Received: 9 January 2023 | Revised: 26 June 2023 | Accepted: 12 August 2023

DOI: 10.1002/dev.22420

Developmental Psychobiology WILEY

BRIEF REPORT

The effects of early rearing experiences on mutual eye gaze among captive olive baboons (*Papio anubis*)

Angela M. Achorn | **Michele M. Mulholland** | **William D. Hopkins**

Department of Comparative Medicine, The University of Texas MD Anderson Cancer Center, Bastrop, Texas, USA

Correspondence
Angela M. Achorn, Department of Comparative Medicine, The University of Texas MD Anderson Cancer Center, Bastrop, TX 78602, USA.
Email: amachorn@mdanderson.org

Funding information
National Institutes of Health, Grant/Award Numbers: HD-103490, NIH OD-024628; National Science Foundation, Grant/Award Number: 2021711

Abstract

Among human and nonhuman primates, mutual eye gaze (MEG) and gaze following are believed to be important for social cognition and communicative signaling. The goals of this study were to examine how early rearing experiences contribute to individual variation in MEG and to examine the potential role of genetic factors underlying this variation. Subjects included 93 female and 23 male baboons (*Papio anubis*) ranging from 3 to 20 years of age. Within the sample, there were 55 mother-reared (MR) and 61 nursery-reared (NR) baboons. MEG was assessed in four 60-s test sessions. For each session, the duration, frequency, and bout length were recorded. Mean values were then calculated for each individual from the four sessions. A multivariate analysis of covariance revealed an overall significant main effect for rearing. Subsequent univariate analyses revealed significant rearing effects on mean bout length, but not mean duration or mean frequency, with MR baboons having longer bout lengths compared to NR baboons. Furthermore, mean bout length was found to be significantly heritable. These results indicate that rearing experiences, and to a small extent, genetic factors, affect patterns of mutual eye gaze - in particular, bout length. These results differ from previous findings in MR and NR chimpanzees, further suggesting that rearing may impact MEG in a species-specific manner that reflects the function of gaze in different primate species.

KEYWORDS
early experience, mother–infant relations, primate, social, temperament

1 | INTRODUCTION

Primates rely more heavily on visual signals than do most other mammals (Emery, 2000). These visual cues help with basic survival skills such as finding food, mates, and shelter, but also with the maintenance of complex social relationships that characterize most primate societies (Kaas & Balaram, 2014). Many of the traits typically associated with primate social cognition—for example, coalition formation, tactical deception, reciprocity, and knowledge of third-party relationships—depend on visual cues since these signals can convey emotional or mental states, and they can be directed toward specific individuals (Emery, 2000). The importance of visual signaling throughout primate evolution, particularly in social contexts, is illustrated by the primate brain which contains over 30 regions involved in visual processing, including regions in which neurons respond to visual social signals (Felleman & Van Essen, 1991).

Among these visual signals, eye gaze is believed to be important for social development, social cognition, and communicative signaling (Grossmann, 2017; Hopkins et al., 2020; Kano et al., 2015). In humans, infants and their caregivers often engage in mutual eye gaze, and this early non-verbal communication is believed to play a role in the formation of social bonds and attachment (Farran & Kasari, 1990; Niedźwiecka et al., 2018). Mutual gaze between mothers and infants has also been observed in other apes (e.g., chimpanzees: Bard,

https://doi.org/10.1002/dev.22420

1994; orangutans: Kaplan & Rogers, 2002) and in monkeys (e.g., rhesus macaques: Ferrari et al., 2009). Additionally, eye gaze may relate to the theory of mind by allowing individuals to make inferences about what others see and think (Grossmann, 2017). Gaze following has been reported in all great apes (Bräuer et al., 2005), catarrhine monkeys (e.g., stump-tailed macaques; Anderson & Mitchell, 1999), platyrrhine monkeys (e.g., spider monkeys and capuchins: Amici et al., 2009; marmosets: Burkart & Heschl, 2006), and prosimians (e.g., black lemurs and common brown lemurs: Ruiz et al., 2009). Research on eye structure and the communicative function of gaze across primate taxa demonstrates that information conveyed through mutual eye gaze and gaze following is widespread among primates (Amici et al., 2009; Bräuer et al., 2005; Rosati & Hare, 2009; Tomasello et al., 1998, 2007). Furthermore, studies show that early social experiences may affect the development of species-typical eye gaze patterns in humans (Senju et al., 2015). However, despite the compelling evidence that eye gaze has a strong evolutionary basis, and that it is potentially influenced by social experiences early in life, few studies have investigated the role of genetic factors or early life experiences on mutual eye gaze among a relatively large cohort of primates. To this end, the current study has two main objectives: (1) to examine how early social rearing experiences contribute to individual variation in mutual eye gaze and (2) to examine the potential role of genetic factors underlying this variation.

