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Group Differences in the Mutual Gaze of Chimpanzees (*Pan Troglodytes*)

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A comparative developmental framework was used to determine whether mutual gaze is unique to humans and, if not, whether common mechanisms support the development of mutual gaze in chimpanzees and humans. Mother–infant chimpanzees engaged in approximately 17 instances of mutual gaze per hour. Mutual gaze occurred in positive, nonagonistic contexts. Mother–infant chimpanzees at a Japanese center exhibited significantly more mutual gaze than those at a center in the United States. Cradling and motor stimulation varied across groups. Time spent cradling infants was inversely related to mutual gaze. It is suggested that in primates, mutual engagement is supported via an interchangeability of tactile and visual modalities. The importance of mutual gaze is best understood within a perspective that embraces both cross-species and cross-cultural data.

Keywords: mother–infant, communication, face-to-face, eye contact, intersubjectivity

In the 1970s, developmental psychologists reported on 2-month-old infants' contribution to sustaining mutual engagement. These face-to-face interactions were variously labeled *communicative dance*, *protoconversation*, *entrainment and enculturation*, and *affect attunement* (Bullowa, 1979), but the importance of mutual gaze was noted consistently. Mutual gaze can function as the occasion setter or the marker of the peak of the communication when vocal greetings and smiles occur (Bullowa, 1979; Stern, 1974; Trevarthen & Aitken, 2001). It was implicitly assumed that these interactions were uniquely human. Chimpanzees continue to be regarded as lacking mutual gaze (Hobson, 2002, p. 270) and lacking many of the consequent social functions of eye gaze (Povinelli & Eddy, 1996; Tomasello, 1999). Here we present developmental evidence on the existence of mutual gaze in chimpanzees. Furthermore, the comparison of mutual gaze in two chimpanzee groups documents flexibility in development as a function of parenting characteristics. The comparative developmental framework allows for the specification of whether a characteristic such as mutual gaze is universal (species typical) and unique to humans (species unique).

It has been assumed that eye-to-eye contact occurs in agnostic encounters and not in positive social interactions for nonhuman primates (e.g., Kaplan & Rogers, 2002). Although it is true that direct eye contact with an adult rhesus monkey often elicits a threat, primate species differ both in their agonistic propensity and in the extent to which mutual gaze occurs in prosocial contexts (Bard, 2002). In Japanese macaques, for example, mutual gaze occurs between mothers and infants, but curiously, it is reported

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when infants begin to walk independently (Ehardt & Blount, 1984). Mutual gaze is reported to occur between mother and infant chimpanzees in the wild (van Lawick-Goodall, 1968) and in captivity (Bard, 1994). Human and chimpanzee newborns prefer to look at a face that is gazing at them (Farroni, Csibra, Simion, & Johnson, 2002; Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2003). As adults, some primates use brief eye contact to convey communicative signals (appeasement, sexual interest, and aggression), but sustained eye contact is rare (Kaplan & Rogers, 2002; Kummer, 1968). Exceptionally, some chimpanzees use sustained mutual gaze to initiate reconciliations (de Waal, 2001).

Mutual gaze between mothers and infants is actively nurtured in many human cultures (Bullowa, 1979), although there are wide cultural variations (Keller et al., 2004; Ochs & Schieffelin, 1984). Caregivers encourage eye gaze patterns, as they nurture and support other and different forms of communication, through unconscious, intuitive parenting behaviors (Bullowa, 1979; Keller, Scholmerich, & Eibl-Eiblesfeldt, 1988; Papousek & Papousek, 1987; Trevarthen & Aitken, 2001). Early socialization of eye gaze patterns in human cultures is strongly influenced by (or most easily understood as reflecting) cultural values (Keller, 2003). When traditional subsistence cultures value social cooperation, interdependence, and an apprentice model of developing competence, early parenting practices focus on interpersonal proximity (i.e., emotionally warm physical contact) and motor development stimulation. This focus on physical contact seems to minimize mutual gaze. Although mutual engagement is important, the modality of engagement in traditional societies is primarily tactile (both passive as in cradling contact and active as in motoric stimulation). In traditional societies, "Eye contact, object play and contingency toward positive infant signals occur as well, yet they are not the caregivers' priorities" (Keller, 2003, p. 295). When Western industrial cultures value independence, individual achievements, and an equality model of developing competence, early parenting practices focus on establishing self-regulation and a communicative dialogue. This focus depends crucially on mutual gaze (Keller, 2003). In industrialized societies, the visual modality is emphasized for mutual engagement (such as in face-to-face protoconversations and object play).

