pathology *per se* (Simons et al., 2022, p. 8). Yet questions remain about how the niche of social ranking is constructed: what proportion of individual differences among young macaques is explained by their mother’s rank, and how early in life do such differences emerge? What are the mechanisms by which the subordinate versus dominant phenotypes emerge? And finally, how are these developmental processes modulated by contextual factors like social instability or the size and composition of the social group?

SUMMARY OF STUDIES

The main goals of this dissertation were to: (1) investigate the role of matrilineal social rank in the social development of male rhesus macaques during the first year of life and (2) to identify measures of macaque behavior from early infancy that serve as reliable "predictors" of social competency in the juvenile stage. Towards these goals, the analyses presented here made use of an extensive, longitudinal dataset generated as part of an "Autism Center of Excellence" (ACE) grant (P50-MH100029), which was first awarded in 2012 to our collaborators at the Marcus Autism Center (Atlanta, GA), then subsequently renewed for 2017 – 2023. The Emory National Primate Research Center (ENPRC) collaborated on Project V of the ACE study, the aim of which was to apply methods used to study social development in human infants to the study of species-typical developmental mechanisms in an NHP model (see Ford et al., 2023; Kovacs-Balint et al., 2021; Muschinski et al., 2016; Parr et al., 2016; Wang et al., 2020). Through methods including eye-tracking and behavioral observations, development was tracked longitudinally from birth through one year of age for male rhesus macaque infants born and housed at the ENPRC Field Station (Lawrenceville, GA). Focal infants were reared by their mothers in large, multigenerational social groups. This environment provided infants with species-typical social experiences, while still allowing for variables like diet and housing to be standardized. Only male infants were included to allow for greater power in statistical analyses, as well as to align with the broader translational goals of the ACE grant. The prevalence of neurodevelopmental disability, including social-cognitive challenges associated with schizophrenia, Attention-Deficit/Hyperactivity Disorder, and ASD, is increased among males (reviewed by Santos et al., 2022). In the case of ASD, the male-female ratio is approximately 3:1 (Loomes et al., 2017, Ochoa-Lubinoff et al., 2023).

In Study I, maternal behaviors, mother-infant interactions, and focal infants' interactions with other groupmates were observed and analyzed from 2 weeks through one year of age. A central aim of Study I was to assess the role of matrilineal social ranking in the expression of adaptive social behaviors in infant and juvenile rhesus macaques. I hypothesized that individual variation in mother-infant interactions and, later in life, how juveniles interact with others in their social groups, may be explained in part by differences in ranking within the group hierarchy. Another major aim of Study I was to assess the degree of continuity and predictability in the social development of NHPs by identifying potential behavioral predictors for later social behavior. My expected results/predictions were as follows: (1) subjects that demonstrate high sociality in early infancy will continue to do so as juveniles at 1 year, and (2) subjects that receive more rejecting and less protective maternal care will show greater social confidence as juveniles.

In Study II, I describe the “reverse translation” of eye-tracking methods developed by our collaborators at the Marcus Autism Center (see Jones & Klin, 2013) for use with rhesus macaque infants. Eye-tracking was conducted over 14 sessions spanning the first six months of life. The primary aims of Study II were to: (1) assess the role of matrilineal social rank in the typical developmental trajectory of social-visual attention in rhesus macaques during the early postnatal months, (2) assess the degree of continuity and predictability in the social development of NHPs by identifying features of early social-visual attention as potential predictors of later social behavior, and (3) further test and build on the findings of Wang et al. (2020) and Ford et al. (2023) regarding macaque infants’ attention to the eyes. I also explored a novel, data-driven method for identifying normative developmental milestones in social-visual attention. My main hypothesis was that individual variation in social-visual attention in infant macaques ages 1 – 24 weeks old is explained in part by differences in mother-infant social ranking. In particular, I predicted that infants born to lower-ranking females would show earlier peaks in preferential attention towards salient social cues, compared to higher-ranking infants, as well as an accelerated developmental trajectory at later ages, thus confirming previous findings by Ford et al. (2023).

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Study I: Social Status Shapes Maternal Style towards Rhesus Macaque Infants in the First Year of Life

ABSTRACT

Young monkeys interact closely with their caregivers and are embedded in a complex social environment as they mature. For rhesus macaques (*Macaca mulatta*), this environment is shaped from birth by their dams' rank within the matrilineal dominance hierarchy and, across multiple nonhuman primate (NHP) species, a substantial body of research shows that subordinate females experience high levels of psychosocial stress and thus tend to be more protective of and attentive to their offspring. It is not clear, however, to what extent matrilineal rank explains individual differences in the development of social behavior during infancy, or how early in development such differences emerge. In this study, we investigated the role of matrilineal social status in the behavioral development of 17 typically developing male infant rhesus macaques from birth – 1 year of age. We also aimed to identify behavioral variables at younger ages that were predictive of subjects' social behavior upon their reaching juvenescence at 1 year of age. The majority of behaviors analyzed did not vary by matrilineal rank. The few significant effects of rank were on behaviors related to the mother-infant relationship; infants born to low-ranking dams spent less time in proximity with her and being carried, in addition to experiencing a steeper decline in the overall sensitivity of maternal care received as they approached juvenescence, compared to high-ranking infants. In 1-year-old juveniles, we found that the frequency of initiating social play was negatively predicted by the frequency of withdrawing from peers, as well as by maternal cradling duration, at younger ages. We conclude by discussing the importance of factors including the sex of offspring, species of NHP, and the complexity and stability of the wider social environment in studies of early development.

INTRODUCTION

Among social mammals, the position of a given individual in a group dominance hierarchy is in many species established by way of *maternal rank inheritance*, as it is referred to in the literature (Holekamp & Smale, 1991). For rhesus monkeys (*Macaca mulatta),* the position of an adult female's family in the dominance hierarchy, and her individual ranking within that family, is the most important variable predicting the future status of her daughter(s) (Altmann, 1962; Bernstein, 1976; Bernstein & Williams, 1983). Rhesus macaques live in large, multigenerational, polygynous, and matriarchal societies. Of the over 20 species falling under genus *Macaca*, rhesus macaques are among the least socially tolerant (Abbott, 2003; Thierry, 2007), living in social groups organized by linear, rigid, and highly stable matrilines. As such, the external rearing environment of an infant macaque is shaped from the moment of birth by its mother's status (Bernstein & Williams, 1983; Rowell et al., 1964; White & Hinde, 1975; Wooddell et al., 2020). There is yet much ambiguity, though, about whether social rank –and/or its associated traits - are congenital, presenting at birth or shortly afterwards (Paukner et al., 2017; Suarez-Jimenez et al., 2013), or whether differences based on matrilineal rank emerge later in development (Mandalaywala et al., 2014; Weinstein & Capitanio, 2008).

The social environment is especially dangerous for the offspring of lower-ranking females (Hinde & Spencer-Booth, 1967; Rowell et al., 1964). Subordinate animals, including infants and juveniles, receive frequent aggression and harassment from more dominant animals. Dominance relations are first acted out through social play, with the "rules" of play being circumscribed by matrilineal social rank (Hinde & Spencer-Booth, 1967; Holekamp & Smale, 1991; Wooddell et al., 2017). In agonistic interactions between infants, for example, the aggressor is almost always the infant of higher social status. Infants born to subordinate females begin to experience aggression, and to exhibit submissive behaviors (e.g., withdrawing, grimacing) in response, around the time of weaning at 3 months of age (Hinde & Spencer-Booth, 1967; Rowell et al., 1964). As infants continue to mature into juveniles, these behaviors increase in frequency. Such acts of aggression are frequently capricious and unprovoked, resulting in a social environment for low-ranking individuals that is fundamentally unpredictable and uncontrollable (Silk, 2002; Godfrey et al., 2016). Beginning in infancy therefore, subordinate rhesus monkeys experience psychosocial stress that drives a phenotype characterized by elevated stress hormones and differences in neurodevelopment, compared with high-ranking peers (Ford et al., 2023; Godfrey et al., 2023; Howell et al., 2014). The subordinate phenotype is associated in young monkeys with increased susceptibility to disease, delayed onset of puberty, emotional dysregulation, and overall worse health outcomes later in life (reviewed by Abbott et al., 2003; Godfrey et al., 2016; Silk, 2002; Simons et al., 2022).

Studies of caregiving behavior in a number of *Cercopithecine* species (reviewed by Fairbanks, 1996; Liu et al., 2018; Maestripieri, 1999), primarily vervet monkeys (*Cercopithecus aethiops*) but also rhesus macaques, Japanese macaques (*Macaca fuscata*), and pigtailed macaques (*Macaca nemestrina*), have provided evidence that social status plays a role in dams' individual variability in maternal behavior, or "style." Maternal style in nonhuman primates (NHPs) has been measured along two orthogonal dimensions: *Protectiveness* and *Rejection*; some studies have identified maternal *Warmth* as a third independent dimension of maternal behavior (Maestripieri, 1998; Maestripieri et al., 2009). Though varying widely between females, maternal style shows high intra-individual stability (Berman, 1990; McCormack et al., 2006, 2015). A dam's *Protectiveness* score towards her previous infants(s) is the strongest predictor of how protective she will be of the next infant she births; similar consistency is observed for *Rejection* (Fairbanks, 1996). Broadly, the more that a dam experiences her social environment as threatening, and the less social support she has, the more protective and less rejecting she will be towards her infant (Brent et al., 2002; Fairbanks, 1996; Fairbanks & McGuire, 1988; Maestripieri, 2001). In attempting to shield their infants from harm, subordinate dams have few options other than limiting its attempts to wander (Fairbanks, 1996; White & Hinde, 1975); thus, subordinate females tend to behave more protectively (Fairbanks & McGuire, 1988). In particular, White and Hinde

(1975) found that low-ranking rhesus macaque dams, compared to intermediate- and high-ranking dams, played an overall greater role in maintaining proximity in the mother-infant relationship, initiating ventral contact with their infants more frequently and rejecting them less. In both vervet monkeys (Fairbanks & McGuire, 1988) and Japanese macaques (Bardi & Huffman, 2002), studies have found that low-ranking mothers never showed a maternal style simultaneously low in *Protectiveness* and high in *Rejection*.

The concept central to attachment theory is that of the caregiver as a “haven of safety” or “secure base” from which to explore the world. In rhesus macaque societies, this is “much more than mere metaphor” (Kondo-Ikemura & Waters, 1995, p. 108; also reviewed by Suomi, 2005). A study of 1 to 3 month-old Japanese macaques found that infants born to high-ranking females scored significantly higher on a version of the Attachment Q-Set (see Waters & Deane, 1985) adapted for use with nonhuman primates (NHPs), compared to infants born to low-ranking females (Kondo-Ikemura & Waters, 1995). Mothers of more securely attached infants were appropriately alert to potential threats in the environment, as well as attentive and responsive to their infant’s needs; these mothers monitored their infant’s location, carried their infant with them when changing locations, only rarely allowed other groupmates to handle their infant, and actively defended or retrieved their infant when adult males or dominant females came too close. Mothers of securely attached infants also appeared relaxed when in non-threatening situations, whereas mothers of less securely attached infants appeared tense, frequently controlling their infants’ activities and preventing infants from exploring novel objects and/or unfamiliar settings (Kondo-Ikemura & Waters, 1995).

Maternal styles higher in *Protectiveness* are thought to keep infants safe and prepare them for a challenging future environment rife with social threats, at the cost of reduced opportunities for exploration, play, and building a broad social network. Maternal *Protectiveness* during the first three months of life has been shown to strongly predict levels of plasma cortisol in infant rhesus macaques, indicating that infants who are protected more by their dams may be more fearful (Maestripieri et al., 2009). Within a nonpathological range of maternal behavior, i.e., excluding cases of neglect or maltreatment/abuse, there is evidence that dams high in *Protectiveness* generally produce timid, behaviorally inhibited offspring, whereas dams high in *Rejection* tend to produce bold, socially confident offspring (Bardi & Huffman, 2002; Fairbanks, 1996; Fairbanks & McGuire, 1988; Maestripieri et al., 2009; Suarez-Jimenez et al., 2013). For example, McCormack et al. (2006) showed that the frequency with which a rhesus macaque dam rejected her infant was positively correlated with the amount of time the infant spent with other groupmates. In addition to the differences identified between low- and high-ranking infants in early life experiences, attachment style, and physiological outcomes, researchers have further described interindividual variation in affiliative behaviors, (Weinstein & Capitanio, 2008), social-visual attention (Mandalaywala et al., 2014; Paukner et al., 2017), and some aspects of emotional temperament (Suarez-Jimenez et al., 2013). Weinstein and Capitanio (2008) found, for example, that high-ranking rhesus macaque yearlings spent more time in proximity to and initiated proximity more frequently with their peers, in addition to having overall larger social networks compared to subordinate yearlings (Weinstein & Capitanio, 2008). Emphasizing the primacy of *psychosocial* stressors specifically, past studies of dominance relations have consistently found effects of individual rank among captive or semi-wild populations even when factors like veterinary care, quality of shelter, predation risk, and access to food are standardized across ranks (Abbott et al., 2003; Simons et al., 2022).

Some studies, however, have reported *no* effect of matrilineal rank on the behavior of rhesus macaque mothers (Dettmer et al., 2016; McCormack et al., 2015; Maestripieri et al., 2009). McCormack et al. (2015) included rank as a covariate in ANCOVA tests and identified no significant effects; similarly, Dettmer et al. (2016) found that a dam’s ranking was not significantly correlated with rates of mutual gaze of grooming, nor with proximity between dam and infant. In some other studies of macaque social behavior, individual social status is not a primary variable of interest and is simply controlled for as a potential confound (e.g., Garner et al., 2023). It is not clear to what extent social status and/or maternal style explain individual differences in the development of social behavior during infancy, how early in development such differences might emerge, or to what extent these dynamics are shared among primate species with varying life histories and levels of social tolerance. Thus, to improve understanding of the role of matrilineal social rank in the development of adaptive social behaviors, we employed a longitudinal design of social development in infant rhesus macaques from birth through 1 year of age. Only male infants were included in this study to allow for greater statistical power given our small sample size, as well as to align with the broader translational goals of funding provided for the studies by the National Institutes of Mental Health through an Autism Center of Excellence (ACE) grant (P50-MH100029) awarded to our collaborators at the Marcus Autism Center (Atlanta, GA).

Focal mother-infant pairs in the current study were socially housed in complex multigenerational groups, thus retaining the social complexity that defines *Macaca mulatta* as a species and enabling us to investigate the following questions: in what specific ways does matrilineal social status shape the early environment? Which factor(s) related to status might play the greatest role(s) in developmental outcomes: maternal style, mother-infant interactions, interactions with others in the wider social group, and/or contextual factors like group instability? Finally, are these factors influential only in the first few weeks of life, or do their effects persist into the juvenile stage? Previous work in rhesus macaques has demonstrated that individual sociality is influenced by external conditions during development, but is also trait-like and highly stable across age (Capitanio, 1999; Simpson et al., 2016; Talbot et al., 2022). Therefore, an additional aim was to assess the degree of intraindividual stability and predictability in the social development of NHPs. We aimed to identify behavioral measures in infancy that strongly predicted the individual's social behavior later in life, at 1 year of age. Our predictions were as follows: (1) subjects that demonstrate high sociality in early infancy will continue to do so as juveniles at 1 year, and (2) subjects born to dams high in *Rejection* and low in *Protectiveness* will demonstrate greater boldness and social confidence as juveniles.

METHODS

Subjects and Housing

As part of a larger programmatic study of early social and neural development (see Ford et al., 2023; Kovacs-Balint et al., 2021; Muschinski et al., 2016; Parr et al., 2016; Wang et al., 2020), behavioral development in 17 typically developing male infant rhesus monkeys (*M. mulatta*) was tracked longitudinally (*n* = 9 high-ranking, *n* = 8 low-ranking; Table 1.) Infant focal observations of social behavior, including mother-infant interactions, were collected from birth through 1 year of life. All subjects were born and housed at the Emory National Primate Research Center (ENPRC) Field Station, allowing for the standardization of variables like diet, climate, housing, and health status, as is typical. Focal infants were reared by their mothers in large, multigenerational and complex social groups. This environment provided infants with species-specific social experiences and opportunities to interact with male and female individuals of varying age and social status. As in free ranging populations of rhesus macaques (Altmann, 1962), each social group consisted of multiple families, or matrilines, with a vertical social hierarchy. Each group was housed in an outdoor compound with access to indoor, temperature-controlled quarters. All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of Emory University, in accordance with the Animal Welfare Act and the U.S. Department of Health and Human Services “Guide for Care and Use of Laboratory Animals.” The wellbeing of each mother-infant pair was monitored for the full duration of the study, and their weights recorded during each session of data collection.

Criteria for inclusion stipulated that all subjects were born to multiparous adult females observed to be competent, non-abusive, and non-neglectful in their care of prior offspring. None of the dams in the study were first-time mothers, although it was not possible to standardize the precise number of previous births among dams. Females were selected to have as little genetic interrelatedness as possible with other mothers in the study, and there was never more than one infant born to any single dam assigned to the study. Subjects were all born full-term and without need of veterinary assistance, weighing a minimum of 450 grams at birth. Dam-infant pairs were also selected from groups known to be relatively socially stable. Subjects were born over the course of four birthing seasons (2018-2021). From 2018 to 2021, a total of 19 mother-infant pairs were assigned to the project at birth. Two of these were dropped within their first month due to health concerns or potential maternal abuse, resulting in a total of 17 pairs included in data analyses (see Table 2).

Behavioral Data Collection

Social rank and group size: Each infant was assigned its mother's matrilineal social rank/status, which is the status of a family/matriline relative to all families in the group. (For example, a rank of 2/9 would indicate the infant was born into the second-ranking family out of nine total families in that social group, and is thus a high-ranking individual.) Matrilineal rank was provided by ENPRC Colony Management staff based on observations of dyadic agonistic interactions. Following established methods (Bernstein, 1976; Embree et al., 2013; Howell et al., 2014), staff considered an adult female as ranking below a groupmate if she invariably responded submissively when that individual approached and/or acted aggressively towards her. Social rank was thus determined from observations not of aggressive behaviors, per se, but of subordinate/submissive behaviors such as withdrawing, grimacing, and fleeing.

As noted under *Subjects & Housing*, roughly equal numbers of subjects were born to low- versus high-ranking mothers (see Table 1 for subjects' social rank and demographic information). The mothers' social ranks were reassessed around the 1 year birthday of her infant, in order to detect any shifts in dominance hierarchies over time. During the course of data collection, only two out of the six compounds experienced social instability or overthrows, resulting in rank shifts of four subjects when they were 2 months of age or older (see Table 1 for details). We used subjects' rank at the time of birth for all data analysis.

Using records maintained by Colony Management staff at the ENPRC Field Station, we further characterized the early social context in terms of the size and complexity of subjects' respective social groups at the time of birth (Table 1). For the purpose of calculating group size, females were considered adults at 3 years of age or older (Resko et al., 1982; Stephens et al., 2015, Wilson et al., 1988). Social group size was quantified in two ways: as the number of families/matrilines and as the number of adult females living in the compound. Two measures of group size were used because the number of animals making up a matriline was highly variable (ranging from 5 to 18 adult females in a single family).

Infant Neurobehavioral Assessment Scale: As part of our larger study, dam-infant pairs were briefly removed from their home compounds at multiple timepoints across early development in order to quantify the infants' visual attention to social stimuli using non-invasive eye-tracking procedures (see data published in Ford et al., 2023, Muschinski et al., 2016; Parr et al., 2016; Wang et al., 2020). We also measured infants' neurobehavioral responses immediately following their eye-tracking sessions using the Infant Neurobehavioral Assessment Scale (INAS; Schneider & Suomi, 1992) at 1 week (n = 17), 2 weeks (n = 17), 3 weeks (n = 16), and 4 weeks of age (n = 15). The INAS is a battery of standard developmental tests assessing orientation responses, neuromotor ability, motor ability, and temperament in infant macaques.

For the purposes of the present analysis, only the portion of the INAS related to temperament was considered, modified by our group (see McCormack et al., 2009) from the *Behavioral Temperament Scale* (Ruppenthal & Sackett, 1992) and the *Neonatal Neurobehavioral Assessment* (Schneider & Suomi, 1992; see also Schneider et al., 1991; Paukner et al., 2020). The temperament portion was completed at the end of INAS testing and reflected the experimenter's overall impression of the infant on eight items: predominant state, vocal response intensity, fearfulness, struggle during testing, ability to be consoled by a human experimenter, cuddliness, aggression towards experimenter, and amount of distress or irritation. Each item was scored following a Likert scale from 0 (low degree of the trait) to 2 (high degree of the trait). Only the item "consolability" was selected as a measure of infant temperament because this measure showed a high degree of intraindividual variability. *Consolability* decreased significantly from one to 4 weeks of age (Mean ± SEM: 1.65 ± 0.13, 1.68 ± 0.11, 1.41 ± 0.18, 0.93 ± 0.16; $F(1.98,31.65) = 11.79$, $p < .001$, partial $\eta^2 = .42$). We therefore chose to sum values across age, using interpolation with the age-specific mean for missing datapoints, yielding a score for each infant with a possible range of 0-8 ($M = 5.66$, $SEM = 0.42$). This overall score was then used as a covariate in the statistical analyses described below.

Infant focal observations: The frequencies and durations of the behaviors of each infant while in their social groups, including solitary behavior as well as social behaviors exhibited towards or received from other group members or from their dam, were coded real-time by experienced observers at seven ages: 2 weeks ($n = 16$), 4 weeks ($n = 16$), 6 weeks ($n = 15$), 8 weeks ($n = 14$), 12 weeks ($n = 15$), 24 weeks ($n = 14$), and 1 year ($n = 13$). For two subjects, their dam was not present in the home compound due to health concerns when the 1 year data were collected (Table 2). A complete longitudinal dataset was available for nine subjects. The presence of younger siblings at the time that observations were conducted at 1 year was also noted, i.e., whether the subject's mother had another birth in the spring before the conclusion of data collection. The majority of dams in the study did become pregnant again, though a younger sibling was present during data collection at 1 year for only two of our subjects (Table 1).

Infant focal behavioral observations were collected at each age as four 30-minute sessions within a week, for a total of two hours of data collection per subject. Data were collected for the 2018 and 2019 cohorts by two trained observers with a percent agreement > 90% and Cohen's κ > 0.8. One of these observers also collected all data for the 2020 and 2021 cohorts. Observations were conducted from a tower using binoculars and a netbook computer running in-house software (WinObs60). Focal observations were done in the morning (7AM – 12PM), as this is when the groups were most active. Observations were not conducted on those days when the focal infant was removed from the group for an eye-tracking session. We used a well-established ethogram, adapted from Altmann (1962) by our research group for studies of rhesus macaque social and emotional development and mother-infant interactions (Herman et al., 2003; McCormack et al., 2006, 2009, 2015, 2022; Morin et al., 2020; Raper et al., 2014), to quantify behaviors as either *frequencies* (number of discrete occurrences of the behavior per hour) or *durations* (minutes per hour spent exhibiting the behavior). When applicable, the observer noted whether the focal individual was the initiator/actor or the target/recipient of a behavior involving another macaque(s), e.g., grooming or social play. See Table 3 for a full list of coded behaviors with their operational definitions.

Instrument of Macaque Maternal Care: Immediately following each 30-minute observation session, the observer completed the items published in the Instrument of Macaque Maternal Care (IMMC; Table 4), a rating scale developed by our group (McCormack et al., 2006; 2015). Ratings were assigned on a 1-5 Likert scale based on how *often* a particular behavior occurs during a 30-minute period. The IMMC consists of 22 items sorted into four dimensions labelled as: ***Sensitivity/Responsivity*** (Items 1-5), ***Protectiveness*** (Items 8-12), ***Permissiveness*** (Items 14-16), and ***Irritability/Harshness*** (Items 6-7; 17-22). For ease of interpretation, ratings were converted to a proportion of the highest score theoretically possible for that dimension (e.g., individual *Responsivity* score = (Item #1 + Item #2 + Item #3 + Item #4 + Item #5) / 25). Scores closer to 0% indicate a low level of the particular dimension, whereas scores closer to 100% indicate a high level of the dimension at hand. Previous work has found that the IMMC dimensions remain generally stable across at least the first 12 postnatal weeks (McCormack et al., 2015; Wallace et al., 2019).

Data Handling & Statistical Analyses

<u>*Focal infant behavioral measures:*</u> Since the focal animal was the infant, all instances of social behavior were divided into those received from the dam, received from other members of the social group (infants, juveniles, adult females, adult males), or initiated by the focal infant (Table 3). We did not analyze occurrences of abuse or neglect by the focal dam, as none were observed and only females known to be competent mothers were assigned to the study. We then calculated for each behavior and each age the proportion of subjects that had *zero* occurrences of that behavior (see McCormack et al., 2022). If ≤25% of subjects ever exhibited the behavior at the majority (≥four) of the seven ages, we excluded that behavior from analysis entirely (Table 3b).

The remaining behaviors were treated as separate outcome measures, with the exception of three composite scores - total harassment by groupmates (frequency of *harass* + *restrain*), total aggression by groupmates (frequency of *non-contact threat* + *contact aggression*; see Kovacs-Balint et al., 2021; McCormack et al., 2022), and total affiliation by groupmates (frequency of *touch* + *initiation of play*). This process yielded eight outcome variables quantifying maternal behaviors and 12 outcome variables quantifying interactions between the focal infant and groupmates (Table 3a).

Only six of the seven ages were included in the analysis of *infant withdrawal, infant initiates social play, maternal restrain,* and *maternal carrying*. Specifically, the 2 week timepoint was excluded in the case of *infant withdrawal* and *infant initiates social play*, as there were zero occurrences of these behaviors observed at 2 weeks of age. The 1 year timepoint was excluded in the case of *maternal restrain*, for which there were zero occurrences at 1 year of age, and *maternal carrying*, for which there were very few non-zero durations recorded at 1 year. For the remaining outcome variables, observational data collected at all seven ages were included in analysis.

*Mother-Infant proximity*: In order to characterize more subtle dynamics of the mother-infant relationship, moment to moment changes in spatial proximity between the focal dam and her infant were also examined. *Approach* occurred whenever either the infant or dam moved from beyond three meters apart to a space within three meters of each other, from within three meters to within arm's reach, or from within arm's reach to being in direct contact (Table 3a). *Leaving* was operationally defined in a similar way, but in reverse. *Leaving* and *approach* were further categorized based on whether the dam or infant initiated the movement. We then calculated the *Hinde Index* (Hinde & Atkinson, 1970; Hinde & Spencer-Booth, 1967; see also Weaver & de Waal, 2002; Jensen et al., 1968), defined as the difference between the proportion of total *approaches* initiated by the infant and the proportion of total *leaving* events initiated by the infant (Index = $\%\text{APPROACH}_{\text{infant}} - \%\text{LEAVING}_{\text{infant}}$). The resulting percentage serves as an indicator of the extent to which the infant versus the dam plays the primary role in maintaining versus breaking proximity in their relationship.

We conducted repeated measures ANOVA tests (RM-ANOVAs) to examine developmental trends in the Hinde Index, as well as frequencies of *approach* and *leaving* events. The infant's age was treated as a within-subject factor and matrilineal social rank as a between-subject factor. Data were included only through 24 weeks, as four mother-infant pairs had to be dropped early from data collection, resulting in a reduced sample size (N = 11) at 1 year (Table 2). We used interpolation with the age-specific mean for additional missing datapoints. When sphericity could not be assumed, we applied the Greenhouse-Geisser correction. Partial η^2 values were reported as a measure of effect size for statistically significant ($p < .05$) effects (IBM SPSS Statistics 29). Given our small sample size of 17 mother-infant pairs ($n = 9$ high-ranking; $n = 8$ low-ranking), sensitivity analysis conducted using G*Power 3 (v3.1.9.7; Faul et al., 2007) indicated that the study was powered at 80% with a 5% level of significance ($\alpha = .05$) to detect large effect sizes ($f = 0.43$) for longitudinal RM-ANOVAs with six timepoints (Cohen, 1988).

Multilevel mixed modelling: Of the dependent variables defined in the previous section, the majority were right-skewed and zero-inflated. This was expected given the nature of early developmental data. The IMMC dimension of Irritability was right-skewed; the remaining three dimensions were skewed to the left. To address the issue of zero-inflation, we followed procedures described by McCormack et al. (2022); briefly, a behavioral variable was dichotomized if >20% of subjects did *not* exhibit the behavior at three or more ages (out of seven ages total). As a result, nine frequency and two duration behaviors were converted into dichotomous variables (Table 3a). The frequencies of *maternal retrieve, maternal reject, maternal restrain, withdraw by infant, touch by infant, eye gaze, total harassment*, and *total aggression* were converted to 0, if the behavior was never observed, or 1 (McCormack et al., 2022). In the case of *social play initiation by infant*, in order to capture the relatively wide range of the frequency data and to avoid ceiling effects, we chose a threshold of three occurrences per hour. This threshold was selected based on the median frequency of play initiations, calculated to be 2.99 per hour (excluding the 2 week timepoint). Similarly, we chose a threshold duration of 15 seconds per hour for *contact with groupmates* (*Mdn* = 14.91 sec/hour) and 8 seconds per hour for *grooming by groupmates* (*Mdn* = 7.53 sec/hour).

The distributions of the remaining variables were checked for normality at each age using Shapiro-Wilks tests ($\alpha = .01$). Due to the nature of developmental data, and especially given the overrepresentation of younger ages in the study design, normality was tested *within each age* rather than testing variables combined across all ages. A normal distribution could be assumed at four or more of the ages for all the non-dichotomized variables, including the IMMC dimensions; therefore, no transformations were applied. We also tested the non-dichotomized measures for extreme outliers within each age based on the interquartile range (IQR; upper bound = Q3 + 3*IQR; lower bound = Q1 – 3*IQR). There were extreme outliers in the data for *maternal carrying, maternal cradling, maternal grooming*, the composite of *touch + play* received, *nonsocial/solitary play*, frequency of approaches by dam, and for two of the IMMC dimensions, *Protectiveness* and *Permissiveness*. We ran the relevant statistical analyses (RM-ANOVAs or GzMLMs) with and without these extreme outliers to check the robustness of our results and found that the hypothesis test conclusions were not affected. Therefore, all results are presented with outliers included to illustrate individual variability.

Generalized multilevel mixed (GzMLM) models were then constructed for each of the 24 outcome variables defined in the previous section, using a binomial response distribution with a logit link function for dichotomized variables and a continuous, normal response distribution for all other outcomes (Hancock et al., 2019; Kiernan, 2018, Singer & Willett, 2003; Tabachnick & Fidell, 2013; West et al., 2022). In order to accommodate both linear and nonlinear trajectories, age was treated as a categorical, rather than continuous, variable. Matrilineal social rank, the primary factor of interest, was treated as a binary variable (*n* = 8 low-ranking; *n* = 9 high-ranking). Estimates were produced for three fixed effects: Rank, Age, and a Rank*Age interaction term. We also sought to account for the potential influence of infant temperament on behavioral outcomes by examining the fixed effects while holding constant the variable of *consolability* generated by the INAS assessment at the earliest four ages.

To account for the dataset's hierarchical structure consisting of subjects nested within one of five different social groups (and home compounds), random effects were modelled at the subject level and the compound level. Models thus included estimates for three variance components: random variation in intercepts associated with individual subjects, random variation in intercepts associated with the different home compounds, and within-subject residual error (see Appendix 1). For the sake of parsimony, random variation in rates of change was always assumed to be zero. Random effects were further simplified in each model where necessary.

Models were constructed using the GLIMMIX procedure in SAS version 9.4 (SAS Institute Inc), applying Restricted Maximum Likelihood Estimation for normally distributed variables and, for the binomial variables, Maximum Likelihood Estimation with Laplace approximation. A separate GzMLM model was fit for each outcome, following a sequential “step-up” strategy (Appendix 1). An unconditional model, hereafter referred to as the “AGE” model, was constructed first, assessing only random effects and the fixed effect of age. Matrilineal social rank and a Rank*Age interaction term were then added; this model will be referred to hereafter as the “AGE*RANK” model. Finally, a model was fit with the addition of *consolability* as a subject-level covariate. If the inclusion of *consolability* changed the estimate for the fixed effect of Rank by an absolute magnitude of ≥10%, the adjusted model was selected. Similar methods were used to also check for potential confounding by infant birthweight, cohort year (2018, 2019, 2020, or 2021), and the two measures of social group size.