This research leverages a unique population of olive baboons at the Michale E. Keeling Center for Comparative Medicine and Research (KCCMR) at The University of Texas MD Anderson Cancer Center. Specifically, the KCCMR maintains a colony of specific pathogen free (SPF) baboons. To create an SPF breeding colony, newborn infant baboons born to non-SPF females must be separated at birth to prevent maternal transfer of all undesirable pathogens. When removed from the non-SPF females, the neonates are raised in a nursery setting (i.e., nursery-reared [NR] baboons) with same-aged peers for the first 2 years following methods very similar to those previously employed at other facilities (Brent & Bode, 2006). There are also offspring born to SPF females who remain with their biological mother in their natal groups since they are already pathogen free (i.e., mother-reared [MR] baboons). This manipulation of early social rearing between MR and NR baboons offers a unique opportunity to examine how these experiences influence mutual eye gaze measures.

Because the NR baboons in this study had more frequent interactions with humans early in life, we hypothesized that NR baboons would be more inclined to engage in mutual eye gaze (MEG) with a human experimenter than MR baboons. Specifically, we predicted that MEG frequency, duration, and bout length would be higher among NR baboons than MR baboons after controlling for age and sex. Additionally, based on evidence that mutual eye gaze has strong evolutionary foundations among primates, we further hypothesized that MEG measures would be heritable among the baboons in this study.

TABLE 1 Study subjects.

Age/sex	Mother-reared	Nursery-reared	Total
Juvenile/adolescent female	4	17	21
Juvenile/adolescent male	2	5	7
Adult female	41	31	72
Adult male	8	8	16
Total	55	61	116

2 | METHODS

2.1 | Subjects

Subjects included 93 female and 23 male olive baboons (*Papio anubis*) housed at the KCCMR. Within the sample, there were 55 MR and 61 NR baboons ranging from 3 to 20 years of age. Table 1 shows the distribution of subjects across the age and sex within the MR and NR cohorts. Baboons were housed in the SPF colony. The baboons at KCCMR live in indoor/outdoor corrals (~4518 ft^2) or domes (~1000 ft^2). The sliding doors separating indoor and outdoor areas remain open aside from daily cleaning times. The baboons are provisioned a diet of monkey chow and fresh produce, and water is available continuously.

As previously mentioned, newborn infant baboons born to conventional (non-SPF) females are separated at birth to prevent maternal transfer of undesirable pathogens and are subsequently raised in a nursery setting. Nursery rearing typically involves bottle feeding and inanimate surrogates during the first 30 days of life, followed by increasing levels of socialization with same-age peers. Specifically, infants are moved into age-matched peer groups of four to five individuals starting at 3–6 months, then larger age-matched groups of 6–12 individuals at 6–9 months, and finally into the multi-age breeding groups when they are ~2 years old and have cleared viral testing. At the time of testing, all subjects in the current study were housed in multi-age breeding groups comprising both MR and NR baboons. We limited our sample to subjects 3 years of age or older so that NR baboons introduced into the breeding group had been in the group for at least 1 year at the time of testing. All work was approved by the Institutional Animal Care and Use Committee at The University of Texas MD Anderson Cancer Center.

2.2 | MEG procedure

As in the previous study by Hopkins et al. (2020) with chimpanzees, mutual eye gaze of each subject was assessed in four, 60-s test sessions by the same human observer. All subjects were tested in their social groups, and no attempts were made to separate individuals. The observer sat ~0.5 m from a window or mesh of the enclosure so that they were not within touching distance but were close enough to tell when direct eye contact was being made. The observer wore a disposable face mask and face shield when conducting observations, though other humans confirmed that the observer's eyes were entirely visible through the plastic face shield.