Chimpanzee mothers also encourage and support their infants' developing social, communicative, and motor competencies but primarily through the tactile modality (Bard, 1994, 2002). Early communication, evident during play and prelinguistic gestural development, is nurtured through tactile means in many nonhuman primates (Plooij, 1979; van Lawick-Goodall, 1968), and also in some human cultures (Sorenson, 1979; Stack, 2001). Supportive evidence on the importance of the tactile modality in humans includes observations from natural perturbations of the human communication system, such as blindness (Adamson, 1995) and, surprisingly, deafness. Caregivers of blind babies engage in large amounts of tactile and kinesthetic stimulation, which set the occasion for social smiles and an increased use of communicative touch (Fraiberg, 1971). Even though the visual system is intact in babies without hearing, mothers of deaf babies use touch and kinesthetics in face-to-face interactions significantly more than mothers of hearing infants (Koester, 1994). Contact comfort has been found to be important in the early socioemotional development of rhesus monkeys (Harlow, 1958) and human infants, especially those born prematurely, who benefit from tactile stimulation (Field, McCabe, & Schneiderman, 1992). The comparative data, therefore, suggest that mutual engagement via the tactile mode is the primate foundation for engagement.

The comparative study of developmental processes in closely related primate species (i.e., humans and chimpanzees) is useful for a variety of reasons, but it is essential to determine species-unique characteristics. Although the evidence suggests that mutual gaze between infant and caregiver is a human universal, the study of nonhuman primates is necessary to determine if mutual gaze is unique to humans. Perhaps it is not mutual gaze, per se, but the appearance of mutual gaze within a positive communicative setting that is unique to the human species. Therefore, we have chosen to study chimpanzees, an evolutionarily closely related species that shares with humans a rich communicative environment early in infancy. We can further our understanding of the function of mutual gaze in early face-to-face communicative exchanges by using evidence gathered from both comparative perspectives (i.e., by studying mutual gaze in non-Western human cultures; e.g., Keller, 2003) and in other primate species (as in this study). These comparison groups disentangle those variables that are confounded in the prototypic instance: the Western mother–infant pair (Rogoff & Morelli, 1989).

The aims of this study were to describe the development of mutual gaze in chimpanzees and to compare development of mutual gaze across two chimpanzee groups to investigate, for example, how chimpanzee mothers participate in the "socialization of attention" (Tomasello, 1999, p. 35). Differences existed in the eye gaze patterns among adult chimpanzees in the two laboratory settings of this study. At the U.S. center, adult chimpanzees used infrequent and brief eye-to-eye contact in their interactions with other adults (Bard, 1994). In contrast, at the Japanese center, sustained eye gaze was found among adult chimpanzees (M. Tomonaga personal communication, July 2001). The substantial differences in the social lives of the chimpanzees at each site, including differences in the extent of human contact, could be linked with existing adult eye gaze patterns (Tomonaga et al., 2004). Although mutual gaze has been found to occur between adult chimpanzees, we do not fully understand the processes by which mutual gaze develops through early mother–infant interactions in chimpanzees.

An ethological approach is advocated that combines developmental data (describing changes in mutual gaze across the first 3 months of life) with comparative data (documenting mutual gaze and parenting behaviors across different groups of nonhuman primates), to provide quantitative data on flexibility in the development of mutual gaze in chimpanzees. If early mother–infant interactions in chimpanzees can be characterized as primarily prosocial and positive, as is found in humans, then we can determine which behaviors, if any, are linked with mutual gaze in chimpanzees. We expect to identify those intuitive parenting behaviors that chimpanzees use to nurture infant development, specifically development of group-specific eye gaze patterns. We expect group differences in mutual gaze to be accompanied by group differences in cradling contact and motor development stimulation, based on evidence from non-Western human cultures. The comparative developmental framework of this study contributes toward the disentanglement of variables to better understand the socialization of attention.