Finally, the intercept (γ_{000}) and coefficients were modelled as fixed effects, then used as fitted values in graphing the modelled trajectories (Figs. 3 – 6). For dichotomized variables, the inverse link transformation was applied to convert the outcomes to predicted probabilities of occurrence. Additional pairwise testing was conducted whenever the fixed effect of age, fixed effect of rank, and/or the interaction term were statistically significant, and for the four IMMC dimensions, developmental change was specifically assessed between 4-12 weeks and 12-52 weeks via pairwise T-tests on estimates from the AGE models.

As with the RM-ANOVA models, we report the effect size whenever $p < .05$ for the fixed effect of Rank in the GLIMMIX analyses. Individual subjects were nested in compounds such that it is was not possible to calculate a single standardized measure of effect size, such as R^2, to capture the multiple sources of variance explained in a multilevel model (Hancock et al., 2019; Rights & Sterba, 2023; West et al., 2022). Therefore, we report effect size as the unstandardized regression coefficient (γ_{010}). The unstandardized coefficient represents the estimated difference between groups for a specific dependent variable, in its original units (e.g., minutes/hour), and allows for a straightforward interpretation of whether the group difference is small or large.

Predictive modelling: We ran Linear Mixed Model (LMM) analysis in SPSS (IBM SPSS Statistics 29) to assess potential predictors at earlier ages for subjects' social behavior upon reaching juvenescence. Rates of *initiating social play* and of *withdrawing* at 1 year of age were used as dependent variables in separate models. *Withdrawal*, defined as "clearly avoiding another macaque," is typically considered to be an indicator of submissiveness (Bernstein, 1976; Embree et al., 2013; Howell et al., 2014; Silk, 2002). We entered four measures as fixed factors: *withdrawals* and *social play initiations* by the infant at 3 months of age, IMMC scores for maternal *Responsivity/Sensitivity* at 3 months of age, and duration of *maternal cradling* in the first postnatal month (see ethogram in Table 3a). These specific behaviors and ages were selected based on plotting the observed data longitudinally and identifying measures with high interindividual variability. We also focused on behavior at 3 months of age because this is a well-known transitional period in rhesus macaque development; around the third postnatal month, maternal rejections and aggression increase, as dams begin weaning their offspring, and infants spend increasing amounts of time engaged in independent exploration and social play (reviewed by Machado & Bachevalier, 2003). For maternal cradling, we calculated each subjects' average duration across 2 and 4 weeks. All independent and dependent variables were treated as continuous. A normal distribution could be assumed for the two dependent variables based on Shapiro-Wilks tests ($\alpha = .01$), so no transformations were applied. For both models, the sample size was $N = 13$ after removing subjects that did not have data at 1 year.

Cohort year (2018, 2019, 2020, or 2021) was added to both models as a random factor. We used the Maximum Likelihood (ML) method to estimate parameters, then calculated the likelihood ratio test to compare the reference model containing all fixed factors to a "reduced" model with one fixed factor removed (West et al., 2022; see also Kaburu et al., 2016). For each reduced model, we also assessed model fit by calculating the change in the Akaike information criterion (AIC) score when one fixed factor was removed (West et al., 2022; see also Simons et al., 2022). When the LRT statistic comparing a reduced model with the reference model was significant ($p < .05$), we checked our results by conducting bivariate linear regression analyses in SPSS (IBM SPSS Statistics 29) for the predictor and the dependent variable.

RESULTS

Mother-Infant Proximity and Hinde Index

The frequencies of changes in spatial proximity were analyzed within dam-infant dyads over the course of development. For leaving by dam, approaches by infant, and leaving by infant, visual inspection of the graphs (Fig. 1) suggests an increase in frequency from 2 to 12 weeks, whereas approaches by dam decreased from 2 to 12 weeks. These changes were confirmed by significant effects of Age (RM-ANOVA tests for the four behavioral categories: dam approaches ($F(3.21, 48.157) = 7.582$, $p<.001$, partial $\eta^2 = .336$), dam leaving ($F(2.84, 42.605) = 17.322$, $p<.001$, partial $\eta^2 = .536$), infant approaches ($F(2.514, 37.717) = 38.851$, $p<.001$, partial $\eta^2 = .721$), and infant leaving ($F(5, 75) = 11.768$, $p<.001$, partial $\eta^2 = .440$). There were no significant main effects of matrilineal social rank or significant interactions between Age and Rank.

To account for the inevitable variability between subjects in their overall levels of movement, whether leaving or approaching, we calculated the Hinde Index, for which a positive value indicates that the infant was primarily responsible for maintaining proximity within the dyad, a negative value indicates the dam was primarily responsible, and a value of zero percent indicates that responsibility was shared equally. This is the case regardless of individuals' baseline activity level or how much time a dam and infant spent near each other overall. We found a substantial main effect of Age ($F(3.241, 48.609) = 45.194$, $p<.001$, partial $\eta^2 = .751$), as the value of the Hinde Index shifted from negative to positive at 6 weeks of age on average (M = 0.37%, SEM = 4.4%, see Figure 2). There was no main effect of Rank

($F(1, 15) = 2.160$, $p = .162$) and no significant interaction between Age and Rank ($F(3.241, 48.609) = 1.459$, $p = .235$).

Focal Infant Behavioral Measures

The results of all GzMLM models are shown in Table 5. Among the final models for the 24 outcome measures, including the four IMMC dimensions, eight measures were adjusted for the effect of temperament; for the remaining 16, the potential confounding effect of temperament was negligible, i.e., less than 10% in magnitude. Even among the models that were ultimately adjusted for the effect of temperament, the fixed effect of *consolability* was not itself statistically significant. The effects of infant birthweight, cohort year, and size of the social group were negligible or nonsignificant ($p < .05$), with the exception of cohort year in the model for *maternal carrying*. As has been recommended for animal behavior studies with small sample sizes (see Nakagawa, 2004), we report *non*-adjusted p-values for all fixed effects.

AGE model: There were only a few behavioral categories for which the Age effect was not significant: *infant touch, infant initiates social play, contact with groupmates, grooming received from groupmates,* and *eye gaze received* (Table 5). Among measures of dam-infant interactions (Figs. 3, 4), there was a significant decrease across age in model-estimated *maternal retrieval, maternal restrain, maternal carrying, maternal cradling, maternal contact,* and *maternal grooming* (all p-values $< .05$, see Table 5), but a significant increase in *maternal rejections* ($p = .007$) and *maternal proximity* ($p = .0002$). The seemingly contradictory findings for time spent in proximity versus in contact are likely due to how the two measures were operationally defined as distinct behaviors (see Table 3; Figs. 3a-b). Infants may have spent increasing amounts of time at later ages in proximity to their mothers (i.e., within an arm's reach) as a consequence of spending *less* time in direct physical contact with her.

For interactions between the infants and other groupmates, the model-estimated durations of both *social* and *nonsocial play* (Figs. 5a, 5b), along with *touch/play received from groupmates* (Fig. 5d), increased rapidly before peaking at 12 weeks of age, after which *nonsocial play* duration (Fig. 5b) decreased precipitously, whereas *social play* duration (Fig. 5a) and *touch/play received* (Fig. 5d) plateaued. These trends are reflected in the overall significant increase across development in the model-estimated *proportion of social play to total play* (Fig. 5c). The developmental changes in play behavior were all statistically significant (*p*-values < .0001 for fixed effects of Age).

The model-estimated probability of an infant receiving *aggression/non-contact threats* rose steadily across development, while remaining at less than 50% probability of occurrence through 12 weeks (*p* = .003; Fig. 5g). In contrast, the estimated probability of receiving *restraining/harassment* increased rapidly to a peak at 12 weeks before gradually declining (*p* = .037; Fig. 5f). We further examined these two categories of agonistic interactions by differentiating occurrences based on whether the initiator was an adult groupmate versus a young (infant or juvenile) peer. As expected based on previous studies (e.g., Hinde & Spencer-Booth, 1967; Rowell et al., 1964), adult males interacted with focal infants only rarely. Subjects were more likely to be restrained or harassed by young peers (typically juveniles) than by the adults in their social group, whereas in the case of aggression and threats, adults (typically adult females), were the sole initiators prior to 12 weeks. Acts of actual physical aggression (e.g., biting, hitting, grabbing, or pinning down the infant) were received by the focal infant infrequently across development. Prior to 6 weeks, we observed physical aggression directed towards only two subjects (40 and 55) at an average frequency of less than once hourly. There was also an increase across age in *infant withdrawals* (Fig. 5e), but this developmental change did not reach significance (*p* = .055).

<u>*AGE*RANK model*</u>*: Maternal contact* was the only behavioral variable with a significant interaction between Age and Rank (*p* = .045). Post-hoc pairwise comparisons revealed that, although high- and

low-ranking mothers spent the same amount of time in contact with their infants in the first 6 months, high-ranking mother-infant pairs spent significantly more time in contact than low-ranking pairs at 6 months and 1 year, by approximately eight minutes (p = .046) and ten minutes (p = .035), respectively (Fig. 3b). A significant fixed effect of Rank on *maternal carrying* was apparent when the cohort year was held constant (Fig. 3c); high-ranking dams spent approximately four minutes/hour more carrying their infants than low-ranking dams (γ_{010} = -4.18 mins/hour, p = .009). Post-hoc pairwise comparisons showed that the group difference in *carrying* was significant at all ages analyzed, except 6 weeks and 12 weeks. In the case of *maternal proximity* (Fig. 3a), there was a significant fixed effect of Rank, but only prior to adjusting for infant temperament (γ_{010} = -3.03 mins/hour, p = .048). (We visually compared versions of the AGE*RANK model plot with versus without holding temperament/*consolability* constant and concluded that the influence of this covariate on *proximity* was not substantial.) High-ranking mother-infant pairs spent significantly more time in proximity at 6 weeks compared to low-ranking dyads (p = .014). There were no significant AGE*RANK interactions or effects of matrilineal rank for any of the other behaviors.

Maternal Style

AGE model: The fixed effect of Age was significant for all four dimensions of maternal style (p-values < .0001; Table 5). Results of the post-hoc T-tests conducted on estimates from the AGE models are depicted in Figs. 6a-d. The model for *Irritability* exhibited a minimal but significant increase (p = .003) from 4 to 12 weeks of age, at which time scores plateaued (Fig. 6a). The model-estimated scores for *Responsivity* (Fig. 6b) and *Protectiveness* (Fig. 6c) decreased significantly with the age of the infant (Week 4 > Week 12: p = .01, p < .0001, respectively; Week12 > Week 52: p-values < .0001). Model-estimated *Permissiveness* (Fig. 6d) rose to a peak from 4 to 12 weeks (p = .0002) before declining gradually through 6 months and 1 year (p = .004).

<u>*AGE*RANK model*</u>*: Responsivity* was the only dimension of maternal style with a significant interaction between Age and Rank (*p* < .001; Table 5, Fig. 6f). The fixed effect of Rank on *Responsivity*, however, was not significant (*p* = .074). We conducted post-hoc pairwise comparisons and found that the group difference was significant only at 1 year (*p* < .0001). At this later age, high-ranking dams exhibited greater *Responsivity* in their maternal style than low-ranking dams. When we conducted post-hoc pairwise tests between different ages, we found divergence between the low- and high-ranking groups for certain comparisons; notably, there were significant decreases in model-estimated *Responsivity* from 2 to 6 weeks, 2 to 12 weeks, and 4 to 12 weeks in the low-ranking group (*p* = .034, *p* = .0003, *p* = .0003, respectively), but *not* for high-ranking dams. Across the entire period of data collection from 2 weeks to 1 year of age, the estimated *Responsivity* score of low-ranking dams decreased by .52 (±.041 *SE*), whereas that of high-ranking dams fell by only .26 (±.037 *SE*).

Predictive Models

Results from the Linear Mixed Models are shown in Table 6. The rate at which 1-year-old juveniles initiated social play with groupmates was significantly predicted by the rate of initiating social play at 3 months of age (Estimate ± SE: 1.22 ± 0.39; LRT = 7.07, LRT *p* < .01), maternal cradling (Estimate ± SE: -0.54 ± 0.23; LRT = 10.16, LRT *p* < .01), and by infants' rate of withdrawing from groupmates at 3 months (Estimate ± SE: -6.68 ± 2.61; LRT = 3.66, LRT *p* = .0556). We retained withdrawing at 3 months as a predictor, despite the LRT not reaching statistical significance (*p* = .0556), because including the variable improved model fit (ΔAIC = +1.66) and the fixed effect was significant (*p* = .049). Examining the model with cohort year as a random factor and including all fixed factors except *Responsivity*, we calculated the marginal pseudo-R^2-value and found that the three predictors together explained 38.9% of the total variance in juveniles' rates of initiating play. Infants that initiated play more frequently as 3-month-olds also did so more frequently as 1-year-olds, whereas infants that withdrew from groupmates more frequently as 3-month-olds went on to initiate play less frequently as 1-year-olds. Finally, infants that received *more* maternal care in their first month, i.e., cradling, went on to initiate play *less* frequently as 1-year-olds. Linear regression confirmed the directionality of the effects of 3-month-old social play initiations (ß = +0.29, R^2 = 4.1%, p = .51), 3-month-old withdraws (ß = -2.14, R^2 = 5.1%, p = .46), and maternal cradling (ß = -0.25, R^2 = 5.3%, p = .47), though the associations were not statistically significant.

In contrast, the rate at which 1-year-old juveniles withdrew from groupmates was significantly predicted only by the rate of withdrawing at 3 months (Estimate ± SE: 3.51 ± 0.43; LRT = 17.6, LRT p < .0001). We tested a LMM with cohort as a random factor and withdrawing at 3 months as the single fixed factor, and found that the rate of withdrawing at 3 months explained 76.3% of the total variance in withdrawing at 1 year. Infants that withdrew from others more frequently as 3-month-olds also did so more frequently as 1-year-olds. Bivariate linear regression analysis confirmed a strong positive relationship between ages for this behavior (ß = +2.05, R^2 = 51.3%, p < .01).

DISCUSSION

In this study, we investigated the role of matrilineal social status in the mother-infant relationship and the behavioral development of infant male rhesus macaques from birth through 1 year of age. Focal infants were raised by their mothers in large, multigenerational social groups, enabling the longitudinal assessment of maternal behaviors, dam-infant interactions, and social interactions between infants and other individuals in the group. Overall, we confirmed previous null findings (Dettmer et al., 2016; Maestripieri et al., 2009; McCormack et al., 2015) for a role of matrilineal rank in the expression of adaptive social behaviors in infant rhesus macaques. We also confirmed and extended the work originally developing the Instrument of Macaque Maternal Care, or IMMC (McCormack et al., 2006, 2015). Consistent with our predictions, we found that sociality showed trait-like stability from three months to one year of age. Further in line with our expected results, the duration of maternal cradling was a negative predictor of later social boldness.

The few significant effects that we identified were effects of ranking on the dam-infant relationship or maternal “style.” This is perhaps unsurprising given the current study’s focus on the early postnatal months. Low-ranking male infants, compared to their high-ranking peers, spent less time in contact with, in close spatial proximity to, and being carried by their mother, in conjunction with experiencing a steeper decline in the responsivity and sensitivity of their mother’s caregiving as they approached 1 year of age. In general, these rank-based differences in caregiving behavior align with a previous finding that infants born to low-ranking females scored significantly lower on a measure of secure attachment (Kondo-Ikemura & Waters, 1995). Matrilineal social status did not significantly impact infants’ interactions with other macaques in their social group, either as the initiator or recipient of specific behaviors.

Taken together, this collection of findings is somewhat puzzling, as much of the literature has reported that low-ranking females experience a highly stressful and threatening environment and are thus more protective and less rejecting of their vulnerable offspring (e.g., Bardi & Huffman, 2002; Brent et al., 2002; Fairbanks, 1996; Fairbanks & McGuire, 1988; Hinde & Spencer-Booth, 1967; Maestripieri, 2001; White & Hinde, 1975). As will be discussed in greater detail below, a number of factors are likely to contribute to divergence in findings between studies on the early social development of NHPs, factors such as the sex of offspring (Dettmer et al., 2016; Jensen et al., 1967; Tomaszycki et al., 2001), the complexity and richness of the social environment experienced by individuals (Capitanio, 1999; Simpson et al., 2016; Wooddell et al., 2017, 2020), the stability (or instability) of the social group (Maestripieri et al., 2001), and the species being studied (Abbott et al., 2003; Bardi & Huffman, 2002; de Lathouwers & van Elsacker, 2004; Thierry, 2007).

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Mother-Infant Proximity

Across development, we found that infants initiated changes in proximity (via leaving or approach) more frequently than dams, a trend also described by Hinde and Atkinson (1970). Examining the Hinde Index, the current data fell within a similar range of values and followed a longitudinal trajectory comparable to that described previously (see *Fig. 12* in Hinde & Spencer-Booth, 1967). Yet whereas the developmental transition from dam to infant being primarily responsible for maintaining proximity (from a negative to a positive Hinde Index) took place sometime between 15-20 weeks in Hinde and Spencer-Booth's (1967) sample, the shift occurred substantially earlier in the current study, at 6 weeks of age on average. The discrepancy could be due to the fact that the foundational work by Hinde et al. was based on observations of rhesus macaques housed in relatively small social groups consisting of one adult male and two to four females with their offspring (Hinde & Atkinson, 1970; Hinde & Spencer-Booth, 1967; White & Hinde, 1975). For the mother-infant pairs in the current study, the complexity of the social context and the availability of more groupmates to interact with, including other adult females in their mother's family, may have pushed the shift in the Hinde Index earlier. In the characterization of infant-caregiver dynamics, these results demonstrate the value of studying micro-interactions within complex social environments (see also Ferrari et al., 2009).

Maternal Care Behaviors

The results of the current study largely confirm the findings by Dettmer et al. (2016) that maternal behaviors such as grooming and mutual gaze are not correlated with matrilineal rank. Our modelling analyses did, however, provide some evidence that a female's social status impacts her caregiving – specifically, the amount of time spent carrying (dorsal and ventral carrying combined), in direct contact with, or in close proximity to her infant. Adjusted for cohort effects, high-ranking mothers spent more time carrying their infants compared with low-ranking mothers. For *maternal contact*, there was a significant Age*Rank interaction; high-ranking mother-infant pairs spent significantly more time in contact than low-ranking pairs, but only later in development, when infants were 6 months and 1 year-old. The model for *maternal proximity* was somewhat more difficult to interpret. High-ranking pairs spent more time in proximity compared to low-ranking pairs, but this effect did not persist after controlling for infant temperament.

Interactions with Groupmates

There was a significant effect of Age for nearly all the modelled outcome measures. The increase across development in interactions with other groupmates was perhaps most noteworthy in the case of agonistic dynamics (i.e., harassment or threats received from groupmates and withdrawal by the infant), though playful, affiliative interactions became more frequent over time as well. The developmental trajectory of infant-directed agonism is particularly intriguing. Showing a similar pattern to that of *nonsocial play* and *touch + play received*, the predicted likelihood of being restrained or harassed by a groupmate rose to a peak at 3 months of age, then began to decline. This is a relatively benign category of actions, more characteristic of other macaques' propensity towards "messing with" infants than an example of agonism *per se*. On the other hand, infant-directed aggression and non-contact threats generally increased in predicted probability across the entire span of early development. Acts of physical aggression or violence towards infants, such as biting or hitting, were observed only rarely, and almost never in the first month of life.

Maternal Style & the IMMC

In designing the IMMC as an index of maternal style, McCormack et al. (2015) found that the dimensions of *Irritability, Responsivity*, and *Permissiveness* did not change across development from 1 to 3 months. Our results here differ in some respects. From 4 to 12 weeks, *Irritability* and *Permissiveness* did increase significantly. *Responsivity* significantly decreased during this early period, but interestingly, this was true only among the low-ranking dams, whereas *Responsivity* among the high-ranking dams followed the pattern described by McCormack et al. from 4 weeks to 3 months.

Given that McCormack et al. studied both male and female infants, whereas the current study included only males, the infants' sex may have accounted, at least in part, for the divergent results, as will be discussed below. For *Protectiveness*, we replicated the significant decrease with age reported by McCormack et al. (2015). The current study is the first to describe maternal style, as quantified by the IMMC, beyond the age of 3 months. From 3 months to 1 year of age, *Protectiveness* and *Responsivity* continued a trend of declining steadily, whereas *Irritability* plateaued. The model for *Permissiveness* showed that its trajectory of change actually reversed direction after 3 months and began a slow decline.

Further confirming the results of McCormack et al. (2015), we did *not* detect any effect of social rank on maternal style in the first 3 months of life. Later in development, however, around 1 year of age, high-ranking mothers exhibited significantly greater *Responsivity* than low-ranking mothers. Paralleling the trend observed for *maternal contact*, the maternal style of high- versus low-ranking dams seemed to diverge gradually over time. This divergence was driven by the apparently steeper decline among low status females in levels of *Responsivity* towards their infant. The current study supports the work of McCormack et al. (2015) by providing further evidence for the utility of the IMMC in reliably indexing features of maternal style. The findings also point to the value of tracking maternal behavior and maternal-infant interactions longitudinally and beyond the first few weeks and months of development, as important interindividual differences between dams, such as those linked to social status, may in some cases only emerge as infants approach juvenescence. A similar point is made by McCormack et al. (2006) in regard to dimensional analyses of infant behaviors across developmental time.

Early Behavioral Markers of Social Functioning in the Juvenile Stage

Based on our LMM results, we identified 3-month *play initiations*, 3-month *withdrawals*, and maternal *cradling* as significant predictors for the rate of *social play initiations* at 1 year. *Withdrawals* at 3 months were also a significant predictor for *withdrawals* at 1 year. In general, 3-month-old infants that initiated social play with groupmates more often and avoided or moved away from groupmates less often exhibited the same pattern of behavior upon reaching juvenescence. Compared to initiating play, withdrawing showed much greater developmental stability within individuals. On its own, the 3-month rate of withdrawals explained over 75% of variation between juveniles in how often they withdrew from others, and the strong positive association was confirmed in a linear regression model. The robust, trait-like stability of this submissive behavior, and the absence of other significant predictors, may be explained by its role in social ranking dynamics (Bernstein, 1976; Embree et al., 2013; Howell et al., 2014; Silk, 2002). It is likely that rates of withdrawing are dictated predominantly by an individual's relative status, which itself tends to be highly stable over time. Finally, we found that the amount of time dams spent cradling their infants in the first four weeks of life was a negative predictor for initiating social play at 1 year, building on previous research showing that more protective and less rejecting macaque mothers, by keeping their infants close and limiting attempts to wander, may prevent harm to their offspring at the cost of reduced opportunities for exploration, play, and creating their early social network (Bardi & Huffman, 2002; Fairbanks, 1996; Fairbanks & McGuire, 1988; Kondo-Ikemura & Waters, 1995; McCormack et al., 2006; Suarez-Jimenez et al., 2013).

Infant Sex Differences

A major limitation of the current project was the exclusion of female infants. The sex of the infants studied could have contributed to the earlier transition in the Hinde Index among our subjects, as well as the divergence in our IMMC results. Previous work in macaques has compellingly demonstrated the role of an infant's sex in shaping various aspects of caregiving. Mothers of male offspring, compared to mothers of female offspring, more frequently groom and engage in mutual gaze with their infants (Dettmer et al., 2016) and are more likely to respond to their distress vocalizations (Tomaszycki et al., 2001). Most notably for the current study, work in pigtailed macaques has demonstrated that, compared to female infants, dams encourage their male infants towards independence at an earlier age, apparently by behaving more harshly and punitively towards male offspring as well as by controlling their activities more frequently with maternal behaviors like restraining and retrieving (Jensen et al., 1968).

Social Instability

As White and Hinde (1975) point out, “we would expect any relations between dominance and the mother-infant relationship to be somewhat subject to change with circumstances…a monkey mother might meet the problem of subordinate status in a number of ways: for instance she might be over-restrictive to protect the infant from others or inattentive as she attended to her own social relationships” (p. 538). Lower-ranking female baboons (*Papio hamadryas*), for example, exhibit abusive behavior towards their infants more frequently than intermediate- or high-ranking females (Brent et al., 2002). Abuse represents a maladaptive form of caregiving and is thus outside the scope of the current study; nevertheless, the finding in female baboons serves to illustrate the point that NHP mothers may adapt to the demands of caregiving and “the problem of subordinate status” with a wide range of behavioral strategies. This may be true particularly when the social environment is unstable - as was the case for four mother-infant pairs (three low-ranking, one high-ranking) living in compounds where rank overthrows took place during the course of the study. In fact, there is some evidence that typical effects of ranking in NHP groups are exaggerated – or even “directionally reversed” – in times of social instability (reviewed by Simons et al., 2022, p. 9).

Subject 43, one of three infants living in compound #6 when a rank overthrow took place, is an especially interesting case. This infant’s dam not only belonged to the lowest-ranking matriline (fifth-ranked of five in her social group) at the time that Subject 43 was born, but likely experienced additional psychosocial stress due to the instability in her social environment. Examining the Hinde Index plot, we note that this mother-infant pair had values above the group average at all ages except 4 weeks and that Subject 43 was the only infant at two weeks with a positive value (14.6%, *M* = -36.4%), meaning he was the primary actor in maintaining proximity with his dam at a very young age. The high values for the Hinde Index appear to have been driven by high rates of leaving by the dam paired with low rates of leaving by the infant at most ages across development, including at 8 weeks of age, which was around the time the overthrow occurred.

Interspecies Differences

Finally, in addition to the divergences discussed above between our findings and those of the extensive literature on rhesus macaque development (Bernstein & Williams, 1983; Ford et al., 2023; Hinde & Atkinson, 1970; Hinde & Spencer-Booth, 1967; Howell et al., 2014; Liu et al., 2018; Maestripieri, 2001; Maestripieri et al., 2009; Mandalaywala et al., 2014; McCormack et al., 2006, 2009, 2015, 2022; Paukner et al., 2017; Simons et al., 2022; Suarez-Jimenez et al., 2013; Rowell et al., 1964; Weinstein & Capitanio, 2008; White & Hinde, 1975; Wooddell et al., 2017, 2020), we echo Bardi & Huffman's conclusion (2002) that interspecies differences in caregiving are crucial to explaining disparate results (see also Maestripieri, 1999; de Lathouwers & van Elsacker, 2004). The current findings diverge from those reported in Japanese macaques; in this species, low-ranking females appear to be more protective mothers and reject their infants less, compared to high-ranking females (Bardi & Huffman, 2002; Kondo-Ikemura & Waters, 1995). Japanese macaques, as well as vervet monkeys, are in general highly tolerant of infants; rejection behavior is uniformly rare. This is in addition to the fact that rhesus macaques, relative to other *Cercopithecine* species, show low levels of social tolerance overall and live in rigidly hierarchical, despotic societies (Abbott, 2003; Thierry, 2007). The results of the current study thus emphasize the importance of considering species-specific behavioral features - as well as subjects' housing conditions, social environment, and sex - in future studies examining the role of dominance hierarchies in the social development of nonhuman primates.

Limitations

As previously noted, no significant effects of matrilineal dominance rank were detected on subjects' interactions with other macaques in their wider social environment, either in the case of behaviors initiated or received. Data analyses were, however, limited in statistical power by the small sample size (*N* = 17), which necessitated the analysis of social rank as a binary variable. We were thus unable to investigate potential differences in behavior between low- and high-ranking animals versus intermediate-ranking animals. Many behaviors of interest occurred very infrequently. Such variables were either excluded from analysis entirely or converted to a binomial. The creation of forced dichotomies is generally a nonideal strategy (see Hancock et al., 2019), as it can result in artificial floor or ceiling effects and an overall loss of precision and descriptive nuance. We were careful to dichotomize variables only when truly necessary for the analysis.

It is also possible that few significant effects of rank were found because, as articulated by Simons et al. (2022), dominance rank itself may not be "the proximate driver" of individual differences (p. 8). The authors examined data from a population of captive adult female rhesus macaques and found that summary measures of behavior and social interactions frequently offered explanatory insight into physiological variation beyond that made available by analyzing rank on its own. Importantly, though, the directionality of effects was consistent whether using rank or rank-associated behaviors as the primary predictor (Simons et al., 2022). Similarly, Maestripieri et al. (2009) found no associations between social status and maternal behavior in a free-ranging population of rhesus macaque females, but did find a significant positive correlation between maternal *Rejection* and levels of plasma cortisol, suggesting that rates of rejection depend on how much stress a dam is experiencing.

The designation of "high" or "low" rank is a useful and validated, but crude, index of the daily dynamics "on the ground" that make up an individual animal's psychosocial environment. In this study, we used a measure of ranking based on the matriline/family, which may be less accurate than a measure of ranking based on the status of individual dams relative to all other individuals in the group. Further, some of the subjects in the current study experienced instability within their social groups and even rank overthrow events, though we did seek to account for such contextual factors by including compound-level random variation in our modelling, as well as by investigating potential confounding factors, e.g., cohort year and the size, complexity, and stability of social groups.

Conclusion

The close study of hierarchical dynamics in a highly social NHP has great potential to inform our understanding of the developmental outcomes that are possible within a species-typical range of early environments (Machado & Bachevalier, 2003). Overall, we found support for the conclusion in previous literature that the dam-offspring relationship is a critical early social experience that facilitates a male infant’s adaptation to the niche created by his mother’s – and his family’s - social status. Infants that were cradled more by their dams went on to initiate social play with groupmates less frequently as juveniles. Further, the low-ranking dams provided less maternal care to their infants and, compared to higher-ranking females, quickly declined in the sensitivity and responsiveness of that care as offspring grew older.

FIGURES & TABLES

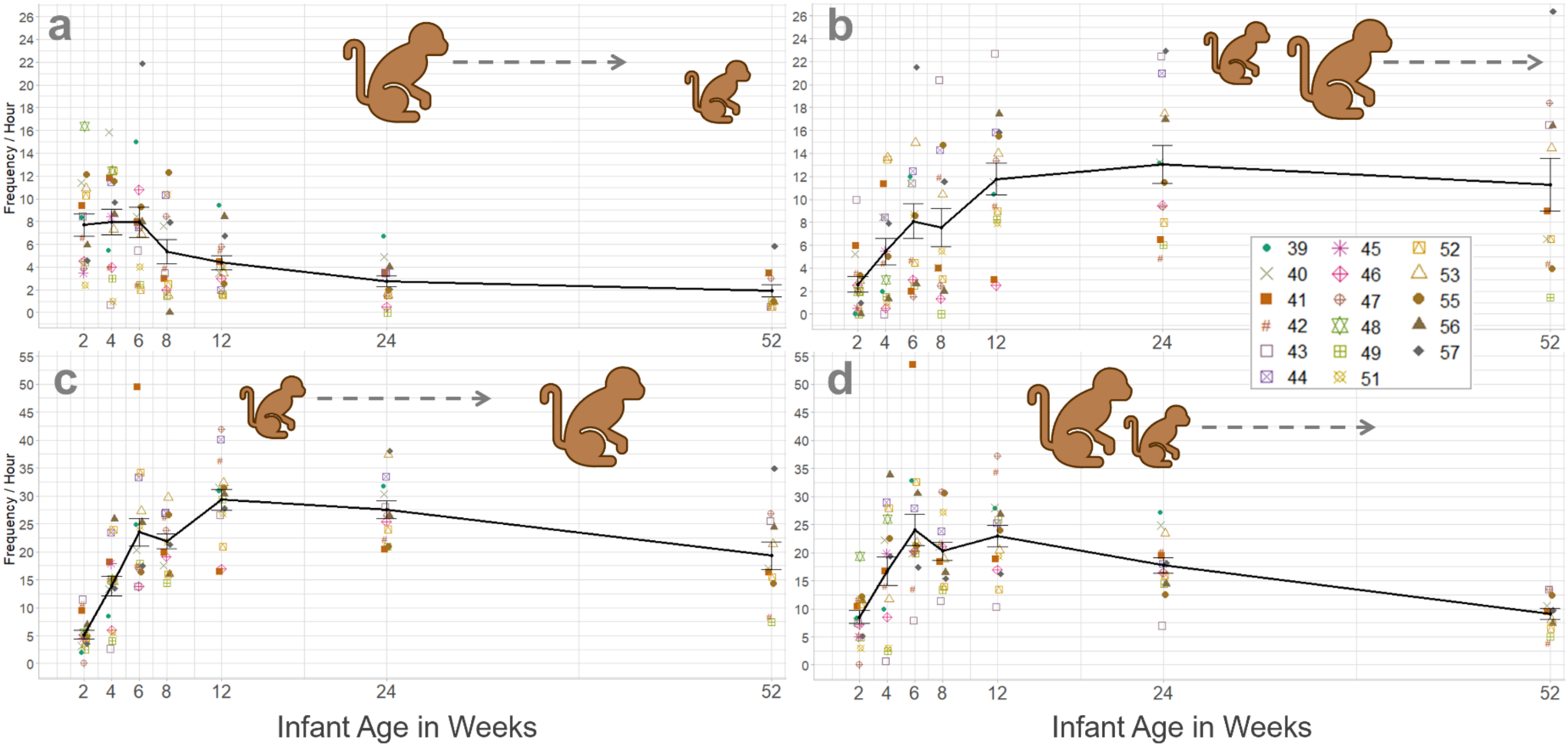


Figure 1: Mother-infant Intra-dyad Proximity Changes across Development. Longitudinal plots showing frequency (occurrences / hour) of approaches and leaving from 2 weeks to 1 year of age (*N* = 17 dam-infant dyads): a) Frequency of dam's approaches to her infant. b) Frequency of dam leaving her infant. c) Frequency of infant's approaches to dam. d) Frequency of infant leaving dam. Group mean is indicated by a solid black line, with vertical bars for standard error at each age. Note the larger scale along the y-axis for infant approaches and leaving (c-d; range 0-55 occurences/hour), compared to the scale for dams (a-b; range 0-26 occurences/hour).