TABLE 2 Pearson correlations between mutual eye gaze (MEG) measures.

MEG Duration				
	Session 1	Session 2	Session 3	Session 4
Session 1	1	0.559	0.635	0.628
Session 2	–	1	0.676	0.651
Session 3	–	–	1	0.647
Session 4	–	–	–	1
MEG Frequency				
	Session 1	Session 2	Session 3	Session 4
Session 1	1	0.547	0.481	0.584
Session 2	–	1	0.410	0.599
Session 3	–	–	1	0.540
Session 4	–	–	–	1
MEG Bout Length				
	Session 1	Session 2	Session 3	Session 4
Session 1	1	0.786	0.837	0.865
Session 2	–	1	0.834	0.809
Session 3	–	–	1	0.855
Session 4	–	–	–	1

Note: All correlations are significant at $p < .01$ (two-tailed).

The 60-s test session began when the subject was sitting or standing with their attention directed toward the observer and when the observer made direct eye contact with the subject. Throughout the session, the observer actively tried to gain and maintain eye contact with the subject by calling their name or making other sounds. All scoring was done live using the program *BORIS* (Friard & Gamba, 2016). On rare occasions (16 times during this study), sessions were discarded if the subject was distracted by external events (e.g., a fight within the group, other humans in the vicinity). The observer repeated this test over four distinct sessions on separate days. During each session, the observer recorded when the subject made or broke eye contact. *BORIS* then provided the duration (i.e., total number of seconds that MEG was maintained within the 60-s session), frequency (i.e., the number of times MEG occurred within the 60-s session), and mean bout length (i.e., total duration divided by frequency) for each observation. The observer was blind to MR or NR status during data collection.

2.3 | Statistical analyses

We used Pearson Product Moment correlations to evaluate individual consistency in MEG measures across the four sessions. Because we found consistent scores within individuals and between the four sessions, we computed mean duration, mean frequency, and mean bout length for each individual. A multivariate analysis of covariance (MANCOVA) was used to examine the effects of sex and rearing on each mean MEG outcome measure. For this analysis, mean frequency, mean duration, and mean bout length were dependent measures, age was a covariate, and sex and rearing history were fixed factors. Subsequent univariate analyses were also used to examine the effects of sex and rearing history on each MEG measure.

2.4 | Heritability

Consistent with previous studies that have utilized pedigree information from captive nonhuman primate populations (Fears et al., 2009; Hopkins et al., 2014; Kochunov et al., 2010; Rogers et al., 2008), we used the software program Sequential Oligogenic Linkage Analysis Routines (SOLAR) (Almasy & Blangero, 1998) to estimate heritability in the MEG measures based on pedigree information from the conventional and SPF baboon colonies at KCCMR. The phenotypes examined included mean MEG duration, mean MEG frequency, and mean MEG bout length. Prior to heritability analyses, all three phenotypes were normalized (due to high kurtosis) using an inverse normal transformation function within SOLAR. Covariates included age, sex, rearing history, sex × age, sex × rearing history, and age × rearing history.

3 | RESULTS

3.1 | Consistency in mutual eye gaze measures

We found significant positive associations among the four observation sessions for all three mutual eye gaze measures including duration, frequency, and bout length (Table 2). Individual responses therefore appear to be consistent and repeatable across test sessions.

3.2 | Heritability

Mean bout length was found to be significantly heritable ($h^2 = 0.309$, SE = 0.175, $p = .026$). Significant covariates for mean bout length included age and age × sex, and the proportion of variance accounted for by these covariates was 0.029. Mean duration was not significantly heritable ($h^2 = 0.210$, SE = 0.232, $p = .161$), nor was mean frequency ($h^2 = 0.039$, SE = 0.321, $p = .450$). Significant covariates for mean duration included age, sex, and sex × age, and the proportion of variance accounted for by these covariates was 0.152. Sex × age was a significant covariate for mean frequency, and the proportion of variance accounted for by this covariate was 0.179.