Method

Participants

One part of the study took place at the Yerkes National Primate Research Center at Emory University. Of the 30 female chimpanzees (*Pan troglodytes*) who gave birth to live offspring at Yerkes from 1987 through 1992, only 9 consistently provided adequate maternal care through the infants' first 3 months. Observations from 8 mother–infant pairs are reported here (see Table 1 for demographic information for chimpanzee mothers and infants), which combine mother–infant pairs from a previous report (n = 5 from Bard, 1994), with three newly reported mother–infant pairs. Food was thrown into the cage twice a day, water was always available, living areas were hosed twice daily and scrubbed biweekly, and additional interactions with humans were minimal. Early rearing histories of the Yerkes mothers varied: Three were hand raised, 2 were probably wild born, and 2 were mother raised. There was no predictable relation between early rearing history (0–18 months) and maternal competence (Bard, 2002).

The other part of the study took place at the Primate Research Institute (PRI), Kyoto University, Inuyama City, Japan. All PRI chimpanzee (*Pan troglodytes*) mothers, who provided adequate maternal care from 1983 to 2000, were videotaped and used in this study (n = 3). Mothers lived in a social group of 11 individuals in an enriched outdoor compound (Ochiai & Matsuzawa, 1998) prior to giving birth. Before giving birth, these mothers interacted with humans for several hours each day, exchanging food, drink, socialization, and toys (Matsuzawa, 2001). Early histories of the PRI mothers varied: One was hand raised, 1 was captive born and mother raised, and 1 was wild born.

Procedures

Naturalistic observations of each mother and infant were videotaped for later detailed microanalysis. Observations occurred when mothers were in their living areas (i.e., not in testing areas), with no restrictions to their activity and with no humans present. One hour of videotape was selected when infants were 2–4 weeks of age (1 month), another hour at 6–8 weeks of age (2 months), and a third hour at 10–12 weeks of age (3 months), as in Bard (1994).

Behavioral coding system. Microanalyses were conducted to document (a) the focus of maternal gaze and (b) the interactive context.

Table 1
Demographic Information for Chimpanzee Mothers and Infants

Mother/Infant	Infant DOB	Infant sex	Previous live offspring
	Yerkes group		
Joice/Olin	Feb. 1988	Male	2
Leslie/Dara	Jul. 1988	Female	1
Vivienne/Wilma	Nov. 1988	Female	1
Barbi/Elvira	Nov. 1988	Female	0
Lil'One/Pollyanna[a]	Mar. 1989	Female	3
Cynthia/Alicia	Jul. 1989	Female	0
Cissie/Travis[a]	Aug. 1989	Male	0
Tai/Daisey[a]	Oct. 1989	Female	4
	PRI group		
Ai/Ayumu[a]	Apr. 2000	Male	0
Chloe/Cleo[a]	Jun. 2000	Female	0
Pan/Pal[a]	Aug. 2000	Female	0

Note. DOB = date of birth; PRI = Primate Research Institute.
[a] Indicates new data from previously unobserved individuals.

Maternal gaze was classified in one of three mutually exclusive and exhaustive categories (at the infant's body, at the infant's face, or not looking at the infant). When mothers looked at their infant's face, a yes–no decision was made as to whether the infant looked at the mother's face (if yes, then mutual gaze was recorded, which is identical to the definition used with humans). Maternal visual attention was the sum of time looking at the infant. For photos exhibiting visual attention, see http://dx.doi.org/10.1037/0012-1649.41.4.XXX.supp

The *interactive context* was classified into mutually exclusive and exhaustive categories (Bard, 1994). These interactive contexts were organized, as detailed below, to address the study of (a) visual exploration, (b) positive versus negative quality of interactions, (c) physical contact, and (d) motor development stimulation. Visual exploration of the infant was assessed with the interactive behaviors of grooming and assess/examine. *Grooming* was defined as a positive interaction consisting of stroking the infant's hair or cleaning of debris from hair or skin. *Assess* was the combined category, defined as checking the infant's state, muscle tone, or both with tactile monitoring (assess) or with visual monitoring (examine).