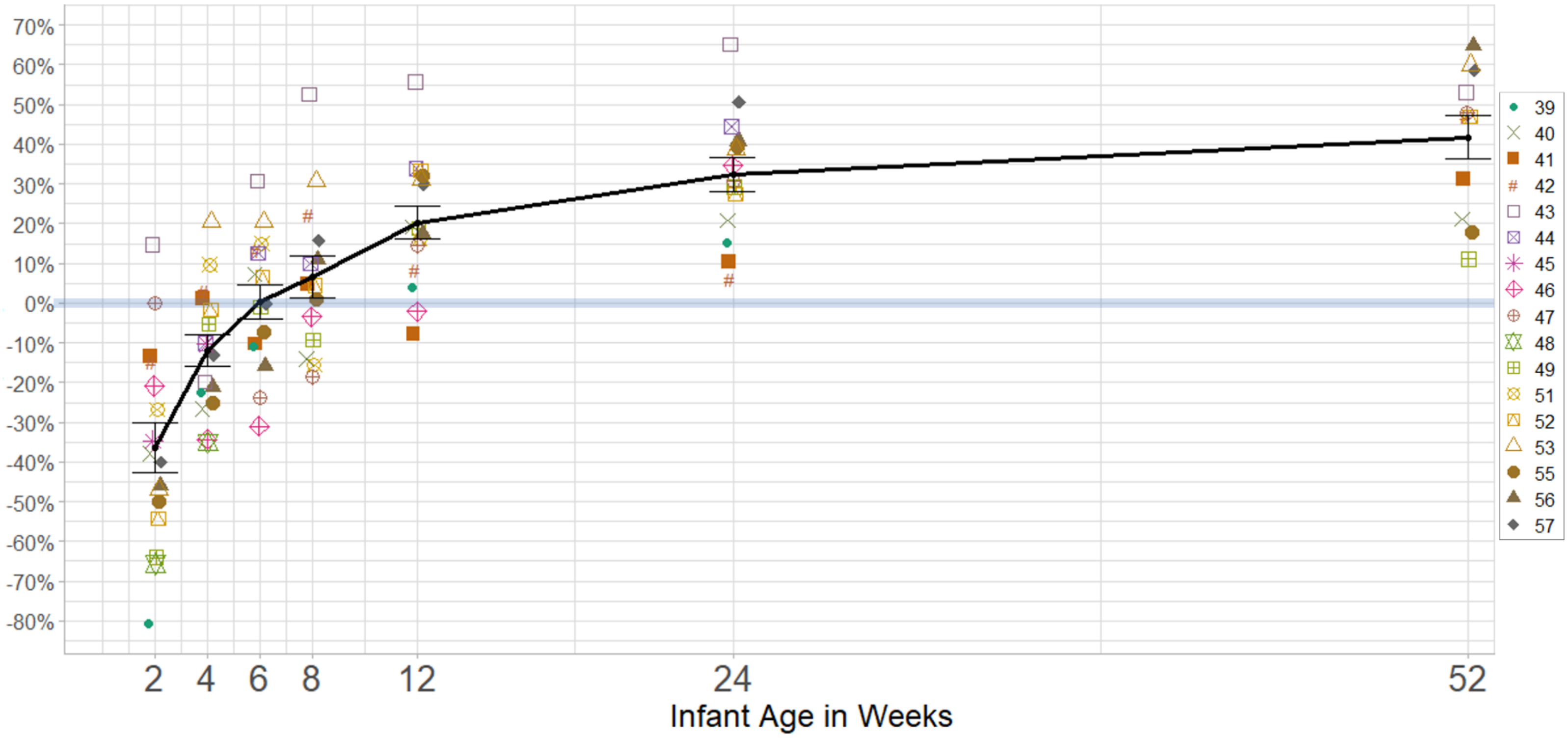


Figure 2: Hinde Index. Individual Hinde Index values (*N* = 17 dam-infant dyads) plotted from 2 weeks to 1 year of age. As described above, the Hinde Index is calculated by subtracting the proportion of total approaches initiated by the infant from the proportion of total leaving initiated by the infant. This value is positive if the infant is primarily responsible for maintaining proximity and negative if the dam is primarily responsible. Responsibility is shared equally within the dam-infant dyad when the Hinde Index equals 0%, marked by a light blue horizontal line. Group mean is indicated by a solid black line, with vertical bars for standard error at each age.

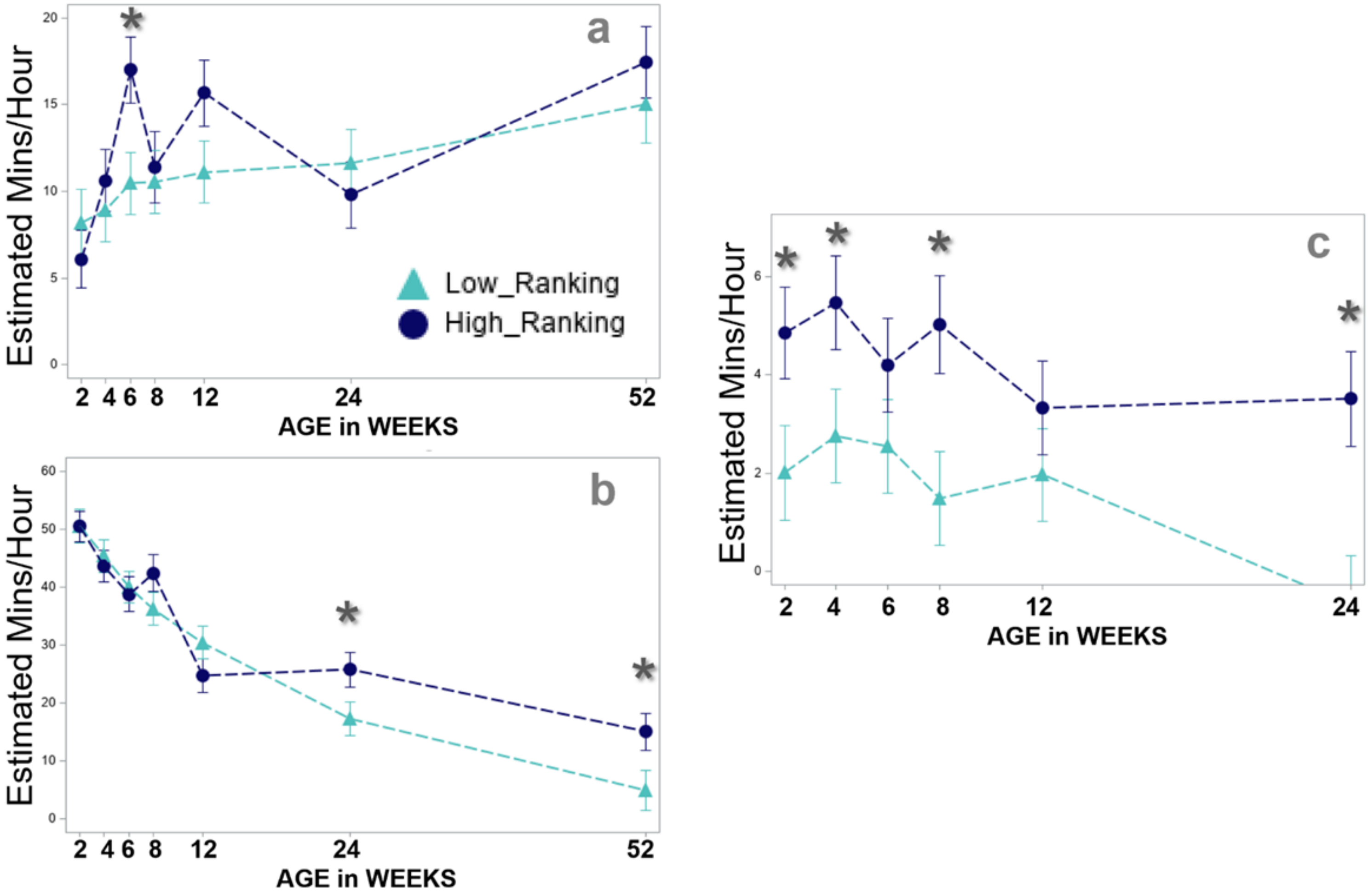


Figure 3: GzMLM Plots of Social Rank Effects. Plots of the AGE*RANK models for the durations of *maternal proximity*, adjusted for infant temperament/*consolability* (a), *maternal contact* (b), and *maternal carrying*, adjusted for cohort year (c). Estimated marginal means for the low-ranking group are indicated by light blue triangles and for the high-ranking group by dark blue circles, with vertical bars representing standard error. Asterisks (*) indicate significant pairwise tests ($p < .05$).

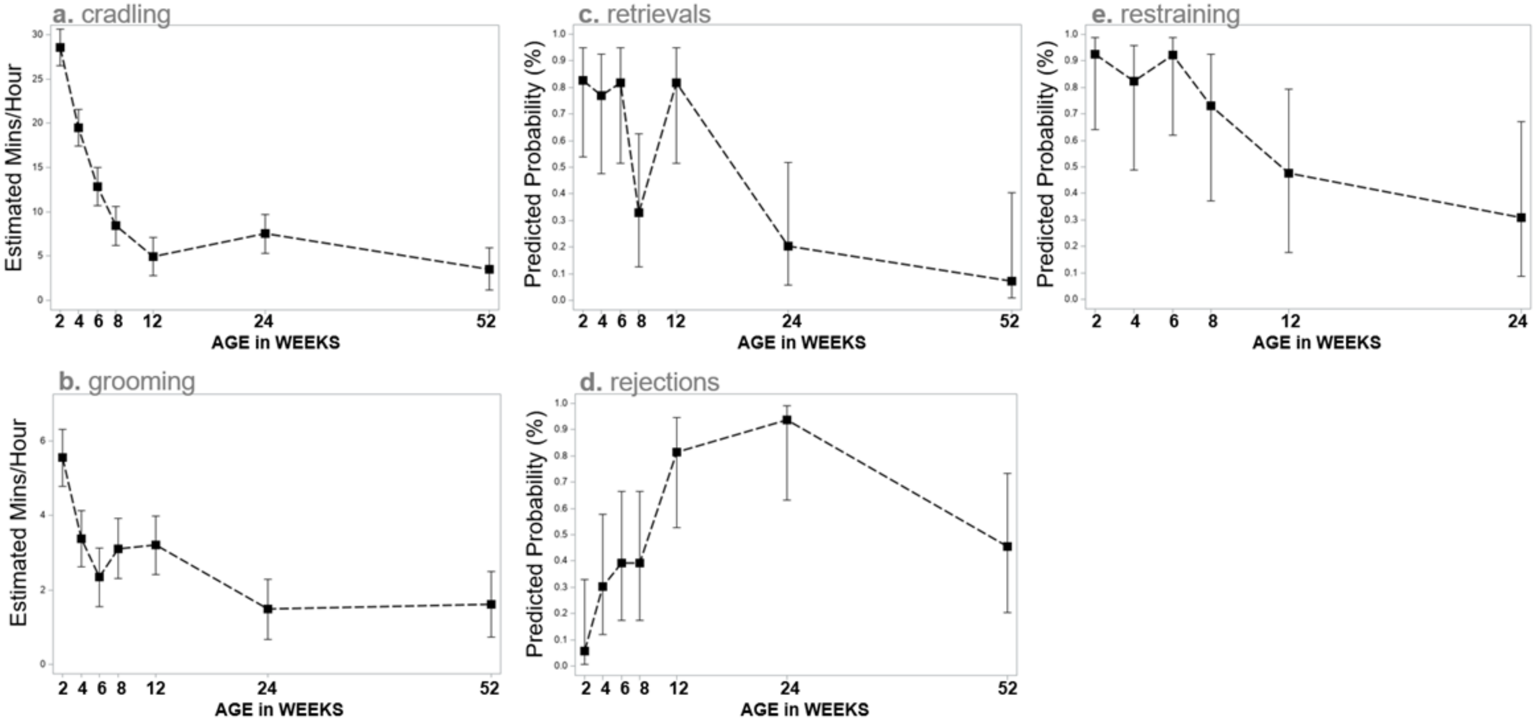


Figure 4: GzMLM Plots of Maternal Behaviors. Plots of the AGE models for *cradling by dam* (a), *grooming by dam* (b), *retrievals* (c), *rejections* (d), and *restraining* through 6 months (e). Data shown are estimated marginal means. Vertical bars represent standard error for continuous variables (a-b) or 95% confidence intervals for predicted probabilities (c-e).

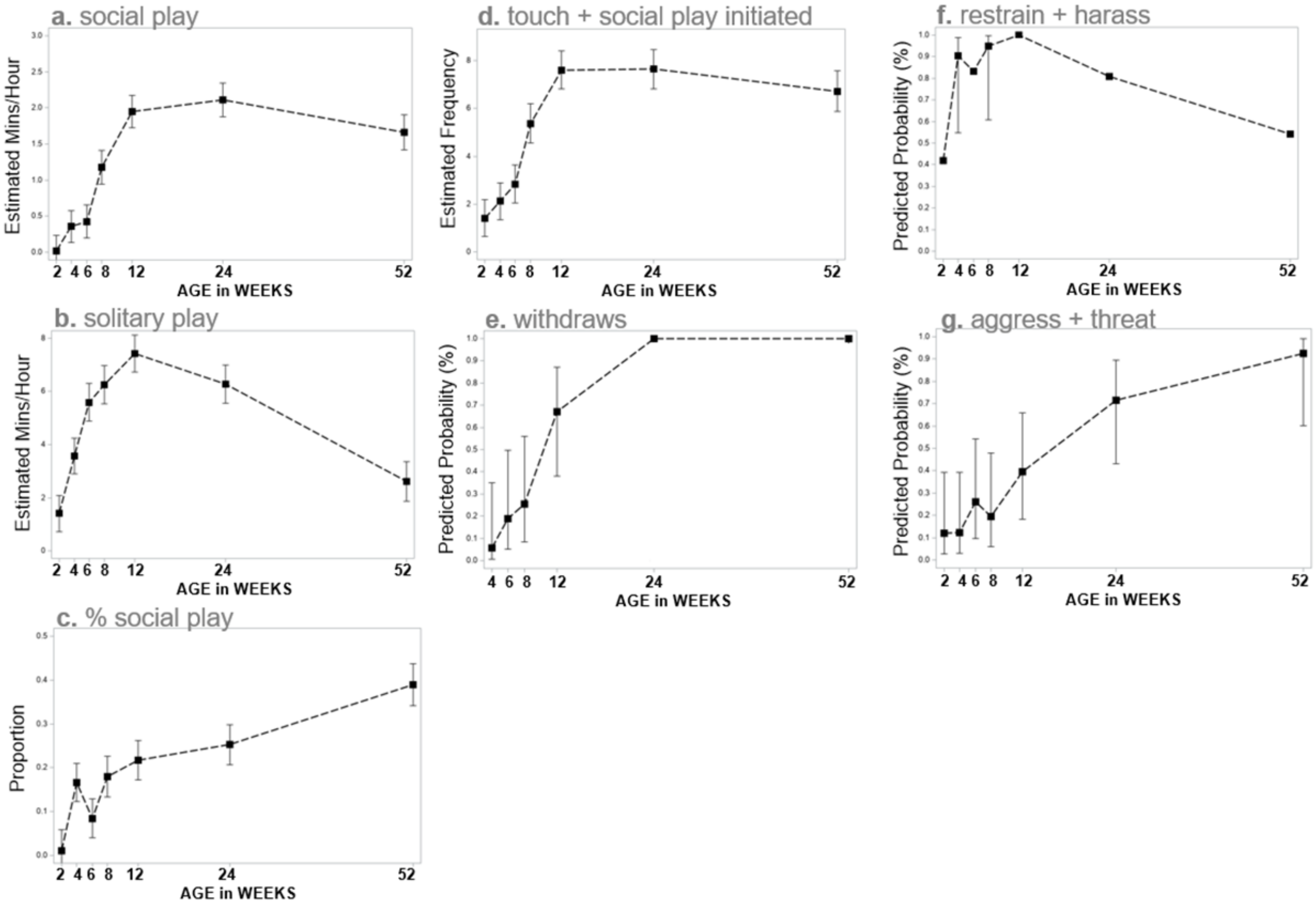


Figure 5: GzMLM Plots of Play and Groupmate Interactions. Plots of the AGE models for social *play duration* (a), *nonsocial play duration* (b), *proportion of social play out of the total play duration* (c), *touch + social play initiated* (d), *withdrawals by infant* after 2 weeks (e), *restraining + harassing* (f), and *aggression + threats* (g). Model plots for *infant touch initiated, initiation of social play by infant* (>3 initiations/hour) after 2 weeks*, contact with groupmates* (>15 sec/hour), *grooming received from groupmates* (>8 sec/hour) and *eye gaze* are not shown, as there were no statistically significant effects of Age for these measures. Data shown are estimated marginal means. Vertical bars represent standard error for continuous variables (a-d) or 95% confidence intervals for predicted probabilities (e-g). (Confidence intervals could not be calculated for *withdraws* at 24 weeks and 1 year, or for *restraining + harassing* at 2 weeks, 6 weeks, 12 weeks, 24 weeks, or 1 year, due to ceiling effects or low variability in the data.)

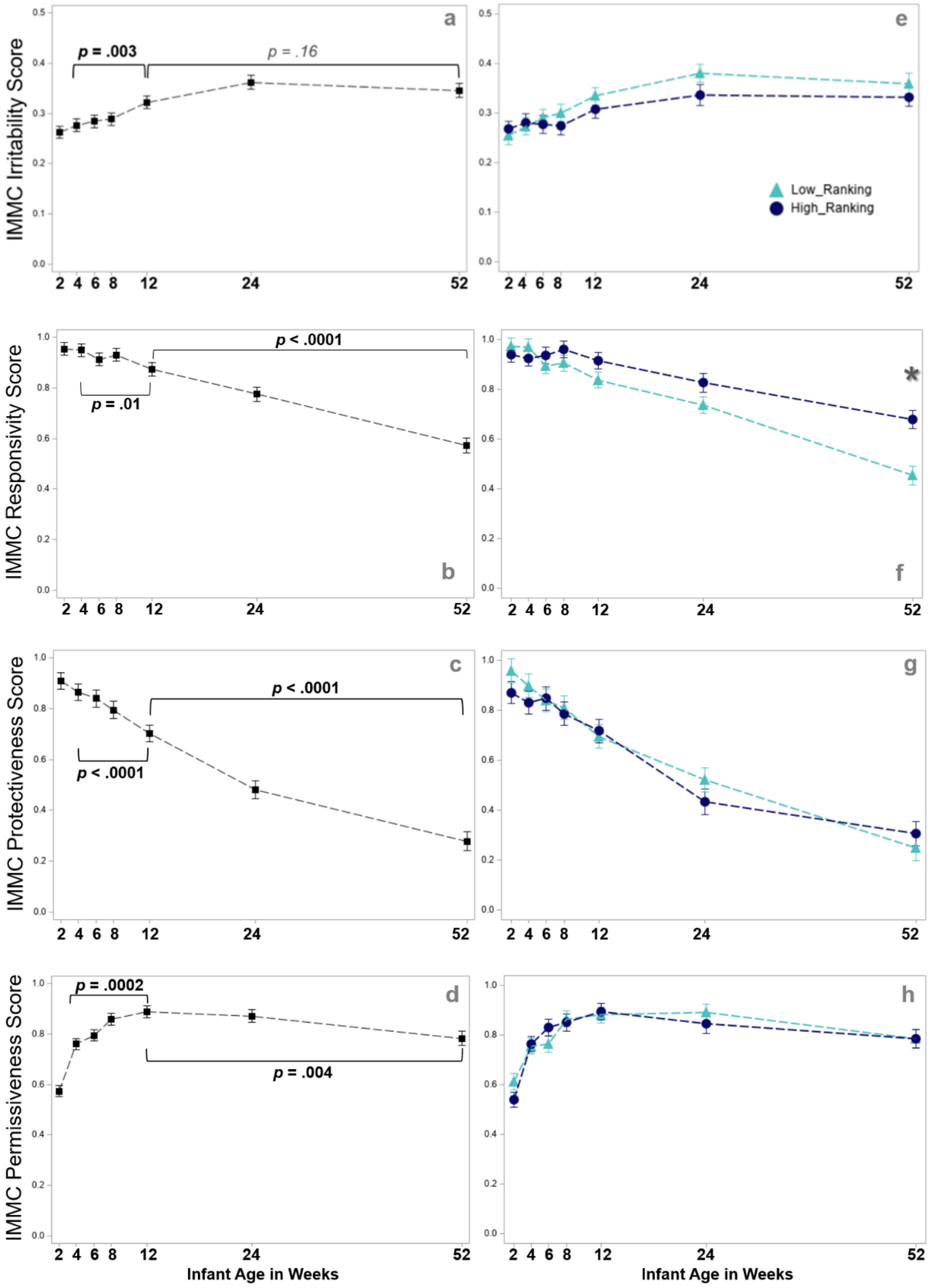
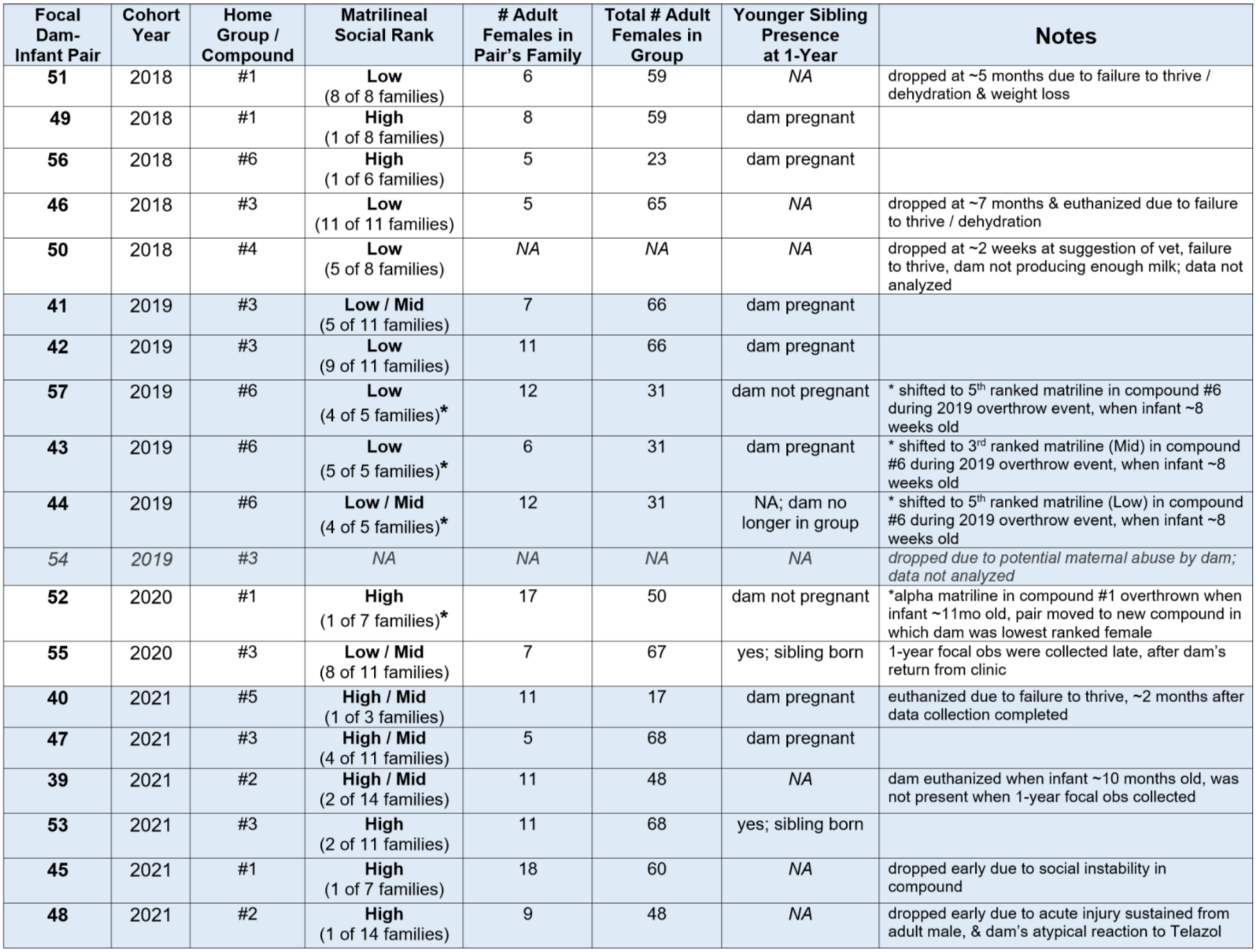


Figure 6: IMMC Dimension GzMLM Plots. Models for *Irritability/Harshness* (a, e), *Responsivity/Sensitivity* (b, f), *Protectiveness* (c, g), and *Permissiveness* (d, h). AGE models are shown on the left (a-d). AGE*RANK models are on the right (e-h). Estimated marginal means for the low-ranking group are indicated by light blue triangles and for the high-ranking group by dark blue circles, with vertical bars indicating standard error. Horizontal brackets reflect pairwise T-tests comparing ages 4 to 12 weeks and 12 weeks to 1 year, based on estimates generated by the AGE models. The asterisk (*) in Fig. f marks a significant difference in model-estimated scores between low- and high-ranking dams ($t(71) = -4.33$, $p < .0001$).

Table 1: Subjects. Social group, rank, and demographic information for the rhesus macaque infants studied (*N* = 17; *N* = 13 with complete longitudinal data). Note that the numerical ranks listed here represent the status of the infant's family/matriline within the social group housed in that compound, rather than the relative rank of the individual dam. Subjects classified as high-ranking were all born into either alpha or beta families (except for Subject 47's dam, which belonged to the 4th-ranked family out of 11). The values for number of animals in a family and number of animals in a compound excluded all juveniles, as well as males of any age. "Adult" females were defined as being of birthing age, or at least 3 years-old (Resko et al., 1982; Stephens et al., 2015; Wilson et al., 1988). Counts were based on the most recently available data from Colony Management (CM) staff at the ENPRC Field Station. Asterisks (*) indicate that an overthrow event occurred during the year of data collection. An overthrow took place in compound #6 when Subjects 43, 44, and 57 were around 8 weeks-old, the result of which was Subjects 44 and 57's family dropping from 4th-ranked to 5th-ranked of the five families in the social group. Subject 43's family rose from 5th-ranked to 3rd-ranked. In compound #1, Subject 52 was around 11 months-old when the alpha matriline, of which his dam was a member, was overthrown by a lower-ranking matriline. CM staff subsequently relocated the former alpha family to a different compound; in this new setting, Subject 52's mother was the lowest-ranking adult female in the group.



Focal Dam-Infant Pair	Cohort Year	Home Group / Compound	Matrilineal Social Rank	# Adult Females in Pair's Family	Total # Adult Females in Group	Younger Sibling Presence at 1-Year	Notes
51	2018	#1	**Low** (8 of 8 families)	6	59	*NA*	dropped at ~5 months due to failure to thrive / dehydration & weight loss
49	2018	#1	**High** (1 of 8 families)	8	59	dam pregnant	
56	2018	#6	**High** (1 of 6 families)	5	23	dam pregnant	
46	2018	#3	**Low** (11 of 11 families)	5	65	*NA*	dropped at ~7 months & euthanized due to failure to thrive / dehydration
50	2018	#4	**Low** (5 of 8 families)	*NA*	*NA*	*NA*	dropped at ~2 weeks at suggestion of vet, failure to thrive, dam not producing enough milk; data not analyzed
41	2019	#3	**Low / Mid** (5 of 11 families)	7	66	dam pregnant	
42	2019	#3	**Low** (9 of 11 families)	11	66	dam pregnant	
57	2019	#6	**Low** (4 of 5 families)*	12	31	dam not pregnant	* shifted to 5th ranked matriline in compound #6 during 2019 overthrow event, when infant ~8 weeks old
43	2019	#6	**Low** (5 of 5 families)*	6	31	dam pregnant	* shifted to 3rd ranked matriline (Mid) in compound #6 during 2019 overthrow event, when infant ~8 weeks old
44	2019	#6	**Low / Mid** (4 of 5 families)*	12	31	NA; dam no longer in group	* shifted to 5th ranked matriline (Low) in compound #6 during 2019 overthrow event, when infant ~8 weeks old
54	*2019*	*#3*	*NA*	*NA*	*NA*	*NA*	*dropped due to potential maternal abuse by dam; data not analyzed*
52	2020	#1	**High** (1 of 7 families)*	17	50	dam not pregnant	*alpha matriline in compound #1 overthrown when infant ~11mo old, pair moved to new compound in which dam was lowest ranked female
55	2020	#3	**Low / Mid** (8 of 11 families)	7	67	yes; sibling born	1-year focal obs were collected late, after dam's return from clinic
40	2021	#5	**High / Mid** (1 of 3 families)	11	17	dam pregnant	euthanized due to failure to thrive, ~2 months after data collection completed
47	2021	#3	**High / Mid** (4 of 11 families)	5	68	dam pregnant	
39	2021	#2	**High / Mid** (2 of 14 families)	11	48	*NA*	dam euthanized when infant ~10 months old, was not present when 1-year focal obs collected
53	2021	#3	**High** (2 of 11 families)	11	68	yes; sibling born	
45	2021	#1	**High** (1 of 7 families)	18	60	*NA*	dropped early due to social instability in compound
48	2021	#2	**High** (1 of 14 families)	9	48	*NA*	dropped early due to acute injury sustained from adult male, & dam's atypical reaction to Telazol

Table 2: Data Summary. Sample sizes for all data types collected (*N* =17 infants total).

	INFANT AGE								
	1 WEEK	**2 WEEKS**	**3 WEEKS**	**4 WEEKS**	**6 WEEKS**	**8 WEEKS**	**12 WEEKS**	**24 WEEKS**	**52 WEEKS**
I.N.A.S.	**17**	**17**	**16**	**15**					
Focal Observations		**16**		**16**	**15**	**14**	**15**	**14**	**13**
Dam-Infant Proximity		**16**		**16**	**15**	**14**	**15**	**14**	**11**
I.M.M.C.		**16**		**16**	**15**	**14**	**15**	**14**	**11**

Table 3A: Ethogram - Analyzed Behaviors. Behaviors measured during infant focal observation sessions. Coding procedures followed a well-established and comprehensive ethogram of rhesus macaque behavior adapted from Altmann (1962) by our research group (see Herman et al., 2003; McCormack et al., 2006, 2009, 2015, 2022; Morin et al., 2020; Raper et al., 2014). Behaviors were measured as frequency rates (number of discrete occurrences of the behavior per hour) and/or duration (minutes per hour spent exhibiting or receiving the behavior). “Groupmates” encompasses all infant, juvenile, and adult macaques, male and female, living in the home compound excepting the focal dam and focal infant.