3.3 | Multivariate analysis of covariance

The MANCOVA revealed an overall significant main effect of rearing $F(3, 109) = 2.796$, $p = .044$ and sex $F(3, 109) = 4.188$, $p = .008$. Age was not a significant covariate $F(3, 109) = 1.516$, $p = .214$. Subsequent univariate analyses revealed significant rearing effects on mean bout length $F(1, 111) = 8.316$, $p = .005$, but not mean duration $F(1, 111) = 3.392$, $p = .068$ or mean frequency $F(1, 111) = 0.738$,

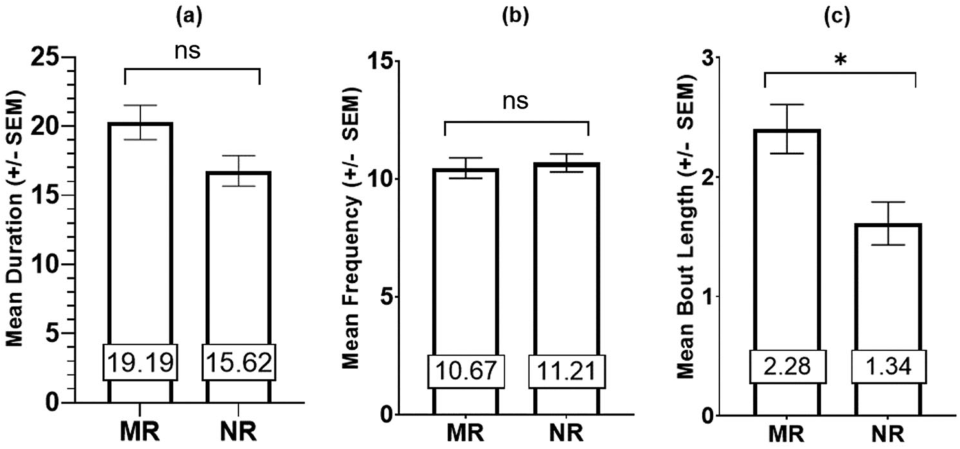

FIGURE 1 Mean and standard errors bars for mutual eye gaze (a) duration, (b) frequency, and (c) bout length in mother-reared and nursery-reared olive baboons (*Papio anubis*). The asterisk indicates significance at the $p < .05$ level.

$p = .392$. Specifically, MR baboons had higher MEG duration and bout lengths compared to NR individuals (see Figure 1). In addition, univariate analyses revealed a significant effect of sex on mean frequency $F(1, 111) = 10.013$, $p = .002$, with females (mean = 11.918, SE = 0.274, $n = 93$) exhibiting higher mean frequency than males (mean = 9.958, SE = 0.555, $n = 23$). To determine the influence of age on MEG measures, we performed a partial correlation analysis. After controlling for sex and rearing, age was found to have a negative association with mean frequency ($r(df = 112) = -0.194$, $p = .039$), indicating that as baboons age, MEG frequency decreases. There was no significant relationship between age and MEG duration or bout length ($p > .05$).

4 | DISCUSSION

4.1 | Mutual eye gaze measures

The results from this study indicate that rearing experiences affect average bout length of MEG among olive baboons. Specifically, MR baboons engaged in significantly longer bouts of MEG compared to NR baboons. This finding is contrary to our first hypothesis that NR baboons would be more inclined to engage in MEG with a human observer than MR baboons. Additionally, the results from this study differ from previous findings in chimpanzees, which show that NR chimpanzees engaged in longer bouts of MEG than both MR and wild-born individuals (Hopkins et al., 2020). One possible explanation for our results could be that when baboon infants are raised by their biological mothers, mothers may engage in frequent MEG with the infants, whereas in the nursery setting, human caretakers do not engage in frequent, sustained MEG with baboon infants. Mother–infant MEG has been described in apes (e.g., (Bard, 1994; Kaplan & Rogers, 2002) and rhesus macaques (Ferrari et al., 2009), though future research involving additional primate taxa, such as baboons, may shed light on the natural variation of this behavior.