Active positive interactions included play and soothe/caress/safeguard. *Play* was defined with the typical definition of activity accompanied by smiles or laughter (Bard, 1998). *Soothe* was defined as behavior that calmed a distressed infant. *Caress* was defined as touching gently with hands or lips (e.g., kisses). *Safeguard* was defined as protecting the infant from harm (e.g., preventing the infant from falling or moving the infant away from the touch of another). Soothe, caress, and safeguard were combined into a single category because these behaviors were similar in emotional tone and each occurred at low frequency. Visual explorations were also considered positive in emotional quality.

Active negative interactions included aggression, restrain, and hold. Although aggressive behaviors were not observed, the negative emotional context was indexed with restrain and hold, as infants' reacted negatively to these maternal actions. *Restrain* was defined as preventing the infant from moving off the mother's body. *Hold* was defined as grasping an arm, leg, or the body. These were combined into a single category, reducing the degree of individual differences among the mothers.

Physical contact was measured with cradling. *Cradling* was defined as any maternal behavior that provided physical support of the infant and/or maintenance of physical contact. Note that cradling was only recorded when no other interactive behavior occurred.

Motor development stimulation was measured with exercise and reposition. *Exercise* was defined as encouraging motor development with kinesthetic stimulation, or engagement in physical activity, such as assisting the infants in supporting their own weight with their legs. *Reposition* was defined as moving the infant to a different location either on the mother's body or off the mother's body.

Data summary. Cradling and maternal gaze were calculated as percentages of visible time, because chimpanzees were occasionally not visible. The number of instances of mutual gaze was determined for each session, and the rate of mutual gaze per hour was calculated. Interactive contexts were calculated as percentage of noncradling time so as to reduce the influence of any differences attributable to time spent cradling.

Observer agreement. Eye gaze was coded by three different coders: Six sessions were coded by a team (JQ + JS = J + J), 10 sessions were coded by JQ alone, and 2 sessions were coded by KB (who coded in Bard, 1994). Eye gaze in chimpanzees can be difficult to observe because of the dark sclera in the eyes of chimpanzees and a small-sized infant, typically held protectively by the mother. Training of observers and assessments of interrater reliability were therefore essential (Bakeman & Gottman, 1986). Good to excellent agreement was determined between all pairs of observers for the analyses of eye gaze (including checking reliability with coders from the Bard, 1994, study). The team of J + J with CH (a coder from previous research, Bard, 1994) achieved 89% observed agreement, with a Cohen's kappa of 0.66. The team of J + J compared with JQ achieved observed agreement of 88%, with a Cohen's kappa of 0.78. The primary

coder from the current study (JQ) with KB (another coder from Bard, 1994) achieved observed agreement of 84%, with a Cohen's kappa of 0.73. KB coded all new sessions of interactive context. Second-by-second comparisons with the categorization from two sessions (120 min) coded by Bard (1994) revealed good-to-excellent intrarater agreement: Observed agreement was 82%, and Cohen's kappa was 0.71.

Results

The present study confirmed previous evidence that mutual gaze occurs in mother-raised chimpanzees ($M = 16.9$ times per hour, $SE = 2.0$). Moreover, as is clearly depicted in Figure 1, mutual gaze occurred in chimpanzees when infants were 1-, 2-, and 3-months and in chimpanzees at both centers. There was a significant group difference: A higher rate of mutual gaze was found at PRI (22 per hour, $SE = 3.4$) than at Yerkes (12 per hour, $SE = 2.1$), $F(1, 9) = 6.52$, $p < .05$, $\eta^2 = .42$. Developmental differences were not significant, $F(2, 18) = 1.62$, *ns*, $\eta^2 = .15$, nor was there a significant interaction between group and age, $F(2, 18) = 1.30$, *ns*, $\eta^2 = .13$.