Behavior	Measure Type	Distribution	Initiator / Actor	Recipient / Target	Ethogram Definition
maternal retrieve	**frequency**	binomial (0, >0)	dam	infant	Dam actively encourages infant to come into contact, i.e., by touching or pulling, usually in response to a threat in the environment
maternal reject	**frequency**	binomial (0, >0)	dam	infant	Dam pushes infant away or prevents infant from nursing or coming in contact
maternal restrain	**frequency**	binomial (0, >0)	dam	infant	Dam physically prevents infant from moving away
maternal carry	**duration**	continuous	dam	infant	Dam carries infant on her back or against her ventrum while standing, walking, or running; does not include limb carrying
withdraw	**frequency**	binomial (0, >0)	infant	groupmates	Infant clearly avoids another macaque; may or may not involve moving out of proximity
touch	**frequency**	binomial (0, >0)	infant	groupmates	Infant touches another macaque; if prolonged, an additional touch is scored for every 3 seconds
contact	**duration**	binomial (<15sec, >15sec)	groupmates or infant	groupmates or infant	An infant and another macaque have at least half of their bodies touching for at least 3 seconds
eye gaze	**frequency**	binomial (0, >0)	groupmates	infant	Another macaque initiates direct eye contact with infant; if prolonged, an additional eye gaze is scored for every 3 seconds
groom	**duration**	binomial (<8sec, >8sec)	groupmates	infant	Another macaque combs through the infant’s hair with hands or mouth for at least 3 seconds
nonsocial play	**duration**	continuous	---	---	Infant plays in the absence of a partner; may be quietly manipulating a toy/object or vigorously jumping and moving around
initiate social play	**frequency**	binomial (<3, >3)	infant	groupmates	Infant initiates play with another macaque; may involve non-agonistic chasing, brief bodily contact, or high intensity “rough-and-tumble” wrestling
social play	**duration**	continuous	groupmates or infant	groupmates or infant	Infant plays with another macaque; may involve non-agonistic chasing, brief bodily contact, or high intensity “rough-and-tumble” wrestling
proportion social play / total play	**duration**	continuous	---	---	100 x (social play duration / social play duration + nonsocial play duration)
composite: touch + social play	**frequency**	continuous	groupmates	infant	Another macaque touches infant or initiates social play with infant
composite: restrain + harass	**frequency**	binomial (0, >0)	groupmates	infant	Another macaque “messes with” infant, i.e., by grabbing or hitting, or physically prevents infant from moving away; infant may or may not show signs of distress
composite: aggression + threat	**frequency**	binomial (0, >0)	groupmates	infant	Another macaque hits, bites, grabs, slaps, or physically pins down infant, or interacts aggressively with infant by lunging, chasing, woofing, threat barking, or making open mouth threat face
maternal proximity	**duration**	continuous	dam or infant	dam or infant	Dam and infant are within an arm’s reach of each other for at least 3 seconds
maternal contact	**duration**	continuous	dam or infant	dam or infant	Dam and infant are in physical contact for at least 3 seconds
maternal cradle	**duration**	continuous	dam	infant	Dam holds her infant against her ventrum
maternal groom	**duration**	continuous	dam	infant	Dam combs through her infant’s pelage with hands or mouth
approach	**frequency**	*NA*	dam or infant	dam or infant	Any move between proximity “zones” that results in dam and infant being closer to each other; e.g., from *beyond* to in *proximity*, from *within 3 meters* to in *contact*, from in *proximity* to in *contact*
leave	**frequency**	*NA*	dam or infant	dam or infant	Any move between proximity “zones” that results in infant and dam being farther away from each other; e.g., from in *contact* to in *proximity*, from in *proximity* to *beyond*, from *within 3 meters* to *beyond*

Table 3B. Ethogram - Low Occurrence Behaviors. Behaviors measured during infant focal observations that were excluded from analyses due to low occurrence. These 16 behaviors were exhibited by ≤ 25% of mother-infant pairs at the majority (four or more) of the ages at which focal observations were conducted. A number of behaviors listed in the full ethogram were not considered in this study are thus not listed here, e.g., sexual behaviors, eating, drinking, scratching, atypical behaviors like stereotypies, and vocalizations, e.g., coos, grunts, and screams.

Low Occurrence Behavior	Measure Type	Initiator / Actor	Recipient / Target	Ethogram Definition
embrace	**frequency**	groupmates	infant	Another macaque momentarily hugs infant
kidnap	**frequency**	groupmates	infant	Another macaque takes control of infant and moves with him; the dam, infant, or both are disturbed; dam may follow the kidnapper or actively retrieve her infant
lipsmack	**frequency**	groupmates	infant	Another macaque makes facial expression directed at infant involving rapid opening and closing of lips; typically indicates affiliation and/or submission
reject	**frequency**	groupmates	infant	Another macaque pushes infant away or prevents infant from coming in contact
genital groom	**frequency**	groupmates	infant	Another macaque grooms, picks at, or mouths infant’s genital area
abuse	**frequency**	groupmates	infant	Another macaque physically abuses infant by dragging infant across the ground by a limb, crushing infant, throwing infant, stepping or sitting on infant, or forcefully pulling out infant’s hair
punish	**frequency**	groupmates	infant	Another macaque stops infant from performing a specific behavior by mouthing or removing him harshly; infant is not injured, but may protest with vocalizations or tantrum
cradle	**duration**	groupmates	infant	Another macaque holds infant against ventrum
carry	**duration**	groupmates	infant	Another macaque carries infant on their back, against ventrum, or on their arm or leg while standing, walking, or running
retrieve from kidnap	**frequency**	dam	infant	Dam physically takes back her infant from kidnapper
body jerk	**frequency**	dam	infant	Dam makes a quick, vertical jerking movement typically indicating annoyance
carry limb	**duration**	dam	infant	Dam carries infant on her arm or leg while standing, walking, or running
genital groom	**duration**	dam	infant	Dam grooms, picks at, or mouth’s infant’s genital area
groom	**frequency**	infant	groupmates	Infant combs through another macaque’s hair with hands or mouth for at least 3 seconds
groom solicit	**frequency**	infant	groupmates	Infant exhibits posture to solicit grooming from another macaque; may involve moving closer, turning to face away from the target animal, and/or lifting tail
grimace	**frequency**	infant	groupmates	Infant opens mouth wide to show teeth while jaw is closed; typically indicates fear and/or submission

Table 4: IMMC Scale. The 22 items comprising the Instrument of Macaque Maternal Care (IMMC) developed by McCormack et al. (2006; 2015). Items were rated by experimenters using a 1-5 Likert scale. “Threatening events” were operationalized as external events that agitated the group (e.g., a hawk flying overhead, staff entering the compound) or social events that could pose a threat to the focal infant (e.g., an attack, kidnapping, a scuffle breaking out nearby, aggressive individuals approaching). Items #10-13 were marked “N/A” if no such event occurred during the 30-minute observation. Note that we reverse coded Item #6 prior to analysis, and Item #13 was dropped from analyses due to the low occurrence of kidnappings. SR = *Sensitivity/Responsivity* dimension, IRR = *Irritability/Harshness* dimension, PROTECT = *Protectiveness* dimension, PERMISS = *Permissiveness* dimension.

N/A ….	**1** ……..…….	**2** ……..…….	**3** ……..…….	**4** ……..………	**5**
	Never	**Rarely**	**Sometimes**	**Often**	**Almost Always**
	0%	1-25%	26-50%	51-75%	76-100%

1. Mother makes herself available when infant approaches her (opens body to infant, does not walk away or block nipple). SR
2. Mother responds to infant’s signals (e.g., distress) and bids for contact/grooming. [Note: bids for contact may be screams/tantrums because mother left it]. SR
3. Mother adjusts caretaking behavior based on infant’s response (e.g., stops grooming if infant doesn’t like it). SR
4. Mother comforts infant when distressed/upset/fearful. SR
5. Mother holds infant on ventrum right away when it is distressed and returns to mother for contact. SR
6. Mother is comfortable and relaxed when in contact with infant. IRR
7. Mother appears distressed/annoyed by infant’s demands. IRR
8. Mother monitors infant when away from her. PROTECT
9. Mother signals infant to follow when she moves away. PROTECT
10. During threatening events, mother makes/maintains contact with infant or prevents it from leaving. [Note: if infant is away, mom knows exactly where it is]. PROTECT
11. Mother retrieves infant right away if it is attacked/threatened or emits distress calls. PROTECT
12. Mother guards infant (restrains/cradles/draws it closer) when a potentially threatening animal walks by (adult male, high-ranking/aggressive female). PROTECT
13. If infant is kidnapped, mother monitors the situation (follows kidnapper, makes bids for contact).
14. Mother allows infant to use her body to play, explore, climb from, etc. PERMISS
15. Mother allows infant to explore its surroundings and/or play. PERMISS
16. Mother allows infant to leave and return to her (refueling: e.g., play and return; explore and return). PERMISS
17. Mother is inconsistent in responding to infant’s needs or bids for contact/interaction. IRR
18. Mother goes from cradling/caring for infant to abuse/rejection (or vice versa) without clear reason. IRR
19. Caretaking bouts are brief. Mother stops infant’s care without clear reason (e.g., interruption, infant signal). IRR
20. Mother uses only physical behaviors to control infant (e.g., restrains, punishes by biting), instead of using facial expressions or gestures (e.g., threat, lipsmacking). IRR
21. Mother punishes infant (bites, slaps) for minor negative behaviors. IRR
22. Mother continues/repeats punishment even after infant stops negative behavior. IRR

Table 5: Model Fitting. Results obtained by fitting generalized multilevel mixed (GzMLM) models in SAS (v. 9.4, SAS Institute Inc.). All reported fixed effects are Type III effects. *N.s.* = not significant. The column labelled "*AGE Fixed Effect*" reports p-values generated by the AGE model, whereas the "*RANK Fixed Effect*" and "*AGE*RANK Interaction*" columns report p-values generated by the selected AGE*RANK" model. The columns describing random effects are only in reference to the selected AGE*RANK model, as the AGE models sometimes differed from each other in the variance components included.

Behavior	**Measure Type**	**Response Distribution**	**AGE Fixed Effect** γ_{100}	**RANK Fixed Effect** γ_{010}	**AGE*RANK Interaction** γ_{110}	**+ Infant Temperament**	**+ Additional Covariates**	**+ Subject Level Random Effect** $\zeta_{0i\|k}$	**+ Group Level Random Effect** ζ_{0k}	**Pairwise Tests**
Maternal Retrieve	frequency	binomial	***p*** **= .002**	*N.s.*	*N.s.*			X		*NA*
Maternal Reject	frequency	binomial	***p*** **= .007**	*N.s.*	*N.s.*	X		X		*NA*
Maternal Restrain	frequency	binomial	***p*** **= .031**	*N.s.*	*N.s.*			X		*NA*
Maternal Carrying	duration	continuous	***p*** **= .0007**	***p*** **= .0087** γ_{010} = -4.18 mins/hour	*N.s.*		X - adjusted for cohort year	X	X	**HIGH > LOW at 2 wks (*p*=.023), 4 wks (*p*=.031), 8 wks (*p*=.005), 24 wks (*p*=.001)**
Maternal Proximity	duration	continuous	***p*** **= .0002**	*N.s.* (when NOT adjusted for temperament, ***p*** **= .048** γ_{010} = -3.03 mins/hour)	*N.s.*	X		X	X	**HIGH > LOW at 6 wks (*p*=.014)** (adjusted for temperament)
Maternal Contact	duration	continuous	***p*** **< .0001**	*N.s.*	***p*** **= .045**			X		**HIGH > LOW at 24 wks (*p*=.046), at 1 yr (*p*=.035)**
Maternal Cradling	duration	continuous	***p*** **< .0001**	*N.s.*	*N.s.*	X		X	X	*NA*
Maternal Grooming	duration	continuous	***p*** **= .0003**	*N.s.*	*N.s.*	X		X		*NA*
Infant Withdraw	frequency	binomial	***p*** **= .055**	*N.s.*	***p*** **= .071**			X		*NA*
Infant Touch	frequency	binomial	*N.s.*	*N.s.*	*N.s.*			X		*NA*
Contact Received	duration	binomial	*N.s.*	*N.s.*	*N.s.*					*NA*
Eye Gaze	frequency	binomial	*N.s.*	*N.s.*	*N.s.*					*NA*
Grooming Received	duration	binomial	*N.s.*	*N.s.*	*N.s.*	X				*NA*
Nonsocial Play	duration	continuous	***p*** **< .0001**	*N.s.*	*N.s.*			X	X	*NA*
Infant Initiates Social Play	frequency	binomial	*N.s.*	*N.s.*	*N.s.*			X		*NA*
Social Play	duration	continuous	***p*** **< .0001**	*N.s.*	*N.s.*			X		*NA*
Social Play / Total Play Duration	proportion	continuous	***p*** **< .0001**	*N.s.*	*N.s.*			X		*NA*
Touch + Social Play Received	frequency	continuous	***p*** **< .0001**	*N.s.*	*N.s.*			X		*NA*
Restrain + Harass Received	frequency	binomial	***p*** **= .037**	*N.s.*	*N.s.*	X		X	X	*NA*
Aggression + Threat Received	frequency	binomial	***p*** **= .003**	*N.s.*	*N.s.*	X		X		*NA*
Irritability / Harshness	IMMC	continuous	***p*** **< .0001**	*N.s.*	*N.s.*			X		*NA*
Responsivity / Sensitivity	IMMC	continuous	***p*** **< .0001**	***p*** **= .074**	***p*** **= .0002**			X		**HIGH > LOW at 1 yr (*p*<.0001). For LOW only, decrease 2-6 wks (*p*=.034), 2-12 wks (*p*=.0003), 4-6 wks (*p*=.036), 4-12 wks (*p*=.0003)**
Protectiveness	IMMC	continuous	***p*** **< .0001**	*N.s.*	*N.s.*			X		*NA*
Permissiveness	IMMC	continuous	***p*** **< .0001**	*N.s.*	*N.s.*	X				*NA*

Table 6: Linear Mixed Model Results. Results of the models testing whether initiating play, withdrawing, and maternal *Responsivity* at 3 months, as well as cradling during the first month of life, predict the two dependent variables, initiating play and withdrawing, at one year of age ($N = 13$). All model versions include cohort year as a random factor. Estimates, t-values, and p-values refer to the “reference” models, which include all four fixed factors (predictors), and to results from Type III tests of fixed effects. For the likelihood ratio tests (LRTs) and AIC values, each row represents a “reduced” model from which that predictor is excluded. Reduced models with a significant ($p < .05$) LRT statistic are bolded. A positive value for ΔAIC indicates that including the predictor improves model fit; a negative value indicates that model fit is improved when the predictor is excluded.

Predictor	DV (1 Year)	Estimate ± SE	*t*	*p*	LRT Statistic	LRT *p*-value	Δ AIC
Infant Initiates Social Play: Frequency at 3 months	Infant Initiates Social Play	1.22 ± 0.39	3.15	.016	**7.07**	**<.01**	+5.07
Infant Withdraws: Frequency at 3 months		-6.68 ± 2.61	-2.56	.049	3.66	.0556	+1.66
Maternal Responsivity: Score at 3 months		21.43 ± 11.05	-0.22	.836	2.85	.091	+0.85
Maternal Cradling: Duration at 1 month		-0.54 ± 0.23	-2.35	.051	**10.16**	**<.01**	+8.16
Infant Initiates Social Play: Frequency at 3 months	Infant Withdraws	-0.05 ± 0.04	-1.29	.237	1.30	.255	-0.70
Infant Withdraws: Frequency at 3 months		3.51 ± 0.43	8.20	<.001	**17.60**	**<.0001**	+15.60
Maternal Responsivity: Score at 3 months		2.53 ± 1.21	2.09	.076	3.128	.077	+1.13
Maternal Cradling: Duration at 1 month		-0.003 ± 0.02	-0.15	.887	0.02	.885	-1.98

APPENDIX: Equations for Generalized Multilevel Mixed Models

We used a step-up strategy to fit the following three-level model for each of our outcome variables ***Y***. Subscripts refer to individual infant ***i*** born in compound ***k*** and assessed at age ***j***. Note that estimates for random variation in slope ($\boldsymbol{\zeta_{1i|k}}, \boldsymbol{\zeta_{1k}}$) were *not* included for the sake of parsimony. When necessary in order to fit a model, residuals related to random variation in intercepts ($\boldsymbol{\zeta_{0i|k}}, \boldsymbol{\zeta_{0k}}$) were also dropped from the equation.

AGE Model:

$$\boldsymbol{Y_{jik} = \gamma_{000} + \gamma_{100}AGE + +\zeta_{0i|k} + \zeta_{0k} + \varepsilon_{jik}}$$

AGE*RANK Model:

$$\boldsymbol{Y_{jik} = \gamma_{000} + \gamma_{010}RANK + \gamma_{100}AGE + \gamma_{110}AGE(RANK) + \zeta_{0i|k} + \zeta_{0k} + \varepsilon_{jik}}$$

AGE*RANK Model Adjusted for Infant Temperament:

$$\boldsymbol{Y_{jik} = \gamma_{000} + \gamma_{010}RANK + \gamma_{020}CONSOLABILITY + \gamma_{100}AGE + \gamma_{110}AGE(RANK) + \zeta_{0i|k} + \zeta_{0k} + \varepsilon_{jik}}$$

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Study II: Developmental Trajectories of Social-Visual Attention in Rhesus Macaque Infants

ABSTRACT

Social-visual attention, an early-emerging attentional bias of infants towards visual cues like the face and eyes of conspecific caregivers, has been linked with social functioning in both typically and atypically developing children. Recent eye-tracking studies have demonstrated the possibility of leveraging the technology to detect divergent patterns of attention in early infancy. Such efforts at early detection benefit from knowledge of typical development gained through studies in rhesus macaques (*Macaca mulatta*). There are striking parallels between macaque and human infants in the developmental trajectory of social-visual attention, with the practical advantage that development in macaques advances roughly four times faster than in humans. Rhesus macaques are a matriarchal species; thus, matrilineal ranking may play a significant role in shaping attentional strategies and determining both the quantity and quality of the social inputs that individuals receive early in life. For the current study, established methods for conducting eye-tracking in human infants (Jones & Klin, 2013) were “reverse translated” for use in rhesus macaques born and reared at the Emory National Primate Research Center (Lawrenceville, GA). Our aims were to: detail the development of basic, evolutionarily conserved social-visual attentional processes in a non-human primate model, investigate the role of matrilineal ranking in social-visual attention, and identify eye-tracking measures as “predictors” of later social behavior. Eye-tracking data were densely sampled over 14 sessions spanning birth through 6 months of age, during which infants voluntarily viewed videoclips depicting a single conspecific or dam-infant interactions. The data suggested that by 4 to 5 months of age, low-ranking infants developed covert viewing strategies in order to monitor social cues while avoiding direct eye contact with conspecifics. We found that rates of initiating social play in juvenescence were positively predicted by saccades to dam-infant videos. In addition, we partially confirmed previous findings by Wang et al. (2020) and Ford et al. (2023), most notably related to infants’ fixation to the eyes of conspecifics.

INTRODUCTION

Newborns acquire vital information about their social world first and foremost through caregivers, relying on dynamic exchanges of facial expressions, vocalizations, and eye contact. Facilitating these interactions is the newborn's attentional preference for visual "cues" like the eye region and face of conspecifics. This attentional bias, referred to as "social-visual attention," is linked with social functioning in both typically and atypically developing children. In recent years, studies have demonstrated the potential of leveraging eye-tracking to identify divergent patterns of attention in infancy (Constantino, 2011, 2018; Constantino et al., 2017; Jones & Klin, 2013; Jones et al., 2023a, 2023b; Klin et al., 2002). In these efforts at early detection, nonhuman primates (NHPs) and, in particular, rhesus macaques (*Macaca mulatt*a) are indispensable as a model system due to their complex social structure, altricial birth, and extended development (reviewed by Machado & Bachevalier, 2003). Female macaques bond with their newborns through reciprocal exchanges of eye contact and affiliative lipsmacking; maternal interactions of this type continue through around 2 months of age, but are especially frequent and robust in the infant's first few weeks (Ferrari et al., 2009). Modelling early development in macaques offers the practical advantage of an accelerated timeline, as 1 week for a newborn macaque is roughly equivalent to 1 month for a human infant (Boothe et al., 1985). Longitudinal data collection can thus be completed in a quarter of the time required for a study of human participants (see Fig. 1). Another practical advantage of modelling development in NHPs is the ability to minimize confounding factors that are difficult to control in human studies (e.g., diet, education, and exposure to prenatal stress).

In adapting eye-tracking procedures for rhesus macaques, our research group has documented striking cross-species parallels in patterns of social-visual attention across development. Like humans, macaques use social-visual attention as a central process for the development of social skills. Converging evidence from eye-tracking studies has led our group to identify a critical period for social development between 5 to 6 weeks. At this age, rhesus macaque infants begin to switch their visual preference from conspecific faces to heterospecific (non-macaque primate) faces (Parr et al. 2016). Similarly, macaques first show preferential attention to direct gaze over averted gaze between 4 and 9 weeks (Muschinski et al. 2016). Wang et al. (2020) identified a peak at 5 to 6 weeks in infants' visual preference for the eye region; that preference declined gradually after 6 weeks before again increasing as infants approached 6 months of age. Importantly, an analogous preference has been described for human infants (Jones & Klin, 2013). Accounting for the relatively accelerated pace of maturation in rhesus macaques, the shared developmental trajectory seems to reflect an evolutionarily conserved transition in primate neurodevelopment (Machado & Bachevalier, 2003). It has been proposed that during this critical period from 5 to 6 weeks, goal-driven cortical processes supporting social-visual attention mature and become increasingly dominant over earlier emerging, reflexive, and stimulus-driven perceptual processes that are grounded in subcortical structures (Distler et al., 1996; Johnson, 2005; Morton & Johnson, 1991).

Studies in rhesus macaques further demonstrate that the developmental trajectory of social-visual attention shows significant interindividual variability and has experience-dependent as well as species-typical features. As stated by Kano et al. (2018), "primate individuals acquire their unique attentional biases through both ontogeny and evolution" (3018p. 1). This interindividual variation in early social-visual attention has been shown to predict individuals' social functioning later in life. For example, Sclafani et al. (2016) presented rhesus macaques with video recordings of aggressive versus neutral behavioral displays and observed that rates of looking at the two types of videos predicted social proficiency at the juvenile stage. The authors proposed that socially impaired juveniles may scan conspecific faces differently from their more prosocial peers, fixating less on the eye region and utilizing a local rather than a global processing strategy. Among similar findings, looking time to the eye region in social stimuli correlated positively with peer-to-peer interactions among male infant rhesus macaques (Ryan et al., 2020). In the case of distinct neonatal behaviors related to social-visual attention, macaque infants who engaged in more mutual gaze with their mother exhibited more frequent prosocial behaviors at both 2 and 5 months of age (Dettmer et al., 2016), and the tendency to imitate facial gestures in the first week of life was predictive of later gaze following ability (Simpson et al., 2016).

One major source of interindividual variability among rhesus macaques is social ranking. This species lives in large, multigenerational, polygynous, and matriarchal societies (Altmann, 1962; Bernstein, 1976; Bernstein & Williams, 1983). Groups are organized by highly stable matrilines, such that the external rearing environment of an infant macaque is influenced from the moment of birth by its mother's status (Rowell et al., 1964; White & Hinde, 1975; Wooddell et al., 2020). Matrilineal ranking thus may play a substantial role in determining both the quantity and quality of the social inputs that infants receive early in life, and in this way, may shape the development of social-visual attention. When 9-month-old rhesus macaques were shown images of conspecific faces, infants born to high-ranking females maintained visual attention towards images of threatening faces, in preference to emotionally neutral faces, for over one second longer on average than infants born to lower-ranking females (Mandalaywala et al., 2014). Significant effects on attention to face and eyes have been detected even in infants younger than 2 months of age (Paukner et al., 2017).

More recently, analysis of eye-tracking data by our group demonstrated a relationship between cortical development and social-visual attention that was modulated by social ranking. Ford et al. (2023) calculated percent fixation to the eye region in 14 male rhesus macaque infants born to middle-ranking females (divided for analysis into relatively low- and high-ranking groups) and found that matrilineal rank was significantly associated with the age at which eye-looking reached a peak in early infancy, as well as the rate of change in eye-looking during late infancy (4 – 6 months). The developmental trajectory of attention to eyes in the first 2 months of life was accelerated in the lower-ranking infants, suggesting that subordinate infants adapt quickly in order to process critical social cues in their environment at a younger age than do their dominant peers. Strikingly, functional connectivity between left primary and extrastriate visual cortical areas was significantly associated with the maturation of eye-looking, predicting an *earlier* peak in eye-looking for low-ranking infants and a *later* peak for high-ranking infants.

Motivated by these findings, we applied eye-tracking technology to further detail the development of basic attentional processes in immature rhesus macaques from birth through 6 months of age. We completed the following aims: (1) we further tested and expanded on the findings by Ford et al. (2023), based on the same category of video stimuli and applying similar statistical methods, but with a larger sample size of 39 mother-infant pairs representing a wider range of social rankings from the highest-ranked (“alpha”) to the lowest-ranked (“omega”) families; (2) we analyzed an additional category of stimuli (videos of mother-infant social interactions) not previously considered; (3) we used the dynamic nature of eye-tracking data to quantify additional features of social-visual attention, such as the frequency of saccades by the viewer, and the amount of missing or lost data due to inattention or gazing offscreen (see Naples et al., 2021; Shic et al., 2022); (4) we expanded on these analyses through exploratory methods to identify developmental milestones in infant macaques’ attention to complex conspecific interactions using a longitudinal “salience mapping” technique (Kreuzman et al., 2017; Micheletti et al., 2017); and (5) we aimed to identify additional features of social-visual attention during infancy as potential predictor variables for the individual’s social behavior later in life, at 1 year of age.

We hypothesized that individual variation in social-visual attention in infant macaques ages 1 – 24 weeks old is explained in part by differences in infant-mother social-ranking within the group hierarchy. In particular, we predicted that infants born to lower-ranking females would show earlier peaks in preferential attention towards salient social cues, as well as an accelerated developmental trajectory at later ages, compared to higher-ranking infants. Finally, we predicted that, similarly to human infants (Micheletti et al., 2017), infant macaques younger than 10 weeks (2.5 months) of age would display scattered and highly variable looking patterns that would then converge on looking patterns similar to those of a 23-week-old macaque at between 10 – 13 weeks (70 – 91 days) of age.

METHODS

Subjects & Housing

As part of a larger programmatic study of early social and neural development (see Ford et al., 2023; Kovacs-Balint et al., 2021; Muschinski et al., 2016; Parr et al., 2016; Wang et al., 2020), behavioral development in 18 typically developing male infant rhesus monkeys (*M. mulatta*) was tracked longitudinally (Fig. 1; Table 1). Only male infants were included to allow for greater statistical power given our small sample size, as well as to align with the broader translational goals of funding provided for the studies by the National Institutes of Mental Health through an Autism Center of Excellence (ACE) grant (P50-MH100029) awarded to our collaborators at the Marcus Autism Center (Atlanta, GA).

All subjects were born and housed at the Emory National Primate Research Center (ENPRC) Field Station in Lawrenceville, GA. Focal infants were reared by their mothers in large, multigenerational social groups. This provided infants with species-typical social experiences and opportunities to interact with both male and female individuals of varying ages and social status, while still making possible the standardization of variables like diet and housing. As in free ranging populations of rhesus macaques (Altmann, 1962), each social group consisted of multiple families, or matrilines, with a vertical social hierarchy. Each group was housed at the Field Station in an outdoor compound with access to indoor, temperature-controlled quarters. All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of Emory University, in accordance with the Animal Welfare Act and the U.S. Department of Health and Human Services “Guide for Care and Use of Laboratory Animals.” The wellbeing of each mother-infant pair was monitored for the full duration of the study, and their weights recorded during each session of data collection.

Criteria for inclusion stipulated that all subjects were born to multiparous adult females observed to be competent, non-abusive, and non-neglectful in their care of prior offspring. None of the dams in the study were first-time mothers, although it was not possible to standardize the precise number of previous births among dams. Females were selected to have as little genetic interrelatedness as possible with other mothers in the study, and there was never more than one infant born to any single dam assigned to the study. Subjects were all born full-term and without need of veterinary assistance, weighing a minimum of 450 grams at birth. Dam-infant pairs were also selected from groups known to be relatively socially stable.

Over the course of four birthing seasons from 2018 to 2021, a total of 19 mother-infant pairs were assigned to the project. One mother-infant pair was removed from the study within a week after birth due to potential maternal abuse, resulting in a total of 18 subjects included in data analyses. We increased the sample size to 39 infants by incorporating additional data collected from macaque infants born in 2016 (*N* = 21) from middle-ranking mothers as part of the same programmatic study (Table 1). See Ford et al. (2023) and Wang et al. (2020) for further details on the 2016 cohort.

Ranking information was provided by ENPRC Colony Management staff based on observations of dyadic agonistic interactions. Following established methods (Bernstein, 1976; Embree et al., 2013; Howell et al., 2014), staff considered an adult female as ranking below a groupmate if she invariably responded submissively when that individual approached and/or acted aggressively towards her. Social rank was thus determined from observations not of aggressive behaviors, per se, but of subordinate/submissive behaviors such as withdrawing, grimacing, and fleeing. Each infant was assigned its mother’s matrilineal social rank/status, which reflects the status of their family/matriline relative to all families in the group/home compound. For example, a rank of 2/8 would indicate the infant was born into the second-ranking family out of eight total families in that group, and is thus a relatively high-ranking individual. Ranks were normalized to a percentile by dividing the family rank by the total number of families, then subtracting this value from one (e.g., 2/8 → 75%), such that percentiles closer to zero represent lower social status and percentiles closer to one represent higher status (Table 1). During the course of data collection, an overthrow occurred in one compound, resulting in rank shifts of three subjects (#'s 43, 44, 57; see Table 1 for details). We used subjects' rank at the time of birth for all data analysis.

Eye-tracking Procedures

Researchers and technicians at the Yerkes NPRC Field Station have developed effective, noninvasive procedures for opportunistically collecting eye-tracking data while infant macaques remain with their mothers. In an effort to increase the translational relevance of the study, these procedures were modelled after those used at the Marcus Autism Center (Atlanta, GA) for collecting longitudinal data on social-visual attention in human infants (see Jones & Klin, 2013). We tracked the development of social-visual attention in male infant rhesus macaques over the course of 14 eye-tracking sessions taking place over 6 months, at 1, 2, 3, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, and 23 weeks postnatally, or 7 – 161 days (Fig. 1). All procedures were previously described (Ford et al., 2023; Muschinski et al., 2016; Parr et al., 2016; Wang et al., 2020) and are summarized below. A detailed description of the procedures is provided in Appendix I.

On the date of testing, the mother-infant pair was removed from their social compound using established procedures (see Herman et al., 2010) and brought to an onsite behavioral testing facility. The mother was lightly anaesthetized via an intramuscular injection of Telazol (3-5 mg/kg). The pair was then positioned comfortably in a chair inside the custom-built testing chamber (Fig. 2), where the infant remained unrestrained and in ventral contact with its mother for the entirety of the session. Stimuli were presented on a computer monitor affixed to one wall of the chamber. An infrared camera was mounted immediately below the video monitor on a motorized gimbal, allowing an experimenter to manually track the infant’s eye and adjust zoom and focus throughout the session (Figs. 2, 3). Due to the smaller size of macaque infants relative to humans, only the infant’s left eye was tracked (Fig. 3). The infant’s gaze was calibrated at the start of each session using a 5-point procedure, then the experimenter initiated presentation of the stimuli “playlist.” At the experimenter’s discretion, any experimental stimuli that the infant did not attend to (due to falling asleep, actively exploring the chamber, etc.) could be repeated at the end of the session. Data were collected using technology developed by ISCAN (http://www.iscaninc.com). A single session lasted 10-15 minutes if calibration proceeded quickly and no stimuli were replayed, extending if necessary to a maximum duration of 30 minutes. Mother and infant were then moved to an adjacent room in the testing facility, where the mother was given time to recover fully from anesthesia before the pair was returned to their social group.