The discrepancy in the impact of rearing on MEG between baboons and chimpanzees (Hopkins et al., 2020) may suggest that rearing impacts MEG in a species-specific manner that potentially reflects different functions of gaze in these two primate species. For instance, mutual eye gaze may have affiliative functions in chimpanzee communication but may serve as an agonistic cue among baboons. Indeed, among captive rhesus macaques (*Macaca mulatta*), eye gaze is believed to be distressing, such that the human intruder test—a test initially designed to measure defensive behavior in infant rhesus macaques (Kalin & Shelton, 1989), which has since been used to measure anxiety and fear (Bethea et al., 2004; Corcoran et al., 2012), behavioral inhibition (Rogers et al., 2008), and aggression (Minier et al., 2011)—often includes a stare phase in which a human observer attempts to make a direct eye contact with the subject. Rhesus macaques tested under the human intruder paradigm have shown increased threat displays (Bethea et al., 2004; Corcoran et al., 2012) and defensive or inhibitory behaviors such as freezing (defined as >3 s of immobility with a tense posture) (Corcoran et al., 2012; Rogers et al., 2008). Furthermore, at least one of these studies shows that rearing history affects responses to the human intruder paradigm with NR macaques showing a decrease in locomotory and exploratory behaviors and a slight increase in freezing compared to MR macaques (Corcoran et al., 2012). Because this study did not record threats or defensive behaviors, it is possible that the tendency to maintain eye contact (i.e., to stare back at the human observer) is an agonistic behavior in baboons rather than an affiliative one. However, the baboons in this study had extensive exposure to the human observer prior to MEG test sessions, the observer was already seated outside the enclosure window when baboon subjects voluntarily approached, and anecdotally, threat behaviors occurred infrequently during this study.

4.2 | Heritability

MEG measures in this study showed relatively low heritability, with only one of the three MEG measures being significantly heritable. This finding partially supports our hypothesis, suggesting that genetic factors potentially play a small role in explaining individual variation in mean bout length among baboons. Given that mean frequency was the one MEG measure that did not significantly differ between MR and NR baboons according to the univariate analyses, it is possible that there was not enough individual variation in this measure to detect stronger heritability. These findings mirror previous research on the heritability of MEG measures in chimpanzees reporting low heritability (Hopkins et al., 2020). Based on the rearing effects found in this study, and the low heritability values, it appears that early life social experiences—such as rearing history—may play a larger role in shaping patterns of MEG. However, our results indicate that genetic factors may explain part of the observed variation as well. This is consistent with other lines of research on heritable measures of temperament and behavioral reactivity in baboons (e.g., behavioral inhibition and vigilance: Rogers et al., 2008).

5 | CONCLUSIONS

Overall, this study shows that social experiences early in life—namely, cross-species rearing histories—influence patterns of MEG among captive olive baboons. Additionally, MEG measures in this study showed low heritability even for the one significantly heritable measure, which is interesting given the accumulating evidence that eye gaze has strong evolutionary foundations among primates. One interpretation of this finding is that social learning and early life social experiences may play a more determining role in shaping patterns of MEG than genetic factors. A limitation of this study is that we quantified MEG between a baboon and a human observer rather than between conspecifics. This limitation may affect the ecological validity of our results. However, measuring MEG with a human observer allows for standardized data collection and is consistent with previous MEG research with nonhuman primates (Hopkins et al., 2020; Mulholland et al., 2020). Despite this concern, subsequent research on naturally occurring mutual eye gaze between mother–infant dyads within the first year of life considered alongside the results of this study may contribute to our understanding of how social learning and conspecific interactions affect eye gaze. Additionally, research on the neuroanatomical basis of mutual eye gaze and on DNA methylation for genes associated with social behavior (e.g., vasopressin and oxytocin receptors: King & Young, 2016) may shed light on the mechanisms that govern interactions between early social environments and behavioral/brain phenotypes in primates.

ACKNOWLEDGMENTS

This work was supported, in part, by the National Institutes of Health (grant numbers HD-103490 and NIH OD-024628) and the National Science Foundation (grant number 2021711). Michele M. Mulholland is funded by NIH grant AG-078411. All work was approved by the Institutional Animal Care and Use Committee at The University of Texas MD Anderson Cancer Center. The authors thank the reviewer and editorial board for their insightful comments which enhanced this article.