Is Mutual Gaze a By-Product of Maternal Visual Attention or Maternal Visual Exploration?

We were interested in specifying the maternal interactive behaviors that support mutual gaze (see Table 2). Perhaps mutual gaze was a by-product of maternal activities that involved visual attention to the infant. First, we asked whether the group difference in mutual gaze was a function of how much the mother looked at the baby. Mothers looked at their infant's body 14% of the time ($SE = 2.2$), which did not differ by group, $F(1, 9) = 0.27$, *ns*, $\eta^2 = .03$; by infant age, $F(2, 18) = 0.50$, $\eta^2 = .05$; or as a function of the interaction of Group × Age, $F(2, 18) = 0.92$, *ns*, $\eta^2 = .09$. Mothers looked at their infant's face for an average of 11% of the time ($SE = 1.4$), which did not differ by group, $F(1, 9) = 0.49$, *ns*, $\eta^2 = .05$; by infant age, $F(2, 18) = 1.26$, *ns*, $\eta^2 = .12$; or as a function of Group × Age, $F(2, 18) = 0.30$, *ns*, $\eta^2 = .03$. Clearly the group difference in mutual gaze was not a function of how much mothers looked at their infants, but rather there were differences in the actions of the mother during the times when mothers were looking at their infant's face. Chimpanzee mothers at PRI appeared to actively encourage mutual gaze by tilting or holding up the infant's chin with their finger while looking into their infant's eyes (see http://dx.doi.org/10.1037/0012-1649.41.4.XXX.supp). This behavior occurred in each of the PRI mothers with their 3-month-old infants but was not observed to occur in any Yerkes mother.

Although group differences in mutual gaze could not be explained by maternal visual attention, it was nevertheless possible that mutual gaze was a by-product of particular interactive con-