Experimental Stimuli

Videoclips depicting a single conspecific or dynamic interactions between conspecifics, rather than static images, have increasingly been used to enhance subject’s visual attention in studies of human children (Karatekin, 2007; van Rijn et al., 2019) and nonhuman primates (Mosher et al., 2011; Ryan et al., 2020). To prioritize ecological validity, high quality video was recorded of freely behaving rhesus macaques located at the ENPRC or the Caribbean Primate Research Center on Cayo Santiago, Puerto Rico and then edited to create short clips of approximately ten seconds in length. None of the individual macaques featured in the videoclips were familiar to our subjects. For the purposes of this study, we analyzed two categories of video stimuli: clips showing a single unfamiliar conspecific (39 unique videoclips; referred to hereafter as “Conspecific” videos) and clips of mother-infant interactions (39 unique videoclips; referred to hereafter as “Mother-Infant” videos). The Conspecific videoclips, which were analyzed in our previous studies (Ford et al., 2023; Wang et al., 2020), showed a single juvenile or adult macaque displaying a neutral facial expression, with males and females represented roughly equally (Fig. 4A). Mother-Infant videoclips showed species-typical dyadic interactions between adult females and infants (Fig. 4B). Infants were shown in close contact with their dam while nursing, playing, exploring, or interacting with another group member. The full bodies of both mother and infant were shown, taking up 30 to 50 percent of the area of the screen. Other conspecifics also appeared briefly in 13 of the Mother-Infant videoclips. Within a given session, approximately 30% of the videos shown were novel and 70% had been shown in at least one previous session. Each unique Mother-Infant and Conspecific videoclip was included in an average of three and no more than six sessions. During testing, the two categories of videos were interspersed with other stimuli categories that are not discussed in this paper. The order of videoclip presentations was pseudorandomized with all subjects viewed the same playlists at the same ages, but in differing orders of presentation. For a detailed overview of calibration success and videos watched by previous cohorts, see Table 1 in Wang et al. (2020).

ROI Analysis

For the Conspecific videos, we used the regions of interest (ROIs) that were previously created by Wang et al. (2020) to capture: total screen area, body, head, eyes, and mouth (Fig. 4A). In order to analyze the Mother-Infant videos, we created ROIs to capture six categories of content: total screen area, infant's eyes, dam's eyes, infant's head, and dam's head, with an additional ROI for other rhesus macaques appearing in the scene, referred to hereafter as "groupmates" (Fig. 4B). ROIs were hand traced frame by frame, using in-house software written in MATLAB (v. r2018b), and stored as binary bitmaps.

We then leveraged in-house software in MATLAB (v. r2018b) to automatically parse the data recorded during eye-tracking sessions into four distinct types of eye movements: fixations, saccades, blinks, and lost/offscreen data. A fixation was counted whenever the infant's gaze rested in the same location on the screen for two frames consecutively (or one-fifteenth of a second given the frame rate of 30 Hz). Each fixation was further tagged with a specific ROI. Saccades were defined by the velocity of eye movements, based on a threshold of 30 degrees/sec. Saccades and blinks were not tagged with ROIs. We then calculated the percentages of fixations, saccades, and lost data relative to the number of frames in a given video (typically around 300 frames). Finally, we calculated percentages of fixation to each predetermined ROI, relative to the total count of fixations for the entire videoclip. For subsequent analyses, we combined the ROIs for dam eyes and head, and for infant eyes and head, to create two ROIs for “dam” and “infant,” due to the small size of the eye region ROIs and low percent fixation (Fig. 4B).

Data were excluded if zero fixations were counted during the presentation of the videoclip. We note that this criterion differed from the exclusion threshold of 20% fixations (approx. 60 frames) applied in some previous eye-tracking studies (e.g., Jones & Klin, 2013; Ford et al., 2023; Wang et al., 2020). We chose a less stringent criterion for the current analyses because we were interested not only in specific ROIs, but also in global measures of viewing behavior and data quality. Further, we wished to avoid the risk of excluding potentially meaningful datapoints, given that monkeys are known to show overall poorer attention towards video stimuli, compared to human participants, and to perform more saccades and covert viewing strategies like brief “check-looks” to the screen, rather than overt fixation (Hu et al., 2013; Mosher et al., 2011; Wang et al., 2020).

Statistical Analysis

FPCA: In this study, we leveraged innovative analytical strategies that have been developed by our colleagues at the Marcus Autism Center in order to generate accurate models of infant development (Jones & Klin, 2013; Klin et al., 2002; see also Dong et al., 2023). Their approach utilizes the tools of functional data analysis in order to describe and quantify features of developmental change itself. A detailed explanation of the statistical procedures is provided in Appendix I. Functional analysis of this type is vital to the study of development because trajectories can be influenced by factors entirely separate from those that influence outcome measures at any one timepoint (Kievit et al., 2021). To identify key derivative features of developmental trajectories in social-visual attention, such as rates of change and the timing of inflection points, we generated longitudinal growth curves using Functional Principal Component Analysis (FPCA) (Chen et al., 2021; Müller, 2005; Ramsay & Silverman, 2005; Wang et al., 2016; Yao et al., 2005). FPCA is a non-parametric, data-driven approach to curve-fitting that does not require making *a priori* assumptions about a curve's true underlying shape.

For these analyses, we used data from the current study (*N*=18) as well as those from the 2016 cohort (*N*= 21) previously published (Ford et al., 2023; Wang et al., 2020) in order to achieve a larger sample size (*N* = 39) and optimize our curve-fitting procedure. We conducted FPCA for 13 measures of social-visual attention - seven measures derived from viewing of Conspecific videoclips (percent total fixations, percent lost/offscreen data, percent saccades, percent fixation to eyes ROI, percent fixation to body ROI, percent fixation to head ROI, percent fixation to mouth ROI) and six measures derived from infants' viewing of Mother-Infant videoclips (percent total fixations, percent lost/offscreen data, percent saccades, percent fixation to infant ROIs, percent fixation to dam ROIs, percent fixation to conspecific groupmate ROI). For each of these measures, Table 2 lists the sample size and number of videoclips included in analysis. We first generated group mean and individual trajectories for each measure of social-visual attention. Mean curve-fitting was done separately for each measure by applying a Gaussian filter to the eye-tracking data. We also examined rates of developmental change by calculating the first derivative of the modelled mean curve. We then leveraged FPCA to identify the predominant modes of variation in these trajectories. Each principal component (PC) function explains a certain proportion of variation relative to the group mean curve, here referred to as the "Fraction of Variance Explained" (FVE). For the current analyses, we report only as many PC functions for each eye-tracking measure as were needed to collectively explain at least 95% of total variance in that measure's trajectory (> 95% FVE). For example, if FPCA for a particular measure yielded four PC functions explaining, respectively, 80%, 10%, 6%, and 4% of the total variance, we would only report and describe the three largest PC functions (combined FVE = 96%) and drop the PC function explaining only 4%.

Linear regression: As a strategy for data reduction, FPCA is useful for between-subject comparisons because it allows for assigning PC scores to individual subjects. These scores are scalar values and thus amenable to standard parametric types of analysis (Chen et al., 2021; Wang et al., 2016). In this study, we used bivariate linear regression models to test for relationships between social-visual attention and an individual's social ranking (IBM SPSS Statistics 29). As described above, rank was treated as a percentile. PC scores were modeled as response variables. We examined all PC scores for extreme individual outliers (3*IQR) and detected extreme outliers among the scores for two functions. When we excluded outliers and conducted the regression analyses again, however, the statistical significance of the associations was not affected. Therefore, all results are presented here with outliers included to preserve individual variability in trajectories.

As one of our major aims in the current study was to further test and expand on the findings by Wang et al. (2020) and Ford et al. (2023) related to the developmental trajectory of percent fixation to eyes, we conducted additional regression analyses for measures of eye-looking using data from different groupings of subjects. We first ran the analyses with infants from the more recent cohorts only (*N* = 18), a sample which included an expanded range of social ranks from very low- to very high-ranking, infants from the 2016 cohort only (*N* = 21), which included mostly middle-ranking subjects, and the combined sample (*N* = 39). All regression models, however, used the same estimated trajectories and PC functions that had been generated based on the full combined sample of 39 mother-infant pairs.

Exploratory salience & convergence analysis: We further analyzed a subset of the Conspecific and Mother-Infant stimuli using "salience mapping" (Kreuzman et al., 2017; Micheletti et al., 2017) to identify developmental milestones in social-visual attention. A detailed explanation of our procedures is provided in Appendix I. Briefly, salience mapping is a data-driven method of quantifying to what viewers are attending at a particular moment in time. Especially when studying attentional biases in nonhuman animals, “top-down” approaches that rely on *a priori* assumptions by human experimenters carry the inherent risk that important stimulus features will be overlooked in analysis. A major benefit of data-driven, “bottom-up” approaches like salience mapping is that they obviate the need to predefine normative regions of interest (Kano et al., 2018). Salience mapping also provides rich insights into both spatial and temporal dynamics of viewing behavior (Tenenbaum et al., 2021), as saliency can be quantified millisecond-by-millisecond (or frame-by-frame). The behavioral saliency of particular visual features can then be intuitively depicted as heat maps and compared across development and between groups of viewers (Fig. 5).

Similarly innovative and data-driven approaches to eye-tracking data have been articulated elsewhere in the literature; i.e., Nakano et al. (2010) and Kano et al. (2018) applied multidimensional scaling to patterns of viewing behavior, Tenenbaum et al. (2021) provided methods for calculating an individual viewer’s “distance from the typical scan path,” and Wang et al. (2018) described how to identify periods of “high cohesion” among viewers of identical stimuli. Through salience mapping, Micheletti et al. (2017) found that typically developing human infants begin to view social scenes in the same way as two-year-old toddlers around 10-13 months of age. For this study, we similarly wished to compare the viewing patterns of the same sample of macaque infants when tested at younger versus older ages. The salience of specific visual stimuli is likely to change over the course of development, and we aimed to identify at what age developing infants begin to exhibit viewing patterns similar to those of relatively mature infants, and to what extent reaching such milestones shows individual variability.

To visualize convergence, we utilized the same modelling and curve-fitting procedures described above. We built separate trajectories for the two categories of video stimuli, using data from 6 Mother-Infant and 9 Conspecific videos that had seen by infants during their final eye-tracking session at 23 weeks, in addition to at least one earlier session. We applied salience mapping methods to these videoclips as viewed across different ages, generating salience values for individuals that were then used to calculate “percentage convergence” relative to the 23-week-old group. Negative values for percentage convergence (< 0%) indicate the individual was fixating to area(s) of the screen that had low salience for 23-week-old infants. Positive (> 0%) convergence values indicate the individual was fixating to highly salient area(s) of the screen, or, in other words, was attending to the same content, at the same moment in the videoclip, as the 23-week-old infants. A developmental milestone was defined as the earliest age at which percentage convergence was greater than or equal to 0%, indicating viewing patterns synchronous with those observed at 23 weeks (161 days) of age. We included data from the 2016 cohort in order to optimize curve-fitting, and generated a mean curve in addition to curves for each individual subject. Pointwise confidence intervals were calculated for the group mean curve; we chose a conservative confidence interval of 99% due to the exploratory nature of the analyses.

<u>*Predictive modelling*</u>: We ran Linear Mixed Model (LMM) analysis in SPSS (IBM SPSS Statistics 29) to assess potential predictors at earlier ages for subjects’ social behavior at 1 year of age. For these analyses, only data from subjects in the 2018-2021 cohorts were used (*N* = 18). Behavioral data at 1 year were operationalized and collected as described in Study One. The sample size was *N* = 13 after removing five subjects that did not have data at 1 year (#’s 45, 46, 48, 50, 51). Subjects’ rates of *initiating social play* and of *withdrawing* at 1 year of age were used as the dependent variables in separate models. *Withdrawal*, defined as “clearly avoiding another macaque,” is typically considered to be an indicator of submissiveness (Bernstein, 1976; Embree et al., 2013; Howell et al., 2014; Silk, 2002). A normal distribution could be assumed for the two dependent variables based on Shapiro-Wilks tests ($\alpha = .01$), so no transformations were applied. We chose which measures to test as fixed factors in the models after considering the results from FPCA. Identity of subjects’ home compound/social group (out of five compounds) was added to both models as a random factor.

We used the Maximum Likelihood (ML) method to estimate parameters, then calculated the likelihood ratio test to compare the reference model containing all fixed factors to a “reduced” model with one fixed factor removed (West et al., 2022; see also Kaburu et al., 2016). For each reduced model, we also assessed model fit by calculating the change in the Akaike information criterion (AIC) score when one fixed factor was removed (West et al., 2022; see also Simons et al., 2022). When the LRT statistic comparing a reduced model with the reference model was significant ($p < .05$), we checked our results by conducting bivariate linear regression analyses in SPSS (IBM SPSS Statistics 29) for the predictor and the dependent variable.

RESULTS

The findings from FPCA for the Conspecific and Mother-Infant videos are presented in Figs. 6 – 10 and Tables 3 – 5. For each eye-tracking measure listed in Table 2, we fit a group mean curve, then extracted principal component (PC) function(s) representing the predominant patterns of individual variation relative to that mean. We then computed individual PC scores, entering them as response variables in bivariate linear regression models.

Analysis of Conspecific Videos

For each of the seven eye-tracking measures (see Table 2), we describe the developmental trajectories across six months of age and report the two PC functions that, when summed, quantify 95% or more of the total variance (*see detailed FPCA methods in Appendix I*).

Functional principal components of percent fixation to eyes: Percent fixation to the eyes increased through the first weeks of life, reaching a plateau between 6 – 10 weeks (42 – 70 days), then declined slightly to a trough at around 15 – 17 weeks (105 – 119 days) and increased sharply thereafter (Fig. 6A-B). Confidence intervals around the mean curve (Fig. 6A) indicate greater individual variability between 7 – 13 weeks (49 – 91 days) and 19 – 23 weeks (133 – 161 days) of age, periods of time which map onto the patterns of variation identified through FPCA (Fig. 6C). The primary PC function (PC1) explained close to three-quarters of total variance in the trajectory (FVE = 72.6%) and quantified difference in levels of fixation to eyes across age, but in particular from 15 weeks (105 days) onward, when mean percent fixation to eyes was increasing. The secondary component (PC2) explained 27.4% of total variance, appearing to capture differences in the timing of the early peak in percent fixation, in addition to the height, or magnitude, of that peak.

We used regression analysis to test for a relationship between matrilineal rank and the two PCs within the most recent cohorts (2018 to 2021; $N = 18$), the 2016 cohort ($N = 21$), and the combined ($N = 39$) cohorts (Table 4). PC1 had an association with social rank, though not statistically significant, for all subject groupings. Lower-ranking infants (those with rank percentiles closer to 1%) tended to display greater proportions of eye-looking across development and, in particular, a steeper increase in later infancy, compared to their higher-ranking peers (Fig. 6D). This association was moderately-sized ($R^2 >$ .06; Gaskill & Garner, 2020) among the 18 infants in the recent cohorts ($R^2 = .077$; $p > .20$) and among the combined 39 infants ($R^2 = .068$; $p = .11$) that included a wider range of low- and high-ranking subjects, but minimal among the infants in the 2016 cohort ($R^2 = .011$; $p > .20$) that included mostly middle-ranking subjects. In order to further test the finding for PC1, we created a targeted measure of the variability captured by this component; we calculated the linear slope (rate of change) during the period of high interindividual variability from 19 to 23 weeks (133 – 161 days). Broadly confirming the results of the regression model for the PC function, social rank was negatively associated with the rate of change in eye-looking during late infancy within all three subject groupings, though this relationship was again not statistically significant and the effect sizes were small: $R^2 = .033$ ($p > .20$) for the 2018-21 subjects, $R^2 = .028$ ($p > .20$) for the 2016 subjects, and $R^2 = .047$ ($p = .19$) for the combined sample.

For all subjects combined (*N* = 39), the average slope was 1.01 increase in percent fixation per week (± 0.12% *SEM*), or 0.145% fixation per day (± 0.018). The average increase for low-ranking infants (ranking percentile ≤ 50%) was 1.11% fixation weekly (± 0.13%), whereas the average increase for high-ranking infants (ranking percentile > 50%) was less than 1% fixation (0.89 ± 0.23%) per week.

PC2 had a moderate association with matrilineal rank for the 2018-21 subjects, which would indicate that lower-ranking infants showed a higher magnitude and later peak in eye-looking, compared to higher-ranking infants. This association did not reach statistical significance, however ($R^2 = .062$, $p > .20$), and was very small for all 39 subjects combined ($R^2 = .002$, $p > .20$). In fact, the association was directionally reversed for the 2016 subjects, which would be indicative of a *lower* magnitude and *earlier* peak in eye-looking among lower-ranking infants and the effect was small and not significant ($R^2 = .021$, $p > .20$).

Functional principal components of percent fixation to mouth, head, & body: The mean curves and predominant PC functions for the remaining social ROIs in the Conspecific videos (the mouth, head, and body regions) are illustrated in Fig. 7; the PC functions for each ROI are listed in Table 3. The shape of the mean trajectory for percent fixation to the mouth (Fig. 7A) resembled the mean trajectories for percent fixation to both eye (Fig. 6A) and head regions (Fig. 7B), with a peak occurring comparatively early in development, at approximately 3 weeks (21 days) of age. The magnitude of this peak was small, though, marking a rise of just 1 – 2% fixation, compared to a rise of around 5 – 7% for the peak in fixation to the eyes (Fig. 6) and 4 – 5% for the peak in fixation to the head (Fig. 7B). After 3 weeks of age, percent fixation to the mouth dropped to below beginning levels (< 5% of total fixations), plateauing at approximately 15 weeks (105 days), before slightly increasing through 23 weeks. The PC functions for fixation to the mouth were notably different from those for the other ROIs in Conspecific videos. PC1 appeared to reflect the magnitude of the difference between the 3-week peak and 15-week trough, i.e., the size of the two “extremes”; PC2 captured general variance in magnitude across the entire developmental period.

For percent fixation to the head (Fig. 7B), the overall trajectory was notably similar to that of percent fixation to eyes (Fig. 6A), although the positive slope during late infancy was steeper for fixation to eyes (Fig. 6B). Percent fixation to the head rose to a peak between 5 – 9 weeks (35 – 63 days) before dropping to a trough at around 17 weeks (119 days), then again gradually increasing. The PC functions of percent fixation to head also appeared quite similar to those for fixation to eyes (Fig. 6C). PC1 of percent fixation to head similarly quantified differences in magnitude, whereas PC2 quantified variance in both the timing and magnitude of the early peak.

Finally, percent fixation to the conspecific’s body dropped sharply from week 1 to a trough at 10 – 11 weeks (70 – 77 days) of age, then slightly rose through the end of data collection (Fig. 7A). PC1 captured variance in the magnitude of percent fixation roughly between 3 – 13 weeks (21 – 91 days), whereas PC2 appeared similar to PC1 of percent fixation to eyes, described above (Fig. 6C), and captured variance in the rate of change during late infancy after approximately 15 weeks (105 days) of age. Any association between matrilineal rank and the PC functions for these three social ROIs had an R^2 value less than .06 and did not reach statistical significance (Table 3), indicating that matrilineal rank had only a small impact, or no impact, on the developmental trajectories of attention to the mouth, head, and body of conspecifics.

Functional principal components of total fixations, saccades, & lost/offscreen data: The group mean curve for percent total fixations increased from 1 – 4 weeks (7 – 28 days) before remaining at approximately the same percentage through the remainder of data collection (Fig. 8A). The group mean for percent lost data showed roughly the same trajectory (Fig. 8C), with a parallel *decrease* from 1 – 4 weeks (7 – 28 days). Percent saccades, in contrast, remained relatively stable across all ages at around 26% (Fig. 8B). The PC2 functions of percent total fixations (Fig. 8A) and percent lost data (Fig. 8C) appeared to capture age-specific variance, with an inflection point at roughly 19 weeks (133 days) of age. Specifically, higher PC2 scores for percent total fixations indicate less fixations relative to the mean curve in early infancy, but more fixations relative to the mean in later infancy. The same pattern of variance was found for lost data. In the case of saccades, PC1 captured variance in the magnitude of percent saccades relative to the mean curve across all ages (Fig. 8B).

For these three measures, only PC2 of percent total fixations (Fig. 8A), PC1 of percent saccades (Fig. 8B), and PC2 of percent lost/offscreen data (Fig. 8C) were associated with matrilineal ranking (see Table 3). None of these relationships reached statistical significance, but their effects were moderately sized ($R^2 > .06$; Gaskill & Garner, 2020). Social rank tended towards a positive association with PC2 scores of percent total fixations ($R^2 = .065$, $p = .12$) and towards a negative association with PC2 scores of percent lost data ($R^2 = .063$, $p = .12$), meaning that lower-ranking animals exhibited *more* fixations and *less* lost data in *early* infancy, whereas in *later* infancy, from around 19 weeks (133 days) of age, they exhibited *less* fixations and *more* lost data. Higher-ranking animals exhibited the reverse pattern in their viewing of Conspecific clips; their percent total fixations *increased* with age, whereas lost data *decreased*. Finally, for saccades (Fig. 8B), PC1 scores were moderately associated with social rank ($R^2 = .064$, $p = .12$) such that higher-ranking infants tended to exhibit *less* saccades across development and lower-ranking infants tended to exhibit *more* saccades.

<u>*Visual convergence milestones*</u>: We found that for viewing patterns to Conspecific videos, the group mean curve (*N* = 36) first “crossed over” the threshold of zero percentage convergence at 27 days (approx. 4 weeks) of age (Fig. 11). All 36 subjects reached convergence in their individual curves (range 17 - 38 days, or approx. 2 – 5 weeks, for first point of convergence). The group mean curve remained at close to zero percentage convergence from 4 weeks through 11 weeks (77 days), then dipped down, indicating viewing divergent from the older reference group. Percentage convergence

reached a shallow trough at 13 – 14 weeks (91 – 98 days) of age, then quickly increased to show convergence for a second time between 17 – 18 weeks (119 – 126 days).

At the level of distinct video frames, when there was significant convergence within the 23-week-old group, the older infants were most often converging on a point in the background of the scene or on the conspecific’s eye region. Very few convergent frames showed convergence to the mouth or body; this was despite the relatively large size of the body in Conspecific videos. When we filtered out all frames that were *non*-convergent within the 23-week-old group before constructing the longitudinal curve for percentage convergence, the group mean was negative across the entirety of development, never showing convergence with the older reference group.

Analysis of Mother-Infant Videos

In the case of percent fixation to infant and percent saccades, we report a single PC function that quantifies 95% or more of the total variance (> 95% FVE) in the trajectory of that measure (FVE: 95.7%, 95.5%, respectively). For percent fixation to groupmate, we report only a single PC function quantifying 92.6% of variance, choosing not to include PC2 because it appeared to largely be capturing stochastic noise in the data, rather than an interpretable pattern of variability. Finally, for percent fixation to dam, percent fixations total, and percent lost/offscreen data, we report two PC functions that quantify > 95% FVE when summed *(see detailed FPCA methods in Appendix I)*.

<u>*Functional principal components of percent fixation to dam, infant, & groupmates*</u>: The mean curves and predominant PC functions for the social ROIs in the Mother-Infant videos are illustrated in Fig. 9. The PC functions for each ROI are listed in Table 5. In scenes showing conspecific mother-infant pairs, the highest percent of total fixations were directed towards the head and face (including the eyes) of the dam. The shape of the trajectory (Fig. 9A) paralleled the trajectory for total fixations to all ROIs (Fig. 10A), rising to a peak from 1 – 4 weeks (7 – 28 days) of age, then declining through the remainder of

the developmental period. Between-subject variability in fixation to the dam was highest during the first 3 months, as shown by PC1 and by the width of the confidence bands around the mean curve. PC2 captured variability later in infancy, starting around 14 – 15 weeks (98 – 105 days) of age. For infants with higher scores on PC2, the curve appeared to plateau at 14 – 15 weeks, whereas the curve for infants with lower PC2 scores continued to slope downwards.

For the infant ROIs (Fig. 9B) and the ROI for other conspecifics/groupmates in the scene (Fig. 9C), percent fixation rose from approximately 5% at 1 week (7 days) to 9% at 23 weeks (161 days). The highest between-subject variability in fixation to the infant occurred roughly between 3 – 19 weeks (21 – 133 days), as captured by PC1 (Fig. 9B). For fixations to other conspecifics (Fig. 9C), between-subject variability was minimal, though PC1 did appear to capture divergence in the rate of change during the last month of data collection, from 20 – 23 weeks (140 – 161 days). Any association between matrilineal rank and the PC functions for these three social ROIs had an R^2 value less than .06 and did not reach statistical significance (Table 5), indicating that matrilineal rank had only a small impact, or no impact, on the developmental trajectories of attention to the dam, infant, and other conspecifics.

Functional principal components of total fixations, saccades, & lost data: The group mean curve for total fixations to Mother-Infant videos (Fig. 10A) showed the same increase from 1 – 4 weeks (7 – 28 days) as the curve for total fixations to Conspecific videos (described above; Fig. 8A) before sloping downwards. The PC functions for total fixations were also comparable between the two video categories, though PC1 and PC2 were reversed. An inflection point at approximately 15 weeks is indicated by PC1 for fixations to Mother-Infant videos (Fig. 10A). Saccades to Mother-Infant videos (Fig. 10B) rose steadily through the entire developmental period, though the increase was small, from approximately 23% to 27%. Like PC1 of saccades for Conspecific videos, PC1 of saccades for Mother-Infant videos captured variance in magnitude, relative to the mean curve, across all ages. For lost data, the predominant variance patterns for Mother-Infant videos (Fig. 10C) were also similar to those described above for Conspecific videos (Fig. 8C). For both categories of video stimuli, the primary components (PC1) showed that in the first 4 weeks, the degree of data loss declined and there was relatively little between-subject variability.

There was a moderately sized ($R^2 > .06$; Gaskill & Garner, 2020) association between matrilineal social rank and PC functions for only two of the measures: percent saccades (Fig. 10B) and percent lost/offscreen data (Fig. 10C). For saccades, PC1 scores were strongly associated with social rank ($R^2 = .106$), revealing that percent saccades were significantly greater across development for lower-ranking infants, compared to higher-ranking infants ($p = .043$; Fig. 10B). This was the only statistically significant relationship from our linear regression analysis, in addition to the most robust effect size ($R^2 = .106$). After 3 weeks (21 days) and continuing through 6 months for Mother-Infant videos, higher-ranking infants had slightly greater percentages of data lost than lower-ranking infants (Fig. 10C); this association did not reach significance, but the effect size was moderate ($R^2 = .061$, $p = .13$; Gaskill & Garner, 2020).

Visual convergence milestones: For Mother-Infant videos, the group mean curve ($N = 34$) first “crossed over” the threshold of zero percent convergence at 34 days (approx. 5 weeks) of age (Fig. 12), with high variability among individual trajectories (range 22 – 73 days, or approx. 3 – 11 weeks, for first point of convergence). Five infants never showed convergence with the older reference group, or at least did not converge prior to 23 weeks. The group mean curve stayed near zero percentage convergence from 5 weeks through 11 weeks (77 days), then began declining, much like the curve for Conspecific videos. Unlike the curve for Conspecific videos, however, infants’ viewing of Mother-Infant videos rose more gradually and did not show a clear second point of convergence prior to 23 weeks.

At the level of distinct video frames, when there was significant convergence within the 23-week-old group, the greatest number of frames showed convergence to an area in the background of the scene, followed by convergence to a conspecific groupmate. We noted, however, that of the three videos that had a groupmate present in the scene, only one had any frames during which the 23-week-old group significantly converged to the groupmate, despite the relatively large screen area taken up by groupmates. Interestingly, in that one videoclip, the convergence seemed to occur specifically during a sequence in which a juvenile approached the infant and initiated mutual gaze. While watching this interaction in the video, which took place over the course of about 100 frames (equivalent to about three seconds), 23-week-old viewers switched between converging on the head/face of the infant and converging on the juvenile (*see Appendix II*). As with the Conspecific videos, when we filtered out all video frames that were *non*-convergent within the older group before constructing the curve, the group mean was negative across the entirety of development and never converged with the reference group.

Predictive Models

We chose three variables to test as fixed factors: (1) the linear rate of change/slope in eye-looking (Fig. 6B) between 19 to 23 weeks (133-161 days) and (2) eye-looking (%) at 8 weeks (56 days) in the Conspecific videos (Fig. 6A), and (3) individual scores for the PC function extracted from percent saccades to Mother-Infant videos (Fig. 10B). We chose the first two fixed factors to quantify the interindividual variation in eye-looking captured by, respectively, PC1 and PC2 of percent fixation to the eyes (Fig. 6C). We were interested in testing the PC for Mother-Infant video saccades because this single component explained over 95% of variance and could thus serve as an effective way to quantify individuals' saccading behavior, in addition to being the only component to show a significant ($p < .05$) relationship with matrilineal rank ($R^2 = 10.6\%$, $p = .043$; Table 5).

Results from the Linear Mixed Models are shown in Table 6. The rate at which 1-year-old juveniles initiated social play with groupmates was significantly predicted by their PC scores for saccades to Mother-Infant videos (Estimate ± SE: 0.137 ± 0.033; LRT statistic = 9.321, LRT $p = .0023$; ΔAIC = +7.32). Examining a LMM with compound/social group as a random factor and the PC scores as the single fixed factor, we calculated the marginal pseudo-R^2-value, which revealed that the PC scores explained 60.6% of the total variance in juveniles' rates of initiating social play. Infants with greater percent saccades when viewing Mother-Infant videos, across age from 1 to 23 weeks (7 to 161 days), went on as juveniles to initiate play with their groupmates more frequently. This effect was confirmed by a bivariate linear regression model (ß = +0.10, R^2 = 58.1%, p = .002). There were no significant predictors, however, for the rate of withdrawing at 1 year.

DISCUSSION

In this study, we used innovative, non-invasive eye-tracking procedures to confirm and expand on previous work detailing the development of social-visual attentional processes in male rhesus macaques, from birth through 6 months of age, while they viewed videos of conspecifics or of mother-infant dyadic interactions. We investigated the role of matrilineal social rank in the developmental trajectories for fixation to social cues, as well as for global measures of social-visual attention. In addition, we assessed whether some of the eye-tracking measures quantifying social-visual attention in the first 6 months of life could serve as potential markers for the social behavior displayed by the same individuals as juveniles. Finally, we explored a data-driven method, previously applied to eye-tracking data from human infants (Kreuzman et al., 2017; Micheletti et al., 2017), for identifying developmental milestones in viewing patterns.

There were several notable results. First, with a larger sample size of 39 infants, selected from the lowest to the highest-ranking families, we largely confirmed the original findings (Wang et al., 2021; Ford et al., 2023) that the developmental trajectory of fixation to the eyes of conspecifics shows two periods of increase (i.e., from 1 – 6 weeks and again from 17 – 23 weeks) and replicated the findings of Ford and colleagues showing that, compared to higher-ranking infants, lower-ranking infants displayed an accelerated rise in fixation to the eyes during late infancy (i.e., 19 – 23 weeks). For the developmental trajectories of fixation to the mouth, head, and body of conspecifics, there were minor divergences between the current study and the previous two; also, percent fixation to these social cues was not associated with matrilineal social rank. In the Mother-Infant videos, which had not been analyzed previously, the developmental trajectories of fixation to the dam and infant (eyes + head regions) also showed no association with rank. Interestingly, the curve for fixation to the dam exhibited an early rise from 1 – 4 weeks followed by a decrease, whereas that for fixation to the infant rose slightly, but continuously, from 1 – 23 weeks. Across both categories of videos, analysis of total fixations, saccades, and lost/offscreen data revealed that percent saccades measured during the viewing of Mother-Infant videos was the only measure significantly associated with subordinate social status. Percent saccades during Mother-Infant videos was also the sole significant “predictor” variable. Among 1-year-old juvenile macaques, their saccades while viewing Mother-Infant videos during their first six months of life positively predicted how frequently they initiated social play with conspecific groupmates. These results are discussed in turn below.