CONFLICT OF INTEREST STATEMENT

the authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Angela M. Achorn https://orcid.org/0000-0002-3425-2551
Michele M. Mulholland https://orcid.org/0000-0003-1957-0436

REFERENCES

Almasy, L., & Blangero, J. (1998). Multipoint quantitative-trait linkage analysis in general pedigrees. *The American Journal of Human Genetics*, *62*(5), 1198–1211. https://doi.org/10.1086/301844

Amici, F., Aureli, F., Visalberghi, E., & Call, J. (2009). Spider monkeys (*Ateles geoffroyi*) and capuchin monkeys (*Cebus apella*) follow gaze around barriers: Evidence for perspective taking? *Journal of Comparative Psychology (1983)*, *123*(4), 368–374. https://doi.org/10.1037/a0017079

Anderson, J. R., & Mitchell, R. W. (1999). Macaques but not lemurs co-orient visually with humans. *Folia Primatologica*, *70*(1), 17–22. https://doi.org/10.1159/000021670

Bard, K. A. (1994). Evolutionary roots of intuitive parenting: Maternal competence in chimpanzees. *Early Development & Parenting*, *3*(1), 19–28. https://doi.org/10.1002/edp.2430030104

Bethea, C. L., Streicher, J. M., Coleman, K., Pau, F. K. Y., Moessner, R., & Cameron, J. L. (2004). Anxious behavior and fenfluramine-induced prolactin secretion in young rhesus macaques with different alleles of the serotonin reuptake transporter polymorphism (5HTTLPR). *Behavior Genetics*, *34*(3), 295–307. https://doi.org/10.1023/B:BEGE.0000017873.61607.be

Bräuer, J., Call, J., & Tomasello, M. (2005). All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology (1983)*, *119*(2), 145–154. https://doi.org/10.1037/0735-7036.119.2.145

Brent, L., & Bode, A. (2006). Baboon nursery rearing practices and comparisons between nursery-reared and mother-reared individuals. In G. P. Sackett, G. C. Ruppentahal, & K. Elias (Eds.), *Nursery rearing of nonhuman primates in the 21st century* (pp. 269–288). Springer US.

Burkart, J., & Heschl, A. (2006). Geometrical gaze following in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology (1983)*, *120*(2), 120–130. https://doi.org/10.1037/0735-7036.120.2.120

Corcoran, C. A., Pierre, P. J., Haddad, T., Bice, C., Suomi, S. J., Grant, K. A., Friedman, D. P., & Bennett, A. J. (2012). Long-term effects of differential early rearing in rhesus macaques: Behavioral reactivity in adulthood. *Developmental Psychobiology*, *54*(5), 546–555. https://doi.org/10.1002/dev.20613

Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, *24*, 581–604.

Farran, D. C., & Kasari, C. (1990). A longitudinal analysis of the development of synchrony in mutual gaze in mother-child dyads. *Journal of Applied Developmental Psychology*, *11*(4), 419–430. https://doi.org/10.1016/0193-3973(90)90018-F

Fears, S. C., Melega, W. P., Service, S. K., Lee, C., Chen, K., Tu, Z., Jorgensen, M. J., Fairbanks, L. A., Cantor, R. M., Freimer, N. B., & Woods, R. P. (2009). Identifying heritable brain phenotypes in an extended pedigree of vervet monkeys. *The Journal of Neuroscience*, *29*(9), 2867–2875. https://doi.org/10.1523/jneurosci.5153-08.2009

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*(1), 1–47. https://doi.org/10.1093/cercor/1.1.1

Ferrari, P. F., Paukner, A., Ionica, C., & Suomi, S. J. (2009). Reciprocal face-to-face communication between rhesus macaque mothers and their newborn infants. *Current Biology*, *19*(20), 1768–1772. https://doi.org/10.1016/j.cub.2009.08.055

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*, 1325–1330. http://www.boris.unito.it/pages/download.html

Grossmann, T. (2017). The eyes as windows into other minds: An integrative perspective. *Perspectives on Psychological Science*, *12*(1), 107–121. https://doi.org/10.1177/1745691616654457

Hopkins, W. D., Mulholland, M. M., Reamer, L. A., Mareno, M. C., & Schapiro, S. J. (2020). The role of early social rearing, neurological, and genetic factors on individual differences in mutual eye gaze among captive chimpanzees. *Scientific Reports*, *10*(1), 7412. https://doi.org/10.1038/s41598-020-64051-y

Hopkins, W. D., Russell, J. L., & Schaeffer, J. (2014). Chimpanzee intelligence is heritable. *Current Biology*, *24*(14), 1649–1652. https://doi.org/10.1016/j.cub.2014.05.076