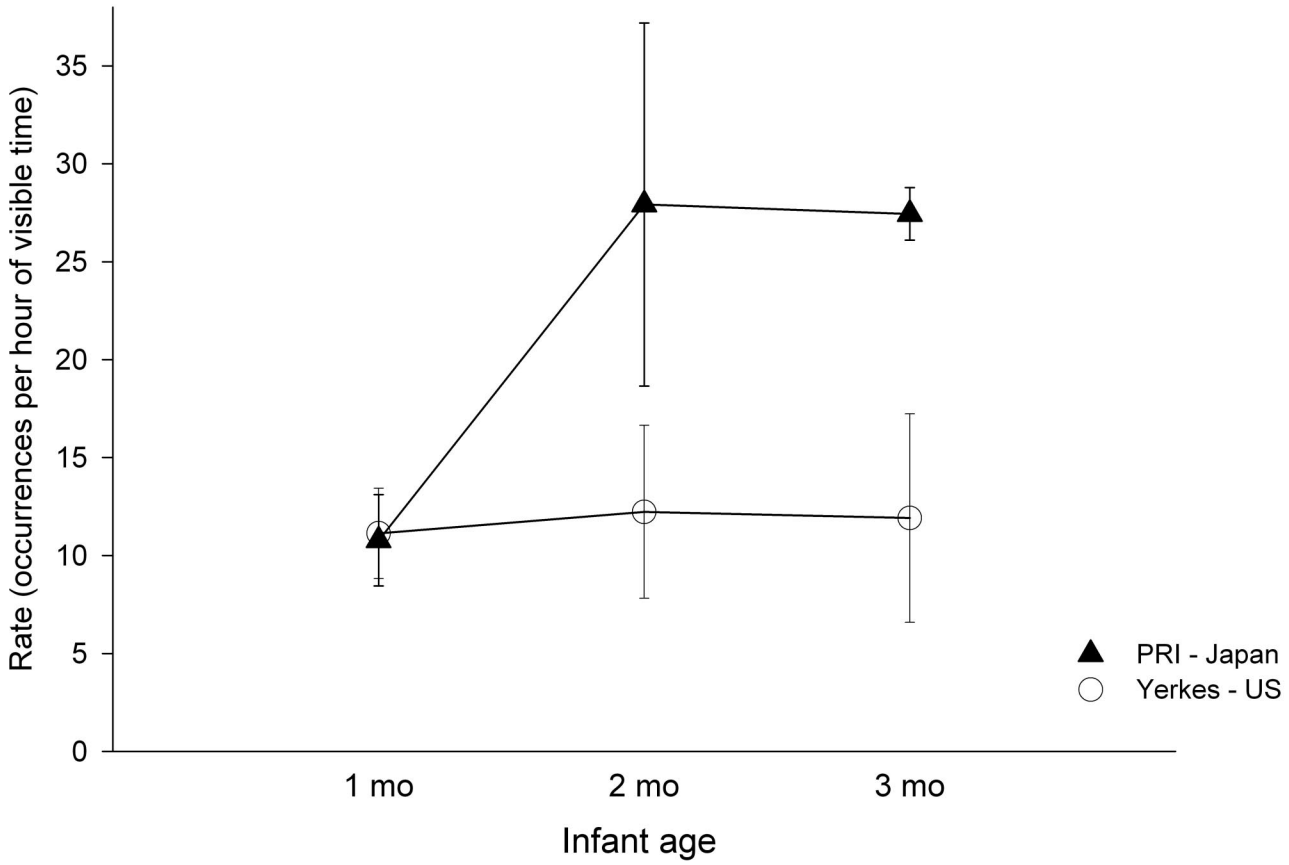

Figure 1. Rate of mutual gaze (mean ± standard error) in mother–infant chimpanzee pairs in the first 3 months of life differs by group. Mother–infant chimpanzee pairs at the Primate Research Institute (PRI) have a significantly higher rate of mutual gaze than do mother–infant pairs at Yerkes National Primate Research Center.

Table 2
Maternal Interactive Behaviors of Chimpanzees From Two Settings With Their 1-, 2-, and 3-Month-Old Infants

	Yerkes						PRI						Significance		
	Month 1		Month 2		Month 3		Month 1		Month 2		Month 3				
Behavior	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	Group	Age	GpxA
M visual attention															
To I's body	15.7	9.6	13.2	8.7	16.7	11.5	8.0	0.4	16.0	9.2	14.5	5.9	*ns*	*ns*	*ns*
To I's face	11.1	6.6	11.1	7.3	7.7	7.5	11.3	11.4	16.4	10.8	8.1	1.6	*ns*	*ns*	*ns*
Visual exploration															
Assess/examine	24.2	24.5	13.6	17.6	6.6	5.2	42.1	31.6	20.3	7.4	6.0	3.0	*ns*	*	*ns*
Groom	31.0	26.4	28.8	29.1	38.5	23.6	13.6	14.5	34.7	13.5	16.4	11.9	*ns*	*ns*	*ns*
Emotional contexts															
Play	17.4	19.1	15.3	23.5	14.2	19.9	2.3	2.9	11.3	6.9	15.7	11.1	*ns*	*ns*	*ns*
Soothe/safeguard	3.4	0.9	6.9	12.9	3.3	3.5	14.5	16.3	4.1	2.0	8.0	3.3	*ns*	*ns*	*ns*
Restrain/hold	13.3	15.6	12.8	17.9	26.5	18.2	10.9	10.6	3.3	1.1	14.1	8.1	*ns*	*ns*	*ns*
Cradling	77.2	5.7	68.6	17.6	71.4	17.3	87.3	2.9	53.5	3.7	39.5	8.4	†	***	***
Motor stimulation															
Exercise	5.4	7.9	17.8	29.0	6.5	8.4	1.6	2.8	11.5	14.7	33.1	16.2	*ns*	†	**
Reposition	5.2	2.6	4.7	3.6	4.4	3.6	14.6	8.5	9.1	9.0	6.6	3.3	*	*ns*	*ns*

Note. M = mother; I = infant. Cradling and visual attention are computed from total observation time; all other interactive behaviors are computed as a percentage of noncradling observation time.
† $p < .10$. * $p < .05$. ** $p < .01$. *** $p < .001$.

texts that involved visual exploration of the infant. So two analyses were conducted on interactive behaviors: (a) A mixed analysis of variance (with age as the repeated measure and group as the between-subjects measure) and (b) a correlation analysis between the rate of mutual gaze and time spent in interactive behavior at 3 months.