Developmental Trajectory of Percent Fixation to Eyes

The shape of the trajectory for the proportion of total fixations directed to the eye region in Conspecific videos was in agreement with the trajectory generated by Wang et al. (2020) using LOESS regression and by Ford et al. (2023) using FPCA/PACE modelling. Eye-looking rose to a peak between 6 – 10 weeks, overlapping the period between 4 – 9 weeks when macaque infants first exhibit a visual preference for direct over averted gaze in conspecific faces (Muschinski et al., 2016). Eye-looking then fell to a trough around 15 – 17 weeks before again rising through the end of data collection. There were two periods when percent fixation to eyes was especially variable between individuals, 7 – 13 weeks and 19 – 23 weeks, which were similar to periods identified previously (Ford et al., 2023). We extracted two principal component functions that roughly mapped onto these variable periods and were, again, similar to the PC functions reported previously (Ford et al., 2023), especially the primary PC function (PC1).

We did not find evidence to support our prediction that the peak in preferential attention to the eyes would occur earlier among low-ranking infants, as had been observed by Ford et al. (2023). We did, however, correctly predict that eye-looking among lower-ranking subjects exhibited an accelerated positive rate of change during late infancy (19 – 23 weeks), compared to eye-looking by higher-ranking subjects, as revealed through our analysis of PC2. We thus replicated the same finding by Ford et al. (2023), although in the results from our regression analyses, the size of the effect was moderate and did not reach statistical significance. The relationship was more robust in the 2018-21 cohorts and in the total combined subjects, compared with the 2016 cohort (respectively, R^2 = 7.7%, *N* = 18; R^2 = 6.8%, *N* = 39; R^2 = 1.1%, *N* = 21). Our results for the overall trajectory of eye-looking also differed slightly in that the mean curve (*N* = 39) increased in late infancy, rising by an average of 1.01% fixation each week from 19 weeks on. This trend was also reported by Wang et al. (2020) using LOESS regression, but *not* confirmed by Ford et al. (2023); the latter study instead found increased variability, and a generally flat slope, during late infancy.

The differences in our findings for PC1 may be due to several factors. First, a lesser fraction of variability (approx. 73%) was explained by PC1 in the current study, compared to over 90% of variance explained by PC1 (with less than 10% explained by PC2) in the results of Ford et al. (2023). This shift in FVE values was as expected given the larger sample size of the current study; in FPCA generally, increasing the amount of available data tends to push a greater fraction of the explained variance to non-primary PC functions. The studies also differed in which subjects were included in analyses. An additional ten macaques were born in 2015 as part of the same multiyear programmatic study; this earlier cohort was excluded from all the analyses described in the current study, but was included by Wang et al. (2020) and Ford et al. (2023) in their analyses. Thus, the previously published studies used data from the 2015 and 2016 cohorts (approximately *N* = 36 total), whereas the current study used data from the 2016, 2018, 2019, 2020, and 2021 cohorts (*N* = 39 total). Comparing percent fixation to eyes in the 2015 versus 2016 cohorts, Wang et al. (2020) found that there was a high level of overlap and no statistically significant difference between the two cohorts. Nevertheless, for the 2016 cohort, the rate of change in later infancy did appear to be relatively accelerated and showed less interindividual variability (see *Fig. 4* in Wang et al., 2020). Therefore, the exclusion of the 2015 subjects (n = 10) from the current analysis may have contributed to the steeper positive rate of change during late infancy and the reduced FVE of PC1.

Importantly, the stronger relationship between PC1 and matrilineal rank for infants from the more recent (2018-21) cohorts suggests that, in order to consistently detect differences between low- and high-ranking macaques in percent fixation to eyes, it is critical to include as wide a range of individual rankings as possible. Among the subjects in the 2016 cohort, no infants were born into their social group's alpha matriline, and just one infant (#11) was born into the lowest-ranked (omega) matriline, representing a range of ranking percentiles from 1% to 80%. The 2015 cohort had a similar range of rankings and contained no infants born into alpha or omega matrilines. Based on the analyses presented here, for the 21 subjects born in 2016, there was only a very small relationship between eye-looking and rank. From 2018 to 2021, more mother-infant pairs were selected from the low and high extremes of their social groups' dominance hierarchies. Of these 18 subjects, six were born to females in the alpha matriline, and two were born to females in the omega matrilines, representing a range of ranking percentiles from 1% to 93%.

Developmental Trajectories of Percent Fixation to Social-Visual Cues

For all other ROIs besides the eyes, there were only small and statistically insignificant associations with matrilineal rank. It is nevertheless worth noting some intriguing features of the mean curves and PC functions for these additional social cues. For percent fixation to the mouth, the two PC functions resembled those reported by Ford et al. (2023; see *SuppMat*), though the primary and secondary component functions were switched. The developmental trajectory of percent fixation to the head had not been analyzed previously, and closely mirrored that of fixation to eyes. That is, fixation to the head rose to a peak in the second month of life and then dropped to a trough at 17 weeks. This is perhaps not surprising since the ROI for the head region immediately surrounded the eye region. The head may also function separately from the mouth and eye regions as a distinct source of social information, e.g., via ear movements corresponding with particular facial expressions (Mosher et al., 2011). Still, the relatively sharp increase during late infancy appeared to be a developmental feature unique to eye-looking.

Finally, the developmental trajectory of percent fixation to the body was similar in shape to the trajectory illustrated in Wang et al. (2020) for the same social cue, although neither that study nor Ford et al. (2023; see SuppMat) described the same distinct trough in fixations to the body between 10 – 11 weeks. Some of these minor discrepancies may be due to the differing data exclusion criteria applied in the initial stages of processing the fixation data; namely, some previous studies (Jones & Klin, 2013; Wang et al., 2020; Ford et al., 2023) applied an exclusion threshold of 20% fixations, whereas in the current study, data were only excluded if there were 0% fixations.

The social cues in the Mother-Infant videos were the dam, infant, and additional conspecifics, when present in the scene. These cues had not been analyzed in previous studies. The greater proportion of fixations were to the dam, likely driven by the larger relative size of the ROIs for the dam's head and eyes. Percent fixation to the dam also rose across the first months of life, peaking at around 4 weeks before beginning to drop. This developmental trajectory aligns with the trajectory for species-typical mother-infant interactions in rhesus macaques, as rates of mutual gaze and lipsmacking are highest in the first 3 weeks of infancy and drop off dramatically thereafter (Ferrari et al., 2009). In contrast, percent fixation to the infant in Mother-Infant videos, as well as to additional conspecifics, rose slightly, but steadily, across the entire 6 month period. It seems that viewers shifted their attention away from adult females and towards other groupmates as they matured, a trend which may reflect an increasing interest in their infant peers and the eventual emergence of social play.

Global Measures of Social-Visual Attention: Total Fixations, Saccades, & Lost Data

In all, subordinate social status was moderately associated with more fixations total and greater attentiveness (that is, lower percent lost data) to Conspecific videos at *earlier* ages, less fixations total and poorer overall attentiveness (that is, greater percent lost data) to Conspecific videos at *later* ages, and greater overall attentiveness to Mother-Infant videoclips from 3 – 23 weeks of age. We found only a small, statistically insignificant associations with social rank for total fixations to Mother-Infant videos. For both types of video stimuli, subordinate status was moderately associated with more saccades across the entire developmental period.

The above findings may seem paradoxical: lower-ranking infants, at older ages after 19 weeks, tended to exhibit an increase in data loss and a reduction in percent total fixations to Conspecific videos, yet exhibited an accelerated increase in the *proportion* of those fixations directed specifically towards the eyes. Eyes were the only social cue for which this was the case. (PC2 of percent fixation to the body did appear to capture variability in slope that was similarly associated with rank, but the relationship was small and not significant). For Mother-Infant videos, however, subordinate infants exhibited *lower* percent data lost, relative to the group mean. One possible explanation for these results is that infants born to lower-ranking females, by 4 – 5 months of age, were already exhibiting greater avoidance of social stimuli and increased rates of gaze aversion - thus the decline in their overall attentiveness, as measured by data lost/offscreen and total fixations - while at the same time continuing to track social cues through covert attentional mechanisms and rapid “check-looks” (Mosher et al., 2011). Direct eye contact functions as an aversive threat signal among rhesus macaques. Thus, the same association with matrilineal rank may not have been observed in the Mother-Infant videos because, for this category, faces and eyes take up a relatively small portion of the screen and direct gaze towards the viewer is rare. This proposed explanation is supported by findings from an eye-tracking study of adult male rhesus macaques (Mosher et al., 2011); subordinate individuals, when presented with videos of conspecific faces, spent less time overall looking at the screen, instead performing frequent check-looks and maintaining eye contact with the conspecific in the video for relatively short durations of time, whereas a dominant male was observed maintaining uninterrupted eye contact for relatively long durations of time.

Beginning at 2 months of age, typically developing macaques perform shorter length fixations towards conspecific faces showing direct gaze (Muschinski et al., 2016) and, from 3 to 4 months, there is a significant increase in the velocity of saccades performed before and after mutual eye contact (Wang, 2019). In fact, the span of time around 4 months of age has been proposed as an additional critical period in the development of social-visual attention in rhesus macaques, during which infants gain an increasingly mature, functional understanding of gaze behavior in others (Wang, 2019). By 4 months of age, weaning has already begun, infants are spending increasing amounts of time engaged in social play, and low-ranked infants have likely begun to receive aggression from groupmates and to respond appropriately via behaviors like grimacing and withdrawing (Hinde & Spencer-Booth, 1967; Rowell et al., 1964). In all, the results of the current study suggest that, during this important transitional period, infants born to low-ranking dams develop a sophisticated, functional understanding of groupmates' gaze behavior, direct eye contact in particular. This understanding is revealed through the adaptive strategies exhibited by lower-ranking infants in order to covertly gather information from their social environment.

Eye-tracking Measures as Predictors of Social Functioning in the Juvenile Stage

In the case of withdrawals by the infant at 1 year, the absence of any significant predictors discovered via Linear Mixed Modelling may be explained partially by the behavior's role in social ranking dynamics (Bernstein, 1976; Embree et al., 2013; Howell et al., 2014; Silk, 2002; see Study One). It is likely that individual rates of withdrawing are dictated predominantly by relative social status, which itself tends to be highly stable. For rates of initiating social play at 1 year, neither potential predictor variable related to eye-looking was predictive of later prosociality, a surprising result given the extant literature showing that looking rates to displays of aggression (Sclafani et al., 2016), looking time to eyes in social stimuli (Ryan et al., 2020), maternal mutual gaze (Dettmer et al., 2016), and neonatal imitation of facial gestures (Simpson et al., 2016) are all positively correlated with social functioning and prosociality. A limitation of our LMM analysis was the small sample size (N = 13) of subjects that had available behavioral data at 1 year.

Rates of initiating social play were, however, significantly predicted by the PC function of percent saccades to Mother-Infant videos. Adjusting for compound/social group as a random factor in the model, PC scores explained approximately 60% of the total variance in juveniles' frequency of initiating play. Infants observed performing more saccades while viewing Mother-Infant videos, across all ages from 1 to 23 weeks (7 to 161 days), went on as juveniles to initiate social play more often. In addition to the significant association with social rank, saccades to Mother-Infant videos seem to be highly consistent within individuals across age. Saccades to Conspecific videos also appear consistent within individuals, though to a lesser extent.

Taken together, the results from LMM and from regression analyses yield findings that: (1) lower-ranking subjects performed more saccades and (2) subjects who performed more saccades went on to initiate play more frequently as juveniles. This pairing of results was somewhat puzzling in light of the solid body of literature demonstrating that infants born to high-ranking dams are more confident and prosocial than their lower-ranking peers (e.g., Fairbanks, 1996; McCormack et al., 2006; Weinstein & Capitanio, 2008). One possible interpretation is that the relationship between the rate of saccades and the rate of initiating play was moderated by ranking, such that among low-ranking subjects, those who performed more saccades also tended to be the subjects that adapted most effectively to their subordinate status, thus developing greater social competency and confidence later in life (at least relative to other low-ranking individuals). Indeed, in the LMM for social play initiations (*N* = 13), the individual with the highest PC score, indicating the most saccades, of all the low-ranking subjects (Subject #42, ranking = 18.2%) also exhibited the highest rate of initiating social play out of all 13 subjects (~ 22 initiations/hour). For high-ranking subjects, perhaps the ability to gather salient information quickly and efficiently from a social scene is not as central to the development of social skills as it is for infants born to subordinate dams.

Convergence Across Age to Salient Areas of Social Scenes

Through salience mapping, we were able to confirm our prediction that patterns of viewing dynamic social stimuli would be scattered and show high between-subject variability early in life. We did *not* confirm our prediction, however, that convergence would appear between 10 -13 weeks (70 – 91 days) of age, on an analogous timeline to that of human infants (Kreuzman et al., 2017; Micheletti et al., 2017). Rather, for both categories of video stimuli, individuals' convergence with the 23-week-old reference group increased rapidly in the first weeks of life, such that milestones were identified at approximately 4 weeks (27 days) for viewing of Conspecific videos and approximately 5 weeks (35 days) for viewing of Mother-Infant videos. The milestone for Mother-Infant videos in particular aligns with the critical period for social-visual attention in rhesus macaques between 5 – 6 weeks (Muschinski et al., 2016; Parr et al., 2016; Wang et al., 2020). After the initial milestone, viewing remained approximately convergent (0% or greater values for percentage convergence) through around 11 weeks for both video categories. After 11 weeks, subjects again diverged temporarily in their viewing patterns, relative to the 23-week-old reference group (though the mean curve for percentage convergence never dropped to the low levels seen in the first few weeks).

The periods of minimally divergent viewing in later infancy may simply reflect habituation to repeated video stimuli; i.e., in their second, third, etc. viewings of the same videoclip, subjects may have visually explored areas of the scene other than the focal cues (Mosher et al., 2011). For example, upon closer examination of a highly salient scene in one Mother-Infant videoclip, which showed a conspecific groupmate initiating mutual gaze with the focal infant, we noted that some younger (17-week-old) viewers fixated on the dam’s head, or on the tail and rump of the groupmate, rather than on the salient exchange of mutual gaze (see *Appendix II*).

To quantify convergence in viewing, we needed to designate a “reference group” that could serve as a normative standard. Overall, the exploratory analyses described in this study were limited in scope due to difficulties in obtaining high quality “reference” data. Monkeys are known to be less engaged by video stimuli than human participants and to rely on saccades and on scanning the screen more so than fixating (Hu et al., 2013; Mosher et al., 2011; Wang et al., 2020). Further, some infants became more active and ambulatory during eye-tracking sessions as they matured, and therefore less attentive to the experimental stimuli (Wang et al., 2020). Ultimately, the number of 23-week-old subjects with usable salience data ranged from a minimum of seven to, at most, 11 subjects per videoclip.

An additional challenge was that only nine Conspecific videoclips and six Mother-Infant clips were usable (see criteria under detailed salience mapping methods in *Appendix I*) and, within each video, there tended to be only a small set of frames for which the 23-week-old reference group demonstrated significant convergence, with some videos only having two or three convergent frames out of ~290 total. The greatest number of convergent frames in a single videoclip was 47 frames. Accordingly, when we filtered out all non-convergent frames before constructing the longitudinal curve for percentage convergence, the group mean was negative across the entirety of development, never showing convergence with the older reference group. For this reason, we were unable to systematically assess convergence to distinct categories of content, though it was possible to qualitatively assess convergence within single videos and frame-by-frame (see *Appendix II*). In general, the convergent frames from Conspecific videos frequently showed the older subjects converging on the eyes, and the convergent frames from Mother-Infant videos frequently showed convergence on a groupmate – though only in the case of one videoclip that featured a groupmate interacting directly with an infant (*Appendix II*).

Future Directions

In sum, data-driven efforts to locate milestones in visual attention offer the benefit of making predetermined ROIs unnecessary, but nevertheless still require that some standard of “typical” development be established against which to compare individual or group data. Indeed, these methods originated in the context of clinical research comparing the gaze patterns of typically- versus atypically-developing children (Kreuzman et al., 2017; Micheletti et al., 2017; Nakano et al., 2010; Tenenbaum et al., 2021; Wang et al., 2018). Here, it was assumed that what 23-week-old rhesus macaques respond to as salient represents “mature,” normative viewing behavior for the species. Such an assumption may or may not be reasonable. To our knowledge, few eye-tracking studies of development in rhesus macaques have collected data beyond 6 months of age. Additional longitudinal studies incorporating dynamic, complex experimental stimuli are needed in order to characterize how a typically developing macaque engages with social visual cues, moment-by-moment and across age. Regardless, salience maps remain a valuable tool for gaining rich qualitative insights into both spatial and temporal dynamics of viewing behavior. Future studies using eye-tracking procedures will also benefit from employing measures of global social-visual attention, beyond fixation to predefined ROIs, in order to gain a more complete picture of individuals’ viewing strategies.

FIGURES & TABLES

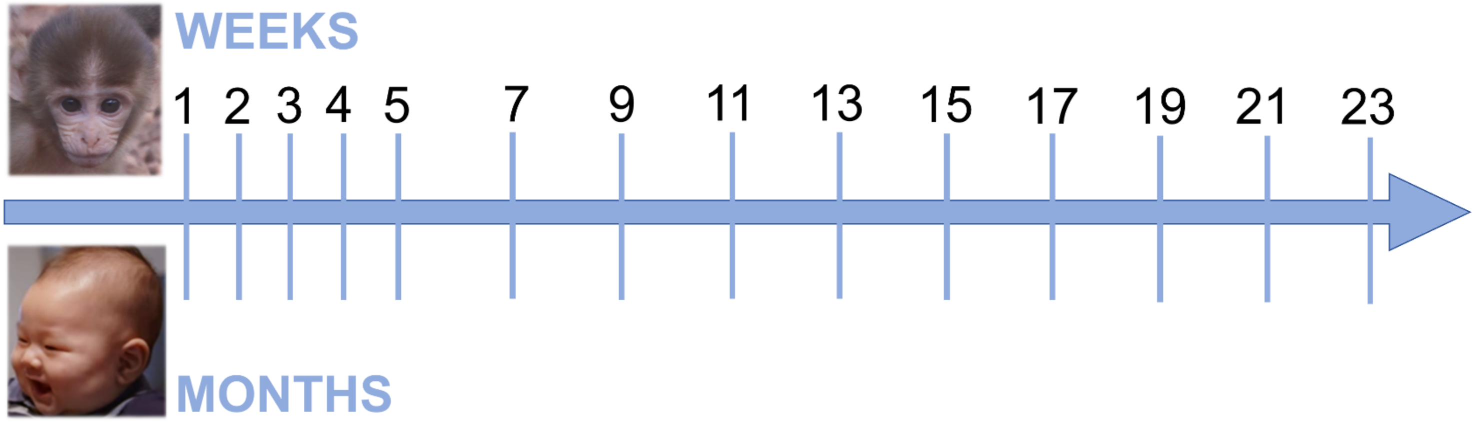


Figure 1: Experimental Timeline. Eye-tracking data were collected over 14 sessions from birth to approx. 6 months of age, roughly equivalent to 24 months (two years), in human development (Boothe et al., 1985).

Figure 2: Eye-tracking Setup. The testing chamber built for eye-tracking of rhesus macaque infants at the ENPRC, with adjustable reclining chair for the dam. The chamber was enclosed at the time of data collection to create a quiet, dark environment, and the infant was free to continue nursing while voluntarily viewing stimuli on the monitor. The yellow arrows indicate the infrared camera, which is mounted on a motorized gimbal and controlled manually by an experimenter during testing.

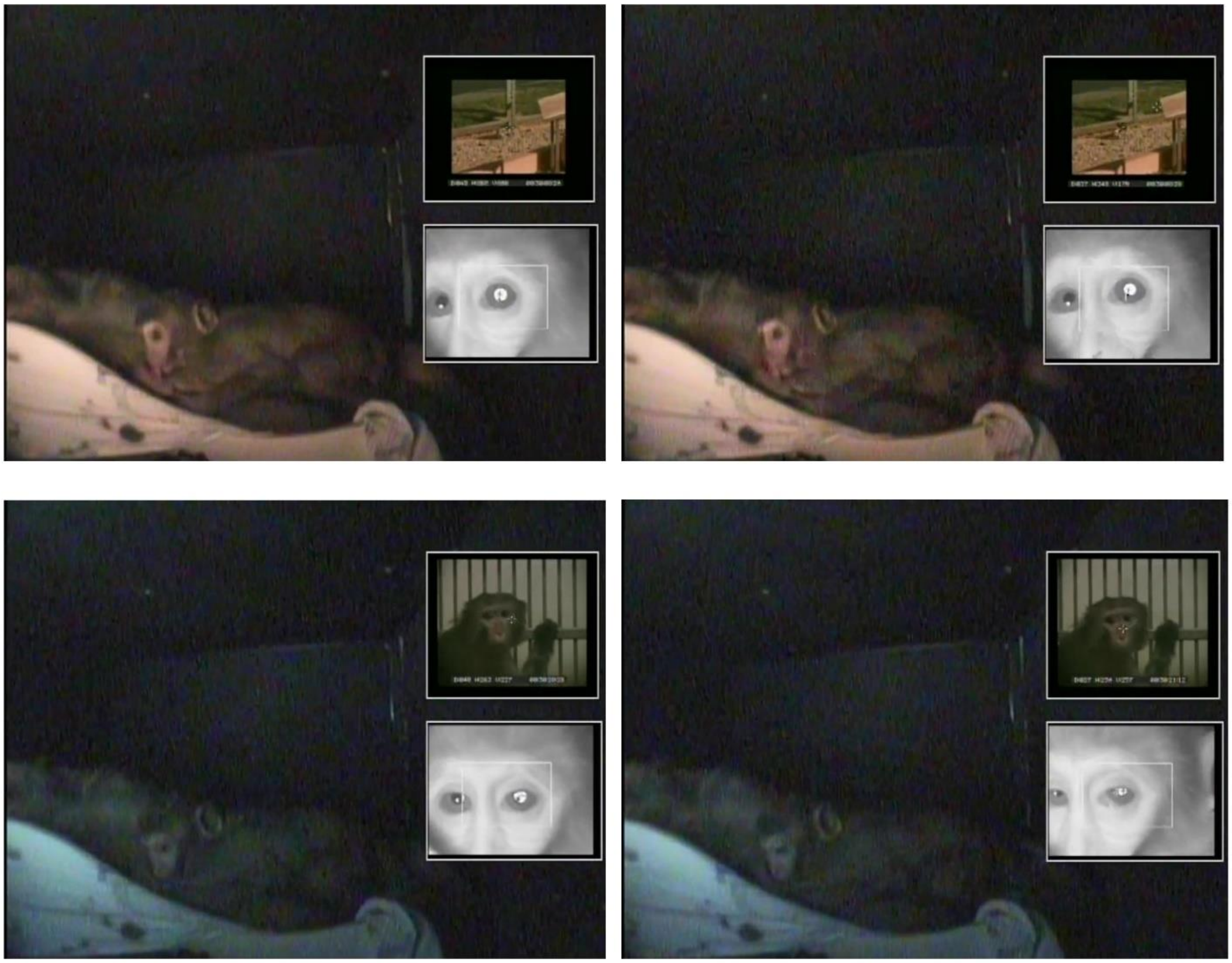


Figure 3: Monitoring of Infant Viewing. Consecutive still frames from video recording of an eye-tracking session in progress. The infant's left eye was manually tracked and kept in focus as shown in the inset grayscale video feed. The inset video feed in the upper right corners shows the stimuli being presented.

Figure 4: Regions of Interest. Consecutive frames with ROIs for Conspecific (A) and Mother-Infant (B) categories of video stimuli. ROIs for Conspecific videos included: eye region (red), mouth region (green), head region (yellow), macaque body (indigo), and total screen area (teal). For the Mother-Infant videos, ROIs included the eye regions (green, red) and heads (pink, indigo) of the dam and infant, respectively. Additional ROIs were drawn for the groupmate in the background (yellow), behind the focal dam-infant pair, and total screen area (teal).

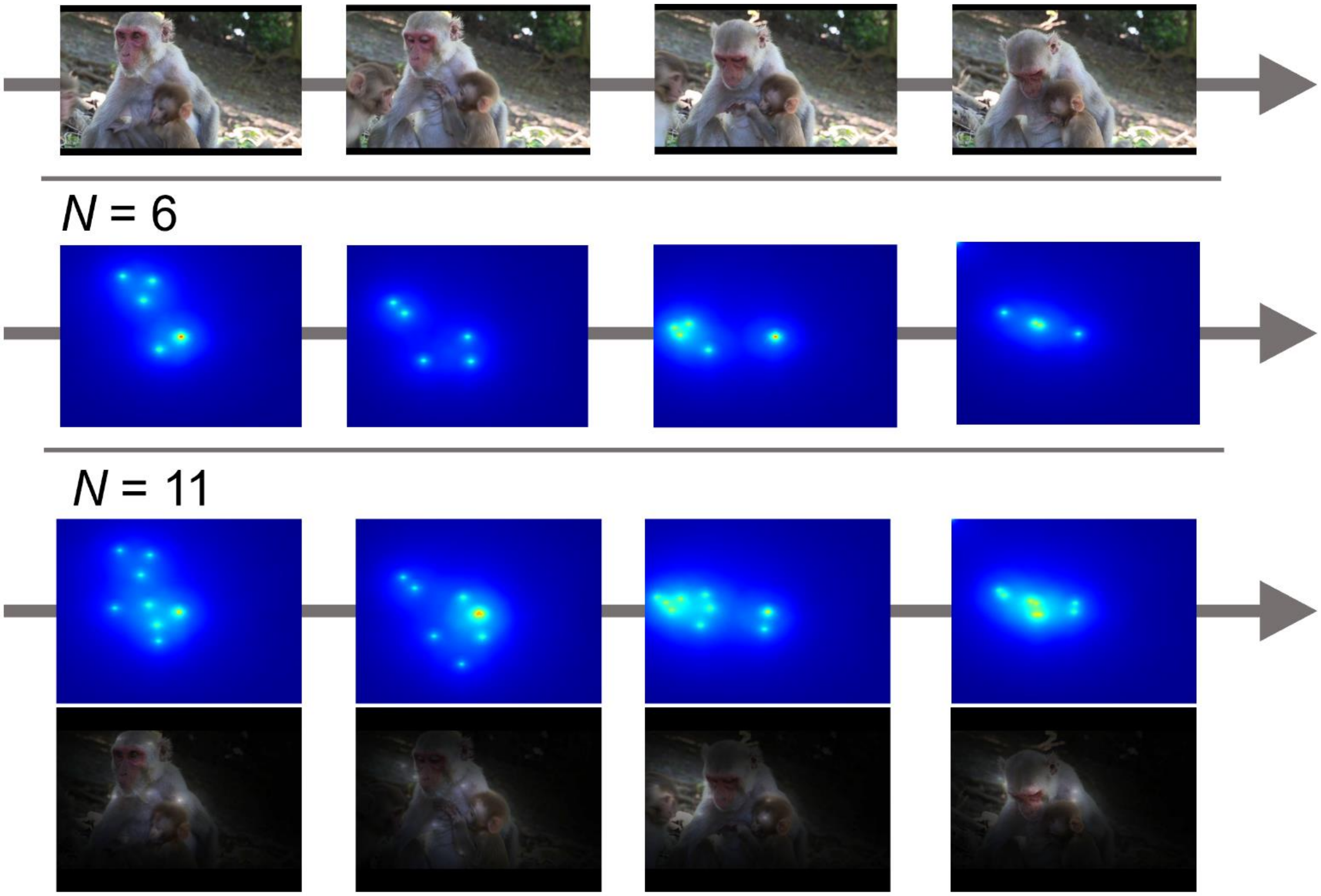


Fig. 5. Salience Mapping. Salience maps for four consecutive frames of a Mother-Infant videoclip. To create a group salience map, the maps from multiple individuals are layered together and summed linearly. Warm colors, or brightened areas of the scene, indicate areas of convergence. Cool colors, or darkened areas, indicate divergence. Comparing the row with data from 6 infants to the row with data from 11 infants demonstrates the effect of adding data from additional viewers.

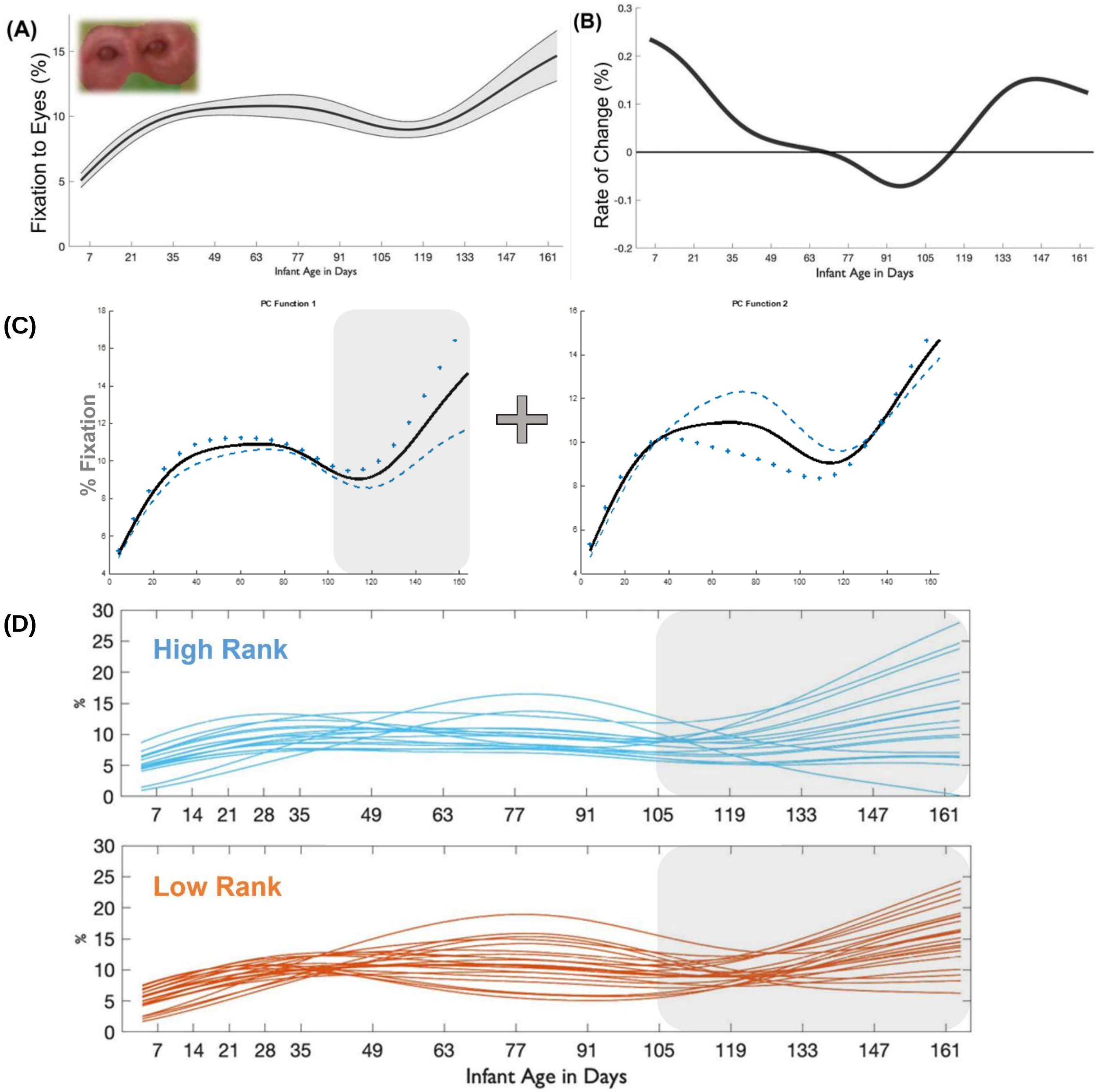


Figure 6: Attention to Conspecific Eyes. Developmental trajectory of attention to the eye region in the Conspecific stimuli (39 unique videoclips) from 1 to 23 weeks (7 to 161 days) of age for all infants combined (*N* = 39). (A) Group mean curve (*N* = 39), mapped using FPCA/PACE. The gray shaded region represents 95% confidence intervals. (B) The first derivative of the mean curve shown in A. The thin horizontal line denotes a rate of change of 0%, i.e., a plateau in attention to eyes. (C) PC functions extracted via FPCA. The blue lines made up of positive (+) and negative (-) symbols depict the effects, respectively, of adding to or subtracting from the mean curve by one standard deviation of the PC curve. For PC1, positive scores denote percent fixation above the group mean and negative scores denote percricricent fixation below the mean, in particular from 15 weeks (105 days) onward (marked by light gray square). For PC2, positive scores denote an earlier peak in percent fixation to eyes that is also lower magnitude, whereas negative scores denote higher magnitude and a later peak. (D) Individual trajectories of attention to eyes. High-ranking infants (*n* = 17) are shown with blue lines; low-ranking infants (*n* = 22) are plotted with orange lines. Light gray squares denote the variance captured by PC1 from 15 weeks onwards.