Kaas, J. H., & Balaram, P. (2014). Current research on the organization and function of the visual system in primates. *Eye and Brain*, *6*, 1–4. https://doi.org/10.2147/EB.S64016

Kalin, N. H., & Shelton, S. E. (1989). Defensive behaviors in infant rhesus monkeys: Environmental cues and neurochemical regulation. *Science*, *243*, 1718–1721. https://doi.org/10.1126/science.2564702

Kano, F., Hirata, S., & Call, J. (2015). Social attention in the two species of pan: Bonobos make more eye contact than chimpanzees. *PLoS One*, *10*(6), e0129684–e0129684. https://doi.org/10.1371/journal.pone.0129684

Kaplan, G., & Rogers, L. J. (2002). Patterns of gazing in orangutans (*Pongo pygmaeus*). *International Journal of Primatology*, *23*(3), 501–526.

King, L. B., & Young, L. J. (2016). Oxytocin, vasopressin, and diversity in social behavior. In D. Murphy & H. Gainer (Eds.), *Molecular neuroendocrinology: From genome to physiology* (pp. 423–441). John Wiley & Sons, Incorporated.

Kochunov, P., Glahn, D. C., Fox, P. T., Lancaster, J. L., Saleem, K., Shelledy, W., Zilles, K., Thompson, P. M., Coulon, O., Mangin, J. F., Blangero, J., & Rogers, J. (2010). Genetics of primary cerebral gyrification: Heritability of length, depth and area of primary sulci in an extended pedigree of Papio baboons. *Neuroimage*, *53*(3), 1126–1134. https://doi.org/10.1016/j.neuroimage.2009.12.045

Minier, D. E., Tatum, L., Gottlieb, D. H., Cameron, A., Snarr, J., Elliot, R., Cook, A., Elliot, K., Banta, K., Heagerty, A., & McCowan, B. (2011). Human-directed contra-aggression training using positive reinforcement with single and multiple trainers for indoor-housed rhesus macaques. *Applied Animal Behaviour Science*, *132*, 178–186. https://doi.org/10.1016/j.applanim.2011.04.009

Mulholland, M. M., Mahovetz, L. M., Mareno, M. C., Reamer, L. A., Schapiro, S. J., & Hopkins, W. D. (2020). Differences in the mutual eye gaze of bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *134*(3), 318–322. https://doi.org/10.1037/com0000247

Niedźwiecka, A., Ramotowska, S., & Tomalski, P. (2018). Mutual gaze during early mother–infant interactions promotes attention control development. *Child Development*, *89*(6), 2230–2244. https://doi.org/10.1111/cdev.12830

Rogers, J., Shelton, S. E., Shelledy, W., Garcia, R., & Kalin, N. H. (2008). Genetic influences on behavioral inhibition and anxiety in juvenile rhesus macaques. *Genes, Brain, and Behavior*, *7*(4), 463–469. https://doi.org/10.1111/j.1601-183X.2007.00381.x

Rosati, A. G., & Hare, B. (2009). Looking past the model species: Diversity in gaze-following skills across primates. *Current Opinion in Neurobiology*, *19*(1), 45–51. https://doi.org/10.1016/j.conb.2009.03.002

Ruiz, A., Gómez, J. C., Roeder, J. J., & Byrne, R. W. (2009). Gaze following and gaze priming in lemurs. *Animal Cognition*, *12*(3), 427–434. https://doi.org/10.1007/s10071-008-0202-z

Senju, A., Vernetti, A., Ganea, N., Hudry, K., Tucker, L., Charman, T., & Johnson, M. H (2015). Early social experience affects the development of eye gaze processing. *Current Biology*, *25*(23), 3086–3091. https://doi.org/10.1016/j.cub.2015.10.019

Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, *55*(4), 1063–1069. https://doi.org/10.1006/anbe.1997.0636

Tomasello, M., Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze following of great apes and human infants: The cooperative eye hypothesis. *Journal of Human Evolution*, *52*(3), 314–320. https://doi.org/10.1016/j.jhevol.2006.10.001

How to cite this article: Achorn, A. M., Mulholland, M. M., & Hopkins, W. D. (2023). The effects of early rearing experiences on mutual eye gaze among captive olive baboons (*Papio anubis*). *Developmental Psychobiology*, *65*, e22420. https://doi.org/10.1002/dev.22420