Chimpanzee mothers spent 17% ($SE = 3.7$) of their interactive time assessing and examining the behavioral and physical state of their infants. There was a significant main effect of age, $F(2, 16) = 4.80$, $p < .02$, $\eta^2 = .37$, with significant contrasts. There were higher levels of assessing at 1 month ($M = 33\%$, $SE = 9.1$) compared with at 3 months ($M = 6\%$, $SE = 1.6$), $F(1, 8) = 7.34$, $p < .03$, $\eta^2 = .48$, with a trend of more assessing at 2 months ($M = 17\%$, $SE = 5.4$) than at 3 months, $F(1, 8) = 4.84$, $p = .06$, $\eta^2 = .38$. There were no group differences, $F(1, 8) = 1.22$, *ns*, $\eta^2 = .13$, and no interaction of age differences by group, $F(2, 16) = 0.57$, *ns*, $\eta^2 = .07$. The amount of time mothers spent assessing their 3-month-old infants was not related to rate of mutual gaze, $r(10) = .19$, *ns*.

Chimpanzee mothers spent approximately 29% ($SE = 4.3$) of their interactive time grooming their infants. There were no group differences, $F(1, 8) = 1.14$, *ns*, $\eta^2 = .12$; no age differences, $F(2, 16) = 0.37$, *ns*, $\eta^2 = .04$; and no interaction between group and age, $F(2, 16) = 0.92$, *ns*, $\eta^2 = .10$ (see Table 2). Amount of time spent grooming the infant was significantly but negatively correlated with rate of mutual gaze, $r(10) = -.64$, $p < .05$. In other words, those mothers who groomed at high levels engaged in less mutual gaze, whereas those who groomed less engaged in more mutual gaze. Thus, we conclude that group differences in mutual gaze were not a by-product of differential maternal visual attention to the infant (evident in looking at the infant's body or face) or differential maternal visual exploration of the infant (evident in assessing infant state or grooming).

Does Mutual Gaze in Chimpanzees Occur in Agonistic Interactions?

Chimpanzee mothers spent 14% ($SE = 3.2$) of their time playing with their infant and 7% ($SE = 1.5$) of the time soothing/caressing/safeguarding their infant. There were no instances of agonism in any mother–infant pair at either facility during these observations (i.e., when infants were 1, 2, and 3 months of age). There were no significant effects in play, by group $F(1, 8) = 0.73$, *ns*, $\eta^2 = .08$; by age $F(1.2, 10.1$, Geisser–Greenhouse correction$) = 0.16$, *ns*, $\eta^2 = .02$; or by Group × Age $F(1.2, 10.1$, Geisser–Greenhouse correction$) = 0.41$, *ns*, $\eta^2 = .05$. Play did not correlate significantly with mutual gaze, $r(10) = .56$, $p = .09$. There were no statistically significant effects in soothe, by group $F(1, 8) = 1.99$, *ns*, $\eta^2 = .20$; by age, $F(2, 16) = 0.43$, *ns*, $\eta^2 = .05$; or by Group × Age interaction, $F(2, 16) = 1.39$, *ns*, $\eta^2 = .15$. Soothe did not correlate with mutual gaze, $r(10) = .33$, *ns*. Chimpanzee mothers restrained their infants 15% ($SE = 2.9$) of the time, but restraint was not accompanied by any aggressive threats or physical punishment. There were no statistically significant effects in restrain by group, $F(1, 8) = 2.20$, *ns*, $\eta^2 = .22$; by age, $F(2, 16) = 1.23$, *ns*, $\eta^2 = .13$; or by Group × Age interaction, $F(2, 16) = 0.21$, *ns*, $\eta^2 = .03$. Restrain did not correlate with mutual gaze, $r(10) = -.39$, *ns*.