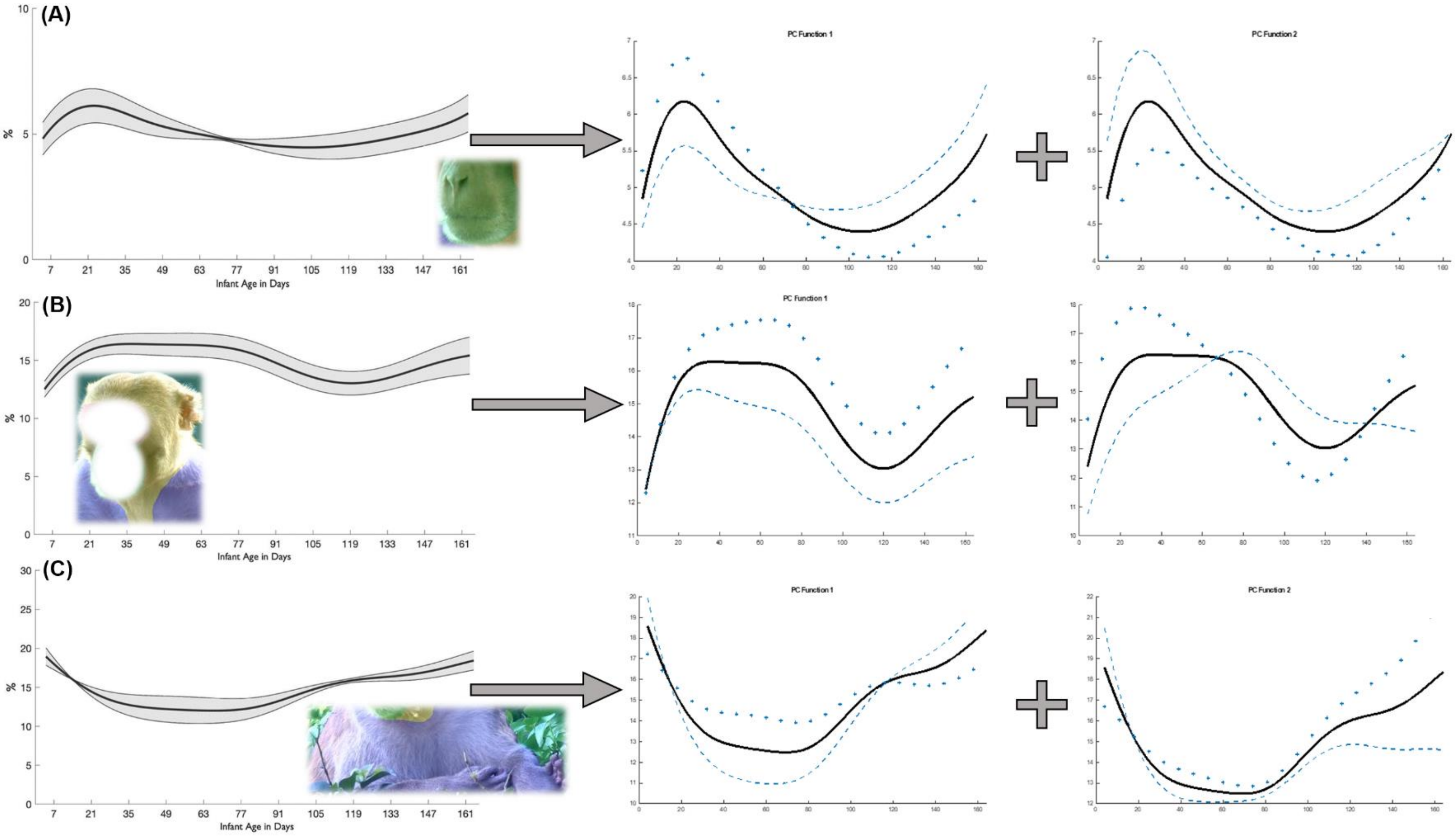
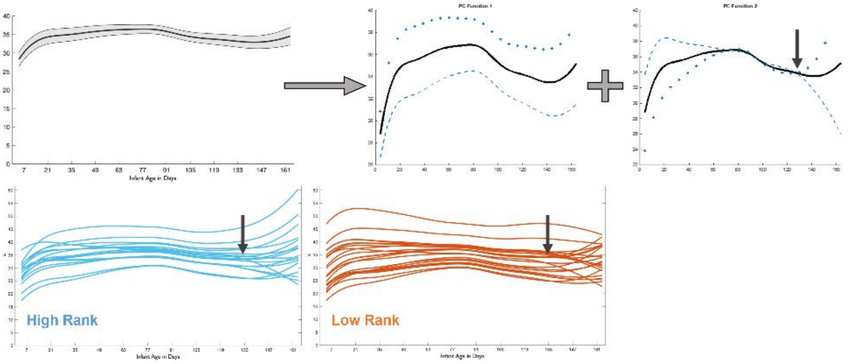
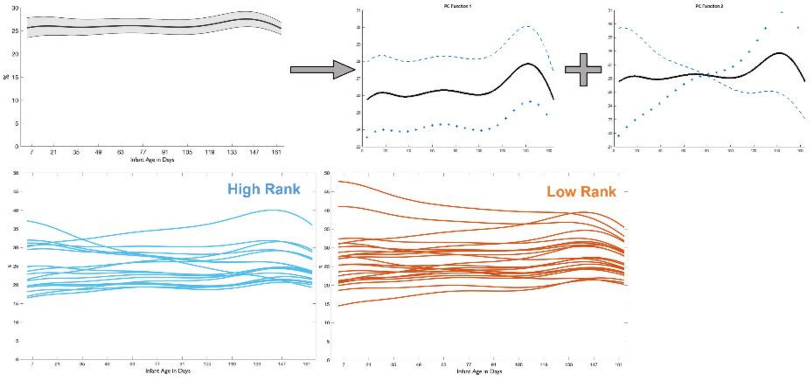


Figure 7: Attention to Conspecific Mouth, Head, & Body. Group mean trajectories (*N* = 39), mapped using FPCA/PACE, for percent fixation to the ROIs for mouth (A), head (B), and body regions (C), with plots for the corresponding PC functions. The gray shaded region around the mean curve represents 95% confidence intervals. In PC score plots, blue lines made up of positive (+) and negative (-) symbols depict the effects, respectively, of adding to or subtracting from the mean curve by one standard deviation of the PC curve.

(A) Total Fixations: Conspecific Videos



(B) Saccades: Conspecific Videos



(C) Lost Data: Conspecific Videos

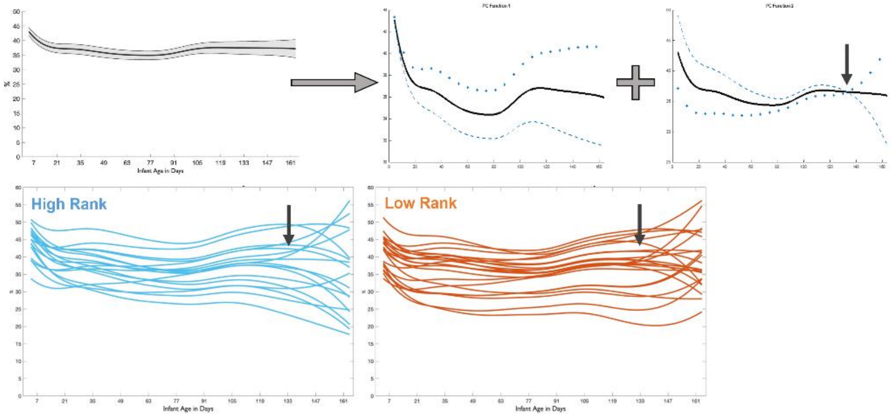


Figure 8: PC Functions for Conspecific Videoclips. For all subjects combined (*N* = 39), group mean curves with 95% confidence intervals, PC functions, and individual curves plotted for: (A) percent total fixations, (B) percent saccades, and (C) percent lost data. In the PC plots, blue lines made up of positive (+) and negative (-) symbols depict the effects, respectively, of adding to or subtracting from the mean curve by one standard deviation of the PC curve. Blue lines indicate high-ranking infants (*n* = 17) in plots on the left; orange lines indicate low-ranking infants (*n* = 22) on the right. Vertical arrows mark the approximate 19-week inflection point in age-specific variance for PC2 in both (A) and (C). In (A), positive PC2 scores indicate fewer total fixations relative to the mean curve in early infancy, but more total fixations relative to the mean in later infancy. Negative PC2 scores indicate the opposite trend. In (B), positive PC1 scores indicate lower percent saccades relative to the mean curve and negative scores indicate greater percent saccades relative to the mean. In (C), positive PC2 scores indicate lower percent data lost relative to the mean curve in early infancy, but greater percent data lost relative to the mean in later infancy. Negative PC2 scores indicate the opposite trend.

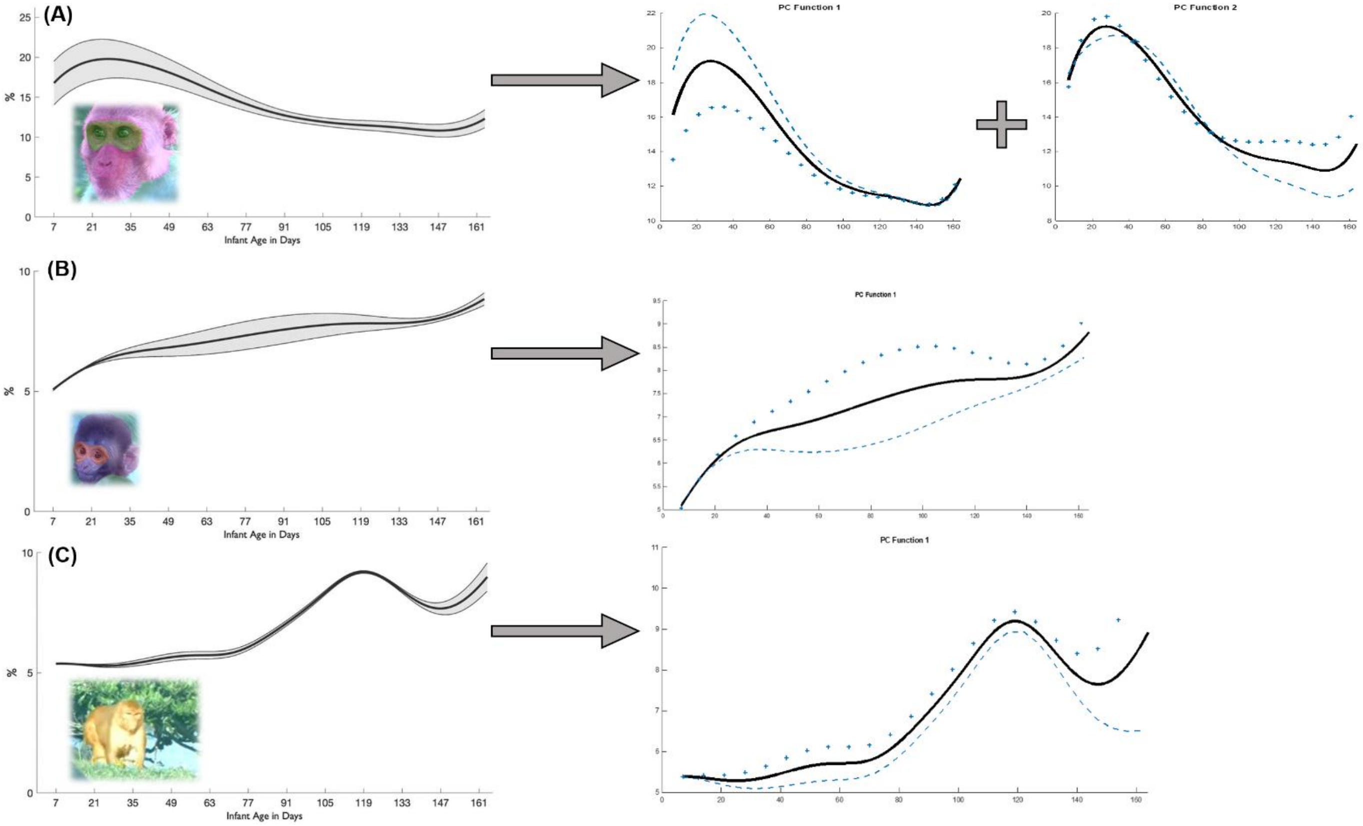
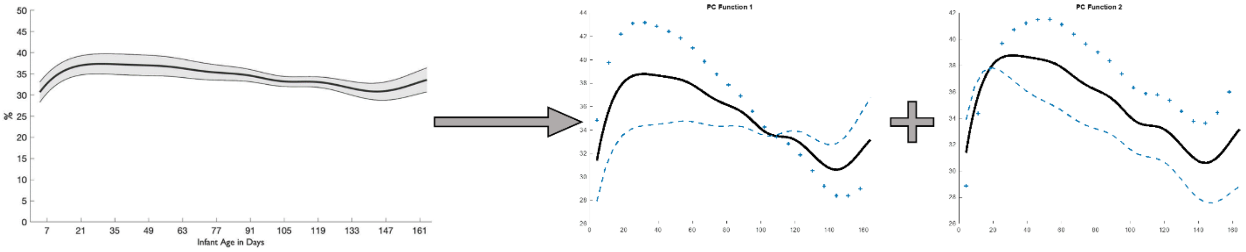
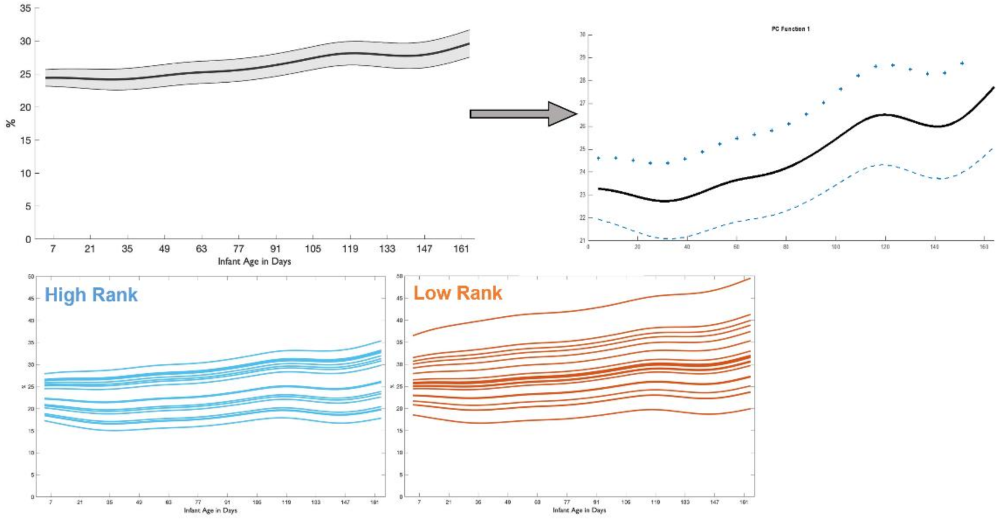


Figure 9: Attention to Dam, Infant, & Groupmate in Mother-Infant Videoclips. Group mean trajectories (*N* = 39), mapped using FPCA/PACE, for percent fixation to the ROIs for dam's head and eyes (A), infant's head and eyes (B), and other conspecifics in the scene (C), with plots for the corresponding PC functions. The gray shaded region around the mean curve represents 95% confidence intervals. In PC score plots, blue lines made up of positive (+) and negative (-) symbols depict the effects, respectively, of adding to or subtracting from the mean curve by one standard deviation of the PC curve.

(A) Total Fixations: Mother-Infant Videos



(B) Saccades: Mother-Infant Videos



(C) Lost Data: Mother-Infant Videos

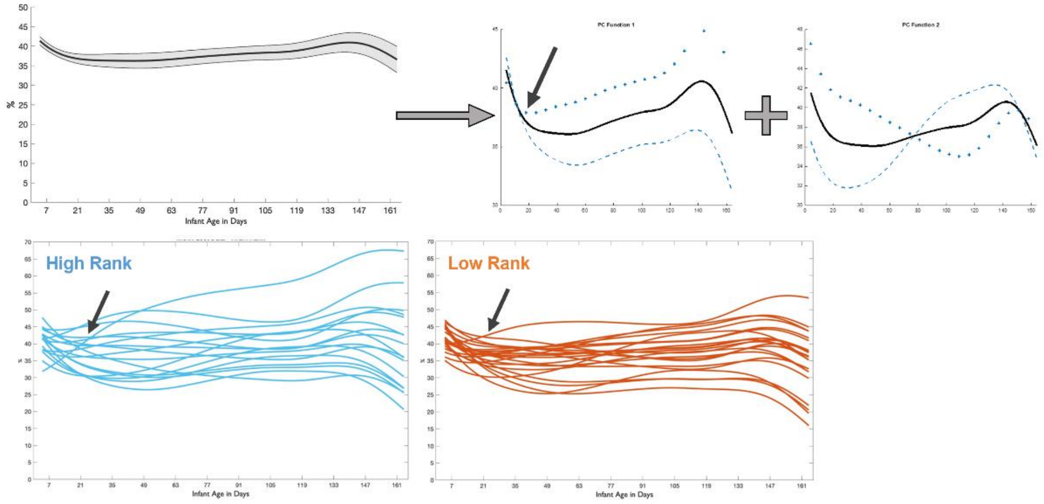


Figure 10: PC Functions for Mother-Infant Videoclips. For all subjects combined (*N* = 39), group mean curves with 95% confidence intervals and PC functions for: total fixations (A), saccades (B), and lost/offscreen data (C). Individual trajectories are also shown for saccades (B) and lost data (C), in order to show the relationship between these measures and rank. In (B), positive PC scores indicate greater % saccades relative to the mean curve and negative scores indicate lower % saccades relative to the mean. In (C), positive PC1 scores indicate greater % lost data and negative PC1 scores indicate lower % lost data, starting from around 3 weeks of age (marked by slanted arrows).

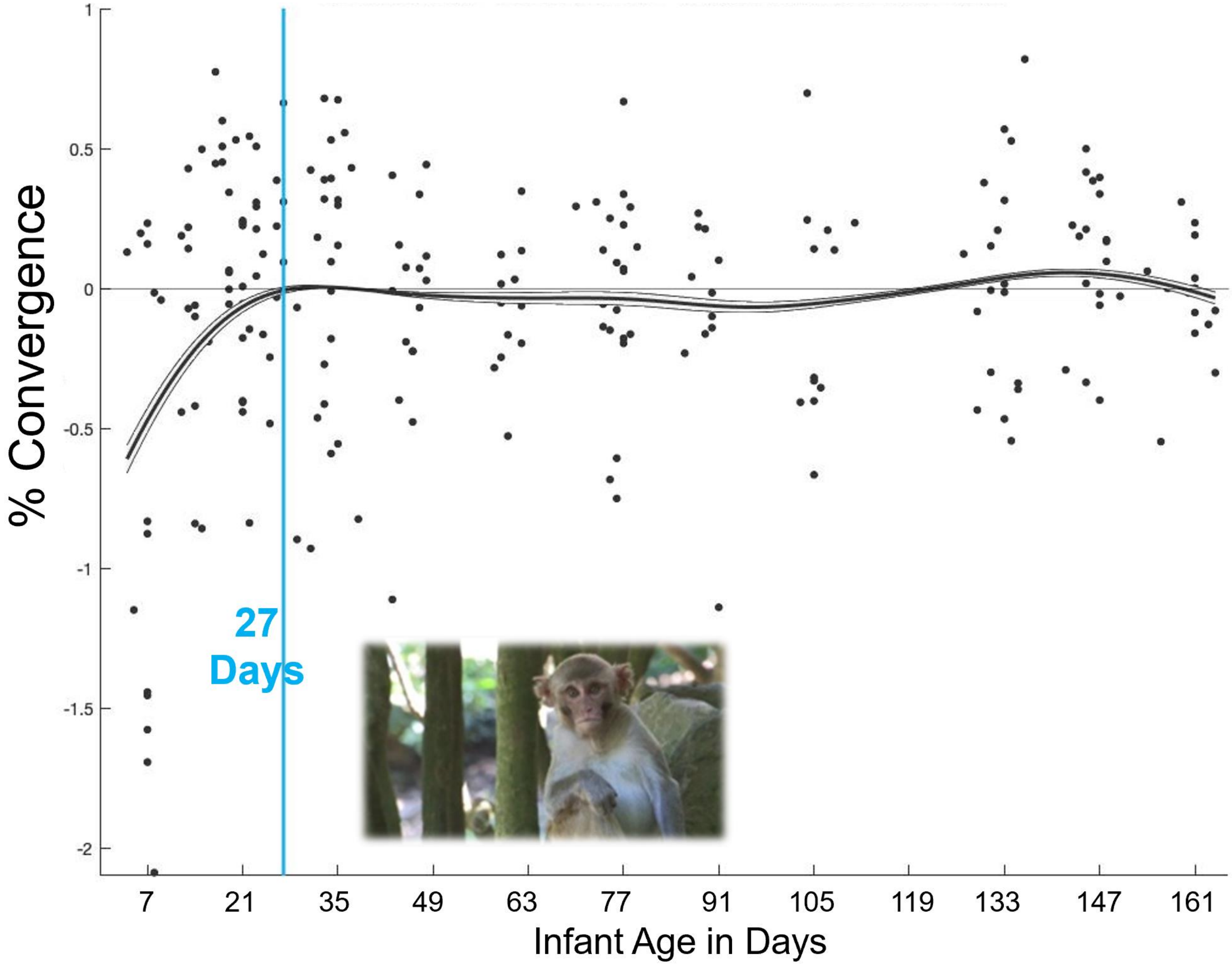


Figure 11: Viewing Convergence for Videos of Conspecifics. Mean curve (*N* = 36) with 99% pointwise confidence intervals. Positive values indicate convergence/synchrony; negative values indicate divergence. The age when the upper confidence limit for the mean percentage of convergence first reaches zero is indicated by a blue vertical line. Data from 9 Conspecific videos are shown, with each dot representing a single subject's viewing of one distinct video during a single eye-tracking session.

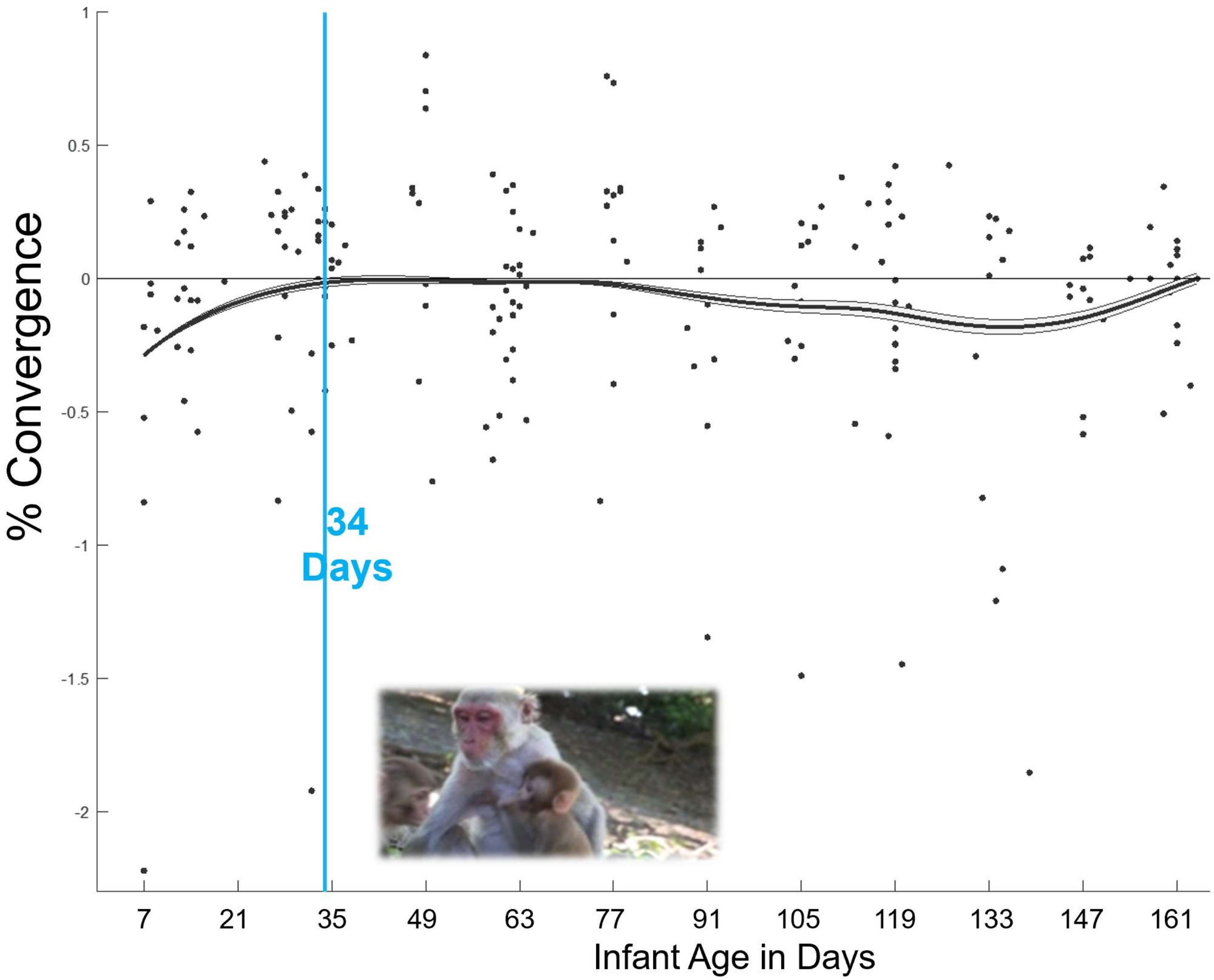


Figure 12: Viewing Convergence for Videos of Mother-Infant Interactions. Mean curve (*N* = 34) with 99% pointwise confidence intervals. Positive values indicate convergence/synchrony; negative values indicate divergence. The age when the upper confidence limit for the mean percentage of convergence first reaches zero is indicated by a blue vertical line. Data from 6 Mother-Infant videos are shown, with each dot representing a single subject's viewing of one distinct video during a single eye-tracking session.

Table 1: Subjects' Demographics. Social rank and year of birth for infant subjects (*N* = 39). Note that the numerical social ranks listed here represent the status of the infant's family/matriline within their social group, rather than the relative rank of the individual dam. The rank percentile was adjusted to 1% from 0% for Subjects 11, 43, 46, and 51. Nine subjects – six infants from the 2016 cohort, one from the 2018 cohort, and two from the 2021 cohort - were removed from the study before reaching 6 months of age due to health concerns, injury, maternal rejection, inability of equipment to accommodate the dam's size, or instability in the social group hierarchy. These subjects are indicated by asterisks (*******). The greatest drop-off in subjects (*N* = 9) occurred in the first 1 to 5 weeks of life. An overthrow took place in group #6 when Subjects 43, 44, and 57 were around 8 weeks (56 days) old, the result of which was Subjects 44 and 57's family dropping from 4th-ranked to 5th-ranked of five families, while Subject 43's family rose from 5th-ranked to 3rd-ranked. For further information on the 2016 cohort, see Wang et al. (2020) and Ford et al. (2023).

Animal Number	Cohort Year	Social Group	Social Rank at Birth	Social Rank (Percentile)
39	2021	#2	2 of 14	85.7%
40	2021	#5	1 of 3	66.7%
***45	2021	#1	1 of 7	85.7%
47	2021	#3	4 of 11	63.6%
***48	2021	#2	1 of 14	92.9%
53	2021	#3	2 of 11	81.8%
52	2020	#1	1 of 7	85.7%
55	2020	#3	8 of 11	27.3%
41	2019	#3	5 of 11	54.5%
42	2019	#3	9 of 11	18.2%
43	2019	#6	5 of 5	1.0%
44	2019	#6	4 of 5	20.0%
57	2019	#6	4 of 5	20.0%
46	2018	#3	11 of 11	1.0%
49	2018	#1	1 of 8	87.5%
***50	2018	#4	5 of 8	37.5%
51	2018	#1	8 of 8	1.0%
56	2018	#6	1 of 6	83.3%
22	2016	#8	2 of 5	60.0%
23	2016	#6	2 of 5	60.0%
9	2016	#9	7 of 10	30.0%
10	2016	#6	3 of 5	40.0%
***25	2016	#7	3 of 5	40.0%
11	2016	#1	10 of 10	1.0%
26	2016	#4	6 of 10	40.0%
12	2016	#8	4 of 5	20.0%
27	2016	#4	3 of 9	66.7%
28	2016	#1	7 of 10	30.0%
29	2016	#2	2 of 3	33.3%
15	2016	#3	12 of 13	7.7%
16	2016	#7	3 of 5	40.0%
17	2016	#1	2 of 10	80.0%
***58	2016	#3	10 of 11	9.1%
***31	2016	#3	10 of 13	23.1%
***32	2016	#1	9 of 10	10.0%
***35	2016	#1	5 of 10	50.0%
20	2016	#6	2 of 5	60.0%
37	2016	#3	4 of 13	69.2%
***38	2016	#3	4 of 13	69.2%

Table 2: Eye-tracking Measures. Variables to be used in Functional Principal Component Analysis (FPCA). Of the 39 unique Mother-Infant videoclips, 12 were shown only to subjects in the 2016 cohort and did not have ROIs drawn. Of the 27 Mother-Infant videos with ROIs, only 13 videos featured additional conspecifics/groupmates in the scene.

Stimulus Type	Eye-Tracking Measure (%)	N	# of Videos
Conspecific	Fixations to Eyes ROI	39	39
Conspecific	Fixations to Mouth ROI	39	39
Conspecific	Fixations to Head ROI	39	39
Conspecific	Fixations to Body ROI	39	39
Conspecific	Fixations Total	39	39
Conspecific	Saccades	39	39
Conspecific	Lost Data	39	39
Mother-Infant	Fixations to Dam ROI (Eyes + Head)	35	27
Mother-Infant	Fixations to Infant ROI (Eyes + Head)	35	27
Mother-Infant	Fixations to Groupmate ROI	34	13
Mother-Infant	Fixations Total	39	39
Mother-Infant	Saccades	39	39
Mother-Infant	Lost Data	39	39

Table 3: Conspecific Video PC Functions & Rank. Results of bivariate linear regression between matrilineal rank (normalized to a percentile) and the principal component (PC) functions extracted from the measures listed in Table 2 for Conspecific stimuli, for all subjects combined (*N* = 39). Each PC function listed with respective Fraction of Variance Explained (FVE). Regression models with moderate effect sizes ($R^2 > .06$; Gaskill & Garner, 2020) are bolded.

Eye-Tracking Measure (%)	PC	FVE	Beta (ß)	R^2	*p*
Fixations to Eyes	**#1**	72.6%	**–**	**.068**	.11
Fixations to Eyes	#2	27.4%	**+**	.002	*.77*
Fixations to Mouth	#1	87.4%	**–**	.005	*.66*
Fixations to Mouth	#2	12.4%	**+**	.007	*.61*
Fixations to Head	#1	82.8%	**–**	.009	*.57*
Fixations to Head	#2	14.8%	**–**	.009	*.57*
Fixations to Body	#1	82.5%	**–**	.004	*.72*
Fixations to Body	#2	17.4%	**–**	.035	*.25*
Fixations Total	#1	87.4%	**+**	.003	*.75*
Fixations Total	**#2**	10.3%	**+**	**.065**	.12
Saccades	**#1**	91.9%	**+**	**.064**	.12
Saccades	#2	7.3%	**–**	.014	*.47*
Lost Data	#1	82.7%	**+**	.002	*.80*
Lost Data	**#2**	13.4%	**–**	**.063**	.12

Table 4: Eye-looking PC Functions & Rank. Results of bivariate linear regression between matrilineal rank (normalized to a percentile) and three measures derived from individual percent fixation to the ROI for eyes in Conspecific videoclips: PC1 scores, PC2 scores, and the linear rate of change/slope from 19 – 23 weeks (133 – 161 days). Results are presented based on three different combinations of subjects. Moderate to large effect sizes ($R^2 > .06$; Gaskill & Garner, 2020) are bolded. FVE refers to Fraction of Variance in eye-looking explained by the PC.

Sample	**19 - 23 Weeks Linear Slope**			**PC #1 (FVE = 72.6%) Scores**			**PC #2 (FVE = 27.4%) Scores**		
	ß	R^2	*p*	**ß**	R^2	*p*	**ß**	R^2	*p*
2018-21 Cohorts (*N* = 18)	**–**	.033	.47	**–**	**.077**	.26	**+**	**.062**	.32
2016 Cohort (*N* = 21)	**–**	.028	.47	**–**	.011	.65	**–**	.021	.53
All Subjects (*N* = 39)	**–**	.047	.19	**–**	**.068**	.11	**+**	.002	.77

Table 5: Mother-Infant Video PC Functions & Rank. Results of bivariate linear regression between matrilineal rank (normalized to a percentile) and the principal component (PC) functions extracted from the measures listed in Table 2 for Mother-Infant stimuli, for all subjects combined (*N* = 39). Each PC function listed with respective Fraction of Variance Explained (FVE). Regression models with moderate effect sizes ($R^2 > .06$; Gaskill & Garner, 2020) are bolded.

Eye-Tracking Measure (%)	**PC**	**FVE**	**Beta (ß)**	**R^2**	***p***
Fixations to Dam (Eyes + Head)	#1	83.3%	–	.013	*.51*
Fixations to Dam (Eyes + Head)	#2	16.3%	–	.006	*.67*
Fixations to Infant (Eyes + Head)	#1	95.7%	+	.001	*.90*
Fixations to Groupmate	#1	92.6%	+	.045	*.23*
Fixations Total	#1	54.0%	–	.0002	*.94*
Fixations Total	#2	44.2%	–	.013	*.48*
Saccades	**#1**	95.5%	–	**.106**	**.043**
Lost Data	**#1**	93.3%	+	**.061**	.13
Lost Data	#2	6.4%	+	.001	*.85*

Table 6: Linear Mixed Model Results. Results of the models testing whether eye-tracking measures predict the two dependent variables, initiating play and withdrawing, at one year of age (*N* = 13). All model versions include home compound/social group as a random factor. Note that for Eyes %Fixation, we used the percent fixation values generated by the FPCA curve-fitting procedure (as depicted in Fig. 6), not actual observed fixation data. Estimates, *t*-values, and *p*-values refer to the "reference" models, which include all three fixed factors (predictors), and to results from Type III tests of fixed effects. For the likelihood ratio tests (LRTs) and AIC values, each row represents a "reduced" model from which that predictor is excluded. Reduced models with a significant (*p* < .05) LRT statistic are bolded. A positive value for ΔAIC indicates that including the predictor improves model fit; a negative value indicates that model fit is improved when the predictor is excluded.

Predictor	**DV (1 Year)**	**Estimate ± SE**	***t***	***p***	**LRT Statistic**	**LRT *p*-value**	**Δ AIC**
Eyes %Fixation at 8 Wks (56 Days)	Infant Initiates Social Play	-0.044 ± 0.45	-0.10	.924	0.009	.924	-1.99
Rate of Change in Eyes %Fixation at 19-23 Wks (133-161 Days)		-14.70 ± 10.85	-1.35	.209	1.209	.272	-0.79
PC Function of %Saccades to Mother-Infant Videos		0.14 ± 0.03	4.17	.002	**9.321**	**.00227**	+7.32
Eyes %Fixation at 8 Wks (56 Days)	Infant Withdraws	0.27 ± 0.16	1.66	.138	0.861	.353	-1.14
Rate of Change in Eyes %Fixation at 19-23 Wks (133-161 Days)		3.66 ± 3.92	0.93	.380	0.563	.453	-1.44
PC Function of %Saccades to Mother-Infant Videos		-0.003 ± 0.01	-0.20	.850	0.015	.903	-1.99

APPENDIX I: Detailed Methods

Eye-tracking Procedures

In order for dam and newborn to bond without disruption, eye-tracking did not begin until at least three days after birth. At the start of a session of data collection, the lights in the room were turned off and a curtain dropped over the open side of the testing chamber, creating a completely enclosed, dark, and sound-attenuated environment. During the session, the infant's behavior was continuously monitored by the experimenter via a video camera mounted on the wall next to the monitor. These video recordings were saved and archived for future behavioral analyses. The mother's breathing and general condition were also monitored throughout the session. Eye-tracking sessions were conducted in the morning so that the pair could be returned on the afternoon of the same day.

Stimuli were presented on a 19" (62.6 cm) computer monitor (1024 x 768 pixels) affixed to one wall of the chamber at a distance of about 76 cm from the infant. Data were collected at a rate of 60 Hz using hardware and software developed by ISCAN (http://www.iscaninc.com) and relying on a dark pupil/corneal reflection technique (see Cognolato et al., 2018). The ISCAN system is accurate to within ±0.3 degrees visual angle (dva) over an area of 20 dva horizontally and vertically. At the start of each session, the infant's gaze was calibrated to the ISCAN software using a 5-point calibration procedure, during which videos unrelated to the experimental stimuli – typically colorful animated patterns or children's cartoons – were played in order to maintain the infant's attention towards the video monitor. Once the calibration was checked for accuracy, the experimenter initiated presentation of the stimuli "playlist." Videoclips were presented at a rate of 30 frames per second. Any accompanying audio were included. In order to recenter the infant's attention between presentations of experimental stimuli, there was an intertrial interval lasting two seconds, during which a spinning target appeared at the center of a black screen. The accuracy of the calibration was also retested in the course of the session as needed.

Functional Principal Component Analysis via PACE

The steps involved in FPCA are essentially the same as those in standard Principal Component Analysis, the goal of both strategies being to identify mutually orthogonal “components” that quantify a specific portion of variation in the data (the “Fraction of Variance Explained,” or FVE). The key distinction is that the components identified in FPCA are two-dimensional functions, quantifying patterns of variance that emerge along a continuum, such as time or age (Ramsay & Silverman, 2005). The “scores” associated with principal component (PC) functions are scalar values that represent the extent to which an individual’s own trajectory aligns with that function’s two-dimensional shape. These values are essentially arbitrary and can be positive or negative. Each individual trajectory can be described as the summation of its individual PC scores and the mean trajectory of the group:

Given ***K*** total PC functions extracted →

Individual Curve = $\text{PCScore}_1 + \text{PCScore}_2 + \text{PCScore}_3 \ldots.. + \text{PCScore}_K$ + Mean Curve

Curve-fitting was conducted in MATLAB (v. 2018b) using a software package for functional data analysis (PACE v. 2.17) made available by the Statistics Department of the University of California, Davis (www.stat.ucdavis.edu/PACE/). This open source package utilizes the Principal Analysis by Conditional Expectation (PACE) algorithm, which offers a number of important advantages for modelling longitudinal data. PACE is designed specifically for the analysis of sparse, irregularly-sampled datasets in which values are unlikely to be available at every age for every individual, resulting in missing data points. The PACE method generates a group mean trajectory along with trajectories for individual subjects, allowing for analysis of both within- and between-subject differences. Trajectories can be generated even for subjects with only a few datapoints, as the PACE algorithm manages data sparsity by “borrowing strength” from the entire sample. The process of fitting separate curves for each of our eye-tracking measures involved dynamically adjusting the input parameters for smoothing; i.e., the mean bandwidth ("*bwmu*") and x-covariance structure bandwidth ("*bwxcov*"). To select the number of PC functions (***K***), we set 95% as the minimum threshold FVE.

Salience Mapping

We conducted salience mapping in MATLAB (v. r2018b) using inhouse, custom written software. Briefly, this software program leverages kernel density estimation in concert with a model of cortical magnification (Duncan & Boynton, 2003; Schwartz, 1994) that overlays the X-Y coordinates of the screen. The resulting "map" (Fig. A1) is a probability density function that effectively quantifies an individual's allocation of visual resources as cortical cells per pixel - or, more intuitively for the purposes of this study, as "salience." The salience maps from multiple subjects are then layered together and summed linearly to generate group salience maps (see Fig. 5 in main text). Based on the combined maps, a *group median salience value* is output for each frame; this quantity represents the extent to which the individuals in the group converge, or "agree," on what is behaviorally salient in that scene. A high median salience value denotes greater synchrony or *convergence*, whereas a low median salience denotes *divergence* (Fig. A2). Finally, permutation testing is done to determine whether the level of convergence is greater than that expected by chance (Fig. A3). Note that it was possible, especially given the complexity of some social stimuli, for subjects to have multiple "peaks" depicting convergence on more than one area in a scene.

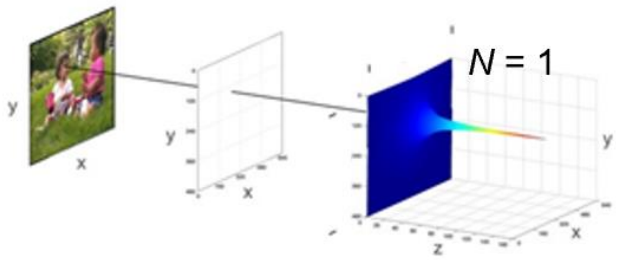


Fig. A1. Individual allocation of visual resources. Pixels are mapped on the x- and y-axes. Salience values are represented on the z-axis as density estimates (arbitrary units), with warm colors indicating convergence and cool colors indicating divergence. Image from Kreuzman et al. (2017) & Micheletti et al. (2017).

The requirements for inclusion of stimuli in salience analyses were as follows: (1) the videoclip was part of the playlist for at least two data collection timepoints, one of those being the final session at 23 weeks (161 days); (2) the “reference” group (23-week-olds) was significantly convergent ($p < .05$) in their viewing for at least two frames (excluding the first 10 frames of a video, as convergence during the first part of the video could be artificially driven by the appearance of the centering stimulus immediately beforehand); and (3) seven or more subjects in the reference group had usable data for that videoclip. Six Mother-Infant videos and nine Conspecific videos were ultimately used in longitudinal salience mapping. Note that the experimental playlist was changed between data collection for the 2016 cohort and later cohorts. After 2016, new Mother-Infant videos were added to the playlist and some Conspecific videos were removed, with the result that four of the six Mother-Infant videos used in salience mapping were presented *only* to the subjects born in 2018 – 2021, and three of the nine Conspecific videos were presented *only* to the 2016 subjects.

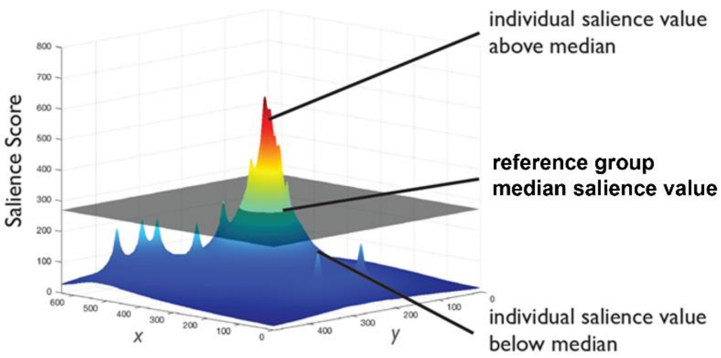


Fig. A2. Individual viewing compared to the reference group’s allocation of visual resources. Pixels are mapped on the x- and y-axes; salience is represented on the z-axis (arbitrary units). Image adapted from Kreuzman et al. (2017) & Micheletti et al. (2017).

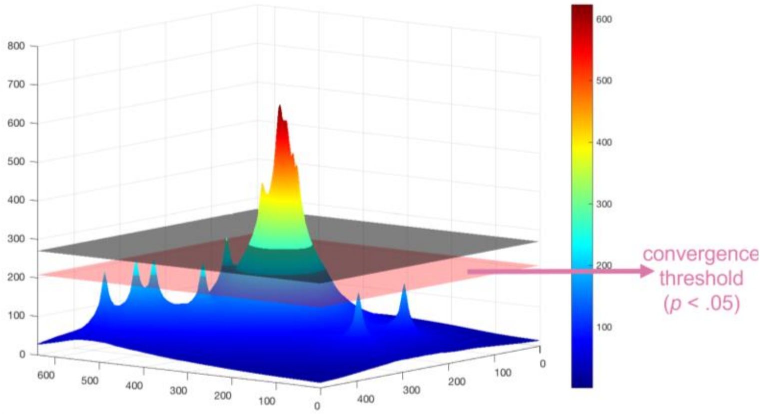


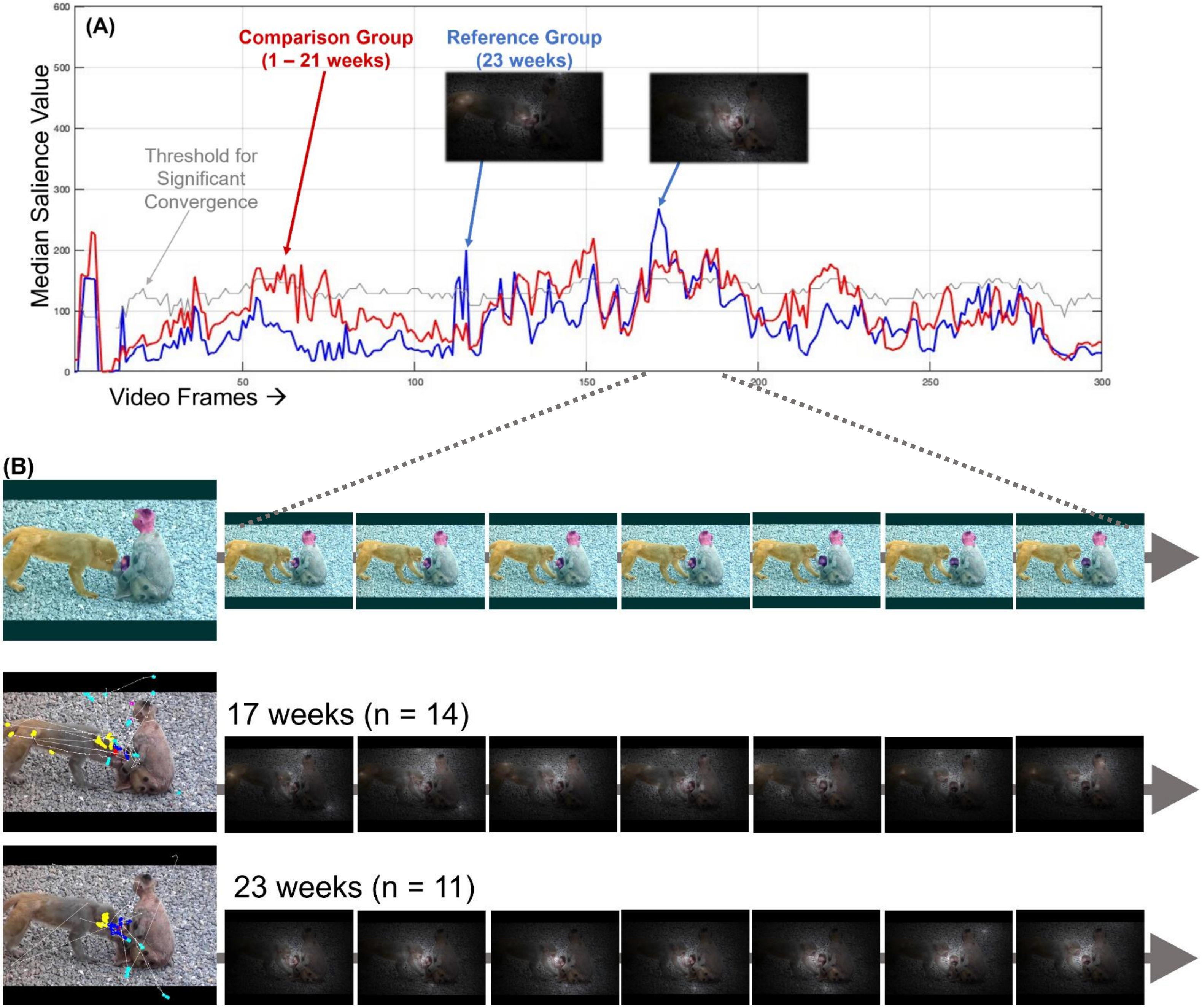
Fig. A3. Significance threshold ($p < .05$) for convergence. Adapted from visual created by M. Micheletti (2017).

We calculated group median salience values for infants in their final eye-tracking session at 23 weeks (161 days) of age, designating these values as the “reference” group. Those same infants at earlier timepoints were the “comparison” group. If an individual’s salience value, at a particular timepoint and at a particular frame, fell below the reference group's median salience value, then that individual's viewing was considered divergent from the reference group (Fig. A2). Likewise, if an individual's salience value was greater than the median salience value, the individual's viewing was considered convergent. For ease of interpretability, we calculated "percentage convergence" values by taking the natural log of the ratio between the individual and reference group salience values:

$$\%\ \text{Convergence} = \ln\left(\frac{\text{individual salience value}}{\text{reference group median salience value}}\right)$$

Percentage convergence was then collapsed across all frames and all videoclips. We again utilized the FPCA-PACE software package to construct longitudinal trajectories of percentage convergence in MATLAB (v. r2018b), following the same modelling and curve-fitting procedures. We constructed trajectories using log salience ratios calculated at all frames (after the first 10), as well as trajectories that included data exclusively from those frames for which the 23-week-old group exhibited significant convergence.

APPENDIX II: Moment-by-Moment Convergence



Appendix II: Frame-by-frame convergence visualized for an exemplar Mother-Infant video (shown in stimuli playlist at 17, 21, & 23 weeks). In (A), the entire length of the video is plotted (~300 frames). The red line shows median salience values collapsed across all younger ages (n = 35 observations/sessions), relative to the reference group of older subjects (n = 11), shown as a blue line. Relative salience was significantly convergent ($p < .05$) when salience was above the convergence threshold, plotted as a light gray line (see Fig. A3 in *Appendix I*). In (B), viewer scan paths and grayscale salience maps are summarized across subjects and across a select series of consecutive frames (23 frames, <1 second) from a highly salient scene in which a juvenile conspecific and infant engage in mutual gaze. In the scan path images, white lines represent saccades by viewers and colored circles represent fixations. (Note: in the grayscale maps, brightness and contrast were altered to improve clarity of the image.)

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GENERAL DISCUSSION

The two studies presented above modelled typical developmental trajectories in a NHP model as a means to improve understanding of atypical development. In the discussion below, I summarize the major findings of each study in turn, then integrate these findings to discuss the main aim of this dissertation: (1) to investigate the role of matrilineal social rank in the social development of male rhesus macaque infants across the first year of life and (2) to identify behavioral measures during early infancy that reliably predict social competency in the juvenile stage. Finally, I discuss implications for future studies of social development and end with concluding remarks.

SUMMARY OF FINDINGS

In Study 1, I analyzed data from behavioral observations conducted at seven ages, beginning at two weeks and spanning the first year of life. My central hypothesis was that interindividual variation in mother-infant interactions, and the infant's interactions with others in their social group, can be explained in part by matrilineal ranking. For a small number of measures related to maternal behavior, there was evidence to support my hypothesis at certain ages. Low-ranking infants, compared to their high-ranking peers, spent less time in direct physical contact with, in spatial proximity to, and being carried by their dam, in concert with experiencing a steeper decline in the responsivity and sensitivity of caregiving as they approached one year of age (indexed by the Instrument of Macaque Maternal Care; McCormack et al., 2006, 2015). For infants' interactions with conspecific groupmates (e.g., play, grooming, aggression received), I did not find evidence to support my hypothesis, suggesting that these behaviors are more strongly influenced by factors other than matrilineal rank. These factors could include the infants' temperament, or characteristics of the social group itself, such as size, sex ratio, time since the group was established, or stability/instability.

In Study 2, I analyzed eye-tracking data collected over 14 sessions spanning the first six months of infancy. My central hypothesis was that interindividual variation in social-visual attention among infant macaques from ages 1 – 24 weeks old is explained in part by matrilineal ranking. Based on this hypothesis, I predicted that lower-ranking infants, compared to higher-ranking peers, would show an earlier peak in attentional bias towards salient social cues in video stimuli, as well as an accelerated developmental trajectory at later ages. Also, I predicted that, similarly to human infants (Micheletti et al., 2017), infant rhesus macaques younger than 10 weeks of age would exhibit scattered, highly variable patterns of looking, which would then converge on looking patterns like those of older macaques at between 10 – 13 weeks of age.

There was some evidence in support of my hypothesis, although the effects of rank on social-visual attention were generally small to moderate and lacking in statistical significance. The peak in preferential attention to the eyes during infancy did not significantly differ by ranking, as had been described by Ford et al. (2023). I did, however, replicate Ford et al.'s (2023) finding that eye-looking in lower-ranking infants exhibited an accelerated positive rate of change during the last month of the study (19 – 23 weeks). My prediction was also confirmed that viewing patterns early in infancy would be scattered and highly variable between subjects, before eventually converging on relatively mature viewing patterns. This convergence appeared earlier than predicted based on past findings in human infants (Micheletti et al., 2017); male rhesus macaque infants demonstrated mature convergence for both categories of video stimuli (Conspecific and Mother-Infant) at just 4 – 5 weeks of age (27 days and 34 days, respectively).

CONTINUITY, DISCONTINUITY, & PREDICTORS

In this dissertation, I assessed the degree of predictability and continuity, or stability, in rhesus macaque social development. In both Study I and Study II, two behavioral variables in 1-year-old juveniles were tested: the frequency of initiating social play with conspecific groupmates and the frequency of withdrawing (avoiding or moving away from a conspecific). Linear mixed models revealed that rates of both behaviors were highly continuous and stable within individuals. The continuity and stability were the case especially for withdrawal; the frequency of withdrawing from others at 3 months of age explained over 75% of variation in the frequency among 1-year-old juveniles. No additional predictors for withdrawal were identified in either Study I or Study II. The robust, trait-like stability of this behavior, as well as the absence of other significant predictors, may be explained by its role in social ranking dynamics. It is likely that rates of withdrawing are dictated predominantly by an individual's relative rank, which itself is highly stable over time. Indeed, researchers often map dominance hierarchies in macaque social groups based on observations of dyadic interactions and, within these observed encounters, withdrawal by one individual is a reliable indicator of subordinate status (Bernstein, 1976; Embree et al., 2013; Howell et al., 2014; Silk, 2002).

In contrast, the rate of initiating social play in juveniles was predicted by: (1) the same behavior at 3 months of age, (2) the rate of withdrawing at 3 months of age, (3) maternal cradling duration in the first month of life, and (4) the principal component function (PC1) of percent saccades to Mother-Infant videoclips. For Study I, my expected results were that subjects demonstrating high sociality in early infancy will continue to do so as juveniles and, in the case of maternal style, that subjects raised by dams that are less protective and more rejecting in their caregiving will demonstrate greater social confidence as juveniles. Both these predictions were confirmed. Three-month-old infants that initiated play with groupmates more often and withdrew from groupmates less often tended to initiate social play more often upon reaching juvenescence. Maternal cradling, like withdrawal, was a negative predictor of initiating play; subjects that were cradled more in their first month of life went on as juveniles to initiate play interactions with their peers less frequently.

Saccading behavior, in contrast, was a positive predictor; infants that performed more saccades when viewing Mother-Infant videos, across all ages from 1 to 23 weeks, went on as juveniles to initiate social play more frequently. This was the only eye-tracking measure identified as a predictor. Levels of saccading were highly continuous and stable within individuals, such that the infants that performed the most saccades at 1 week tended to be the infants performing the most saccades at 6 weeks, especially in the case of Mother-Infant videos.

MATRILINEAL RANK & ONTOGENETIC NICHES

This dissertation builds on an extensive body of research demonstrating the importance of matrilineal ranking in the early social development of rhesus macaques. For both studies, the theoretical framework of ontogenetic niche construction (Flynn et al., 2013) provides insight into the results. In Study I, the only statistically significant effects of matrilineal rank were on variables related to maternal style or the mother-infant relationship and, as discussed above, maternal cradling in early infancy was a negative predictor for initiating social play in the juvenile stage. This latter finding aligns with previous research showing that more controlling or protective primate mothers, by limiting their infants' attempts to wander and explore, may keep their infant safe from harm, but at the cost of reduced opportunities for social play and interactions with groupmates (Bardi & Huffman, 2002; Fairbanks, 1996; Fairbanks & McGuire, 1988; Kondo-Ikemura & Waters, 1995; McCormack et al., 2006; Suarez-Jimenez et al., 2013). As summarized by Fairbanks (1996), "Primate infants inherit more than genes from their mother…they inherit her home range, her social companions, and her rank, and grow up in the developmental niche produced by her individual maternal style. For socially living primates, with a long period of dependency and overlapping generations, maternal behavior is the context of development" (p. 606).

In Study II, lower-ranking infants not only exhibited an accelerated increase in eye-looking across the last month of the study, as discussed above, but also performed more saccades, showed greater attentiveness to the Mother-Infant videoclips from around 3 weeks onwards, and, for the Conspecific videoclips specifically, fixated *more* overall and showed greater attentiveness at earlier ages, but began at 4 -5 months to fixate *less* overall and show lower attentiveness. Taken together, this set of findings indicates that by at least 4 – 5 months of age, lower-ranking infants begin to diverge from higher-ranking infants in their viewing strategies. The span of time around 4 months of age has been proposed as an additional critical period for the development of social-visual attention, in particular for the infant macaque's functional understanding of gaze behavior in conspecifics (Wang, 2019). During this period, infants born to subordinate dams may develop strategies for avoiding direct eye contact with others, while still maintaining their ability to monitor social cues through covert means. Covert attentional strategies could include rapid saccades and "check-looks" towards conspecifics' eyes (Mosher et al., 2011; Muschinski et al., 2016). Such an account would also align with the finding by Ford et al. (2023) that lower-ranking infants had an accelerated developmental trajectory for eye-looking in early infancy, reaching their initial peak in percent fixation at an earlier age than their higher-ranking peers.

Nevertheless, it is important to note that in Study I, ranking did *not* significantly impact the majority of behaviors. Likewise, only small to moderate effect sizes were found for the effects of ranking reported in Study II, and percent saccades to Mother-Infant videos was the only eye-tracking measure for which the relationship with rank was statistically significant. Across both studies, factors other than matrilineal ranking may have had comparatively stronger impacts on maternal style, mother-infant interactions, social-visual attention, and social behaviors. Characteristics of the larger social group - in particular size, complexity, and the stability (or instability) of existing dominance hierarchies - proved especially relevant in interpreting the results of Study I. In a study of adult female rhesus macaques, Simons et al. (2022) found that summary measures of observed social behaviors frequently offered explanatory insight into physiological variation beyond that made available by analyzing rank on its own, though, importantly, the directionality of effects was the same whether rank or rank-associated behaviors were tested as the primary predictor.

In short, social ranking is a well-validated and useful descriptor, extremely valuable as a summary measure to characterize the environment in which social development takes place, but is frequently imprecise. It cannot be assumed that knowing the relative ranking of a mother-infant pair means that we know everything relevant about that infant's social environment and experiences. As articulated by Simons et al. (2022), social ranking is itself likely “not the proximate driver” of phenotypic differences (p. 8). The list of potentially relevant variables quickly expands if we consider wild or semi-wild groups of rhesus macaques. Maternal style and mother-infant interactions have been shown to vary based on the availability and quality of food resources, risk of predation, and overall harshness of the physical habitat (reviewed by Fairbanks, 1996; Liu et al., 2018). In a multi-year study of wild rhesus macaques living at the Nanwan Nature Reserve (Hainan Island, China), Liu et al. (2018) compared the reproductive rates, infant mortality, and maternal style of two groups, one containing around 100 individual macaques and the other, only around 30 individuals. The authors reported finding partial support for their hypothesis that “rank is a main driver of maternal style,” (p. 13), but noted complex interactions between matrilineal rank, group size, and the age of the infant. During the birthing season, when infants were less than 4 months old, effects of rank on maternal style were observed only among females in the larger group, with high-ranking dams spending less time in close physical contact with their infants, compared to low-ranking dams. Within the smaller social group, however, there were no significant effects of rank on maternal style. Findings such as these point to a limitation of the ontogenetic niche construction framework in providing cogent explanations of developmental outcomes, or at least complicate the notion of developmental niches.

IMPLICATIONS FOR FUTURE RESEARCH

Further studies are needed to identify the true “proximate drivers” that may mediate the impacts of matrilineal rank on developmental outcomes for social behavior and social-visual attention. Though labor-intensive, experimental manipulation of social hierarchies, accomplished by controlling individual females' order of introduction to the group (e.g., Tung et al., 2012) is a powerful tool for disentangling causes and consequences of individual ranking. In addition, it will be instructive for future NHP studies to include both male and female infants. There is compelling evidence that dams' caregiving behavior towards male offspring differs significantly from their behavior towards female infants. For example, pigtailed macaque mothers encourage male infants to become independent at an earlier age than female infants. Pigtailed macaque females treat their male infants more harshly and control the movements of male offspring through retrieval and restraint with greater frequency (Jensen et al., 1968; see also Dettmer et al., 2016; Tomaszycki et al., 2001). Rhesus macaques are a matriarchal species; as such, maternal rank "inheritance" is stronger and more reliable in daughters versus sons; young females typically continue to live with kin, integrating into their dam's matriline, whereas young males must negotiate their status upon joining a natal group composed of male peers (Bernstein, 1976; Bernstein & Williams, 1983; Hassett et al., 2009). Given the differing life histories of female versus male rhesus macaques, it is possible that effects of matrilineal rank that were not identified in this dissertation may be found in studies of female infants in the future.

For future eye-tracking studies, in both human infants and non-human primates, the results of Study II demonstrate the value of using dynamic, naturalistic experimental stimuli (Hopper et al., 2020; Karatekin, 2007; Mosher et al., 2011; Ryan et al., 2020; van Rijn et al., 2019). Further, eye-tracking studies should leverage methods for analyzing eye-tracking data that provide holistic views of viewing behavior. These more recently developed and innovative strategies include descriptions of scan paths, which integrate data on saccades, fixations, and covert attentional strategies (e.g., Mosher et al., 2011; Wang, 2019), measures of "missing" or "lost" data and gross data quality (Naples et al., 2021; Shic et al., 2022), and methods for visualizing and quantifying convergence between viewers (Kano et al., 2018; Kreuzman et al., 2017; Micheletti et al., 2017; Nakano et al., 2010; Tenenbaum et al., 2021; Wang et al., 2018). Applying these techniques to eye-tracking data can yield rich insights into individual differences, insights beyond those made available by summary measures of fixation to specific, predefined regions-of-interest.

CONCLUSION

The aim of the current dissertation was to investigate the development of typically-developing male rhesus macaque infants living within a species-typical range of early environments. This dissertation also demonstrated the continued value of NHP models for modelling typical development as a window into atypical development. As a final note, we may wish to interrogate what qualifies as a “typical” range of experiences in the life of a rhesus macaque infant. The current study included male macaque infants only, and selected for experienced, competent mothers with no history of maltreating their offspring. Unlike young macaques in the wild, subjects were never subject to major natural disasters, starvation, or predation. Due to ethical guidelines and concern for animal welfare, infants were dropped from the study if observed failing to thrive or if they experienced serious health challenges or other kinds of early adversity. We might consider this analogous to a study of human development that exclusively recruits upper- or middle-class children from “WEIRD” (Western, Educated, Industrialized, Rich, and Democratic) populations (Henrich et al., 2010). As has been argued forcefully by scholars working in the fields of child development and anthropology, “experiences can be both species-expected and adverse” (Frankenhuis & Amir, 2021, p. 15; see also Kondo-Ikemura & Waters, 1995).

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