Mother chimpanzees spent 66% of their time engaged in positive social interactions with their 1-, 2-, and 3-month-old infants (groom, play, soothe, and assess combined) and only 15% of their time engaged in negative interactions (restrain). No agonism was observed. The context of mother–infant interactions was overwhelmingly positive. The trend for a correlation between play and mutual gaze supports the suggestion that mutual gaze occurs in prosocial contexts in chimpanzees. Prosocial behaviors were not significantly related to mutual gaze and so cannot explain group differences in mutual gaze.

Does Mutual Gaze Relate to Physical Contact or Motor Stimulation in Chimpanzees?

Overall, chimpanzee mothers spent 66% (SE = 2.8) of their time only cradling their infants. There was a significant main effect of age, $F(2, 16) = 11.09$, $p < .01$, $\eta^2 = .58$, and a significant interaction between age and group, $F(2, 16) = 6.21$, $p = .01$, $\eta^2 = .44$. A nonsignificant trend was found for the main effect of group, $F(1, 8) = 4.76$, $p = .061$, $\eta^2 = .37$. Planned contrasts confirmed that the interaction was due to significant group differences comparing 1-month with 2-month, $F(1, 8) = 5.49$, $p < .05$, $\eta^2 = .41$, and 1-month with 3-month, $F(1, 8) = 17.8$, $p < .01$, $\eta^2 = .69$. Chimpanzee mothers cradled their 1-month infants an average of 80% (SE = 2.2). At 3 months, PRI mothers cradled 40% of the time, which was significantly less than Yerkes mothers, who cradled 71% of the time, $F(1, 8) = 8.87$, $p = .018$, $.\eta^2 = .53$. Moreover, there was a significant inverse correlation between mutual gaze and time mothers spent cradling their 3-month infants, $r(10) = -.67$, $p < .05$.

Chimpanzee mothers engaged in motor stimulation of their infants in the forms of exercise (M = 12%, SE = 3.3) and repositioning (M = 6%, SE = 1.0). In exercising, a significant Age × Group interaction was found, $F(2, 16) = 3.65$, $p < .05$, $\eta^2 = .31$, with no effect of group, $F(1, 8) = 0.41$, ns, $\eta^2 = .05$, and a trend for an effect of age, $F(2, 16) = 3.02$, $p = .08$, $\eta^2 = .27$. Exercising increased from 1- to 3-months of age, $F(1, 8) = 20.32$, $p < .01$, $\eta^2 = .72$, but by 3 months of age, PRI mothers spent significantly more time exercising their infants (33%, SE = 6.3) than did Yerkes mothers (7%, SE = 4.1), confirmed with a planned contrast, $F(1, 8) = 17.59$, $p < .01$, $\eta^2 = .69$. At 3 months of age, a trend was found for a positive correlation between exercising and mutual gaze, $r(10) = 0.56$, $p = .094$. Chimpanzee mothers at PRI repositioned their infants significantly more (10%, SE = 1.6) than at Yerkes (5%, SE = 1.0), $F(1, 8) = 8.08$, $p = .02$, $\eta^2 = .50$. The amount of repositioning did not vary by age of the infant, $F(2, 16) = 1.98$, ns, $\eta^2 = .20$, or with an Age × Group interaction, $F(2, 16) = 1.32$, ns, $\eta^2 = .14$. Repositioning at 3 months of age did not correlate with mutual gaze, $r(10) = .02$, ns.

Significant group differences were found in measures of physical contact and motor development stimulation (see Table 2). Moreover, when infants were 3 months of age, these differences in physical contact and motor stimulation were related to mutual gaze (supported by a significant correlation between cradling and mutual gaze and a trend for a positive correlation between exercising and mutual gaze).

Discussion

Chimpanzee and human infants share commonalities in early social communicative exchanges (Bard, 2002; Matsuzawa, 2001; Plooij, 1979; van Lawick-Goodall, 1968), which can now be said to include mutual gaze. When observed naturalistically, mutual gaze occurs at comparable rates in 3-month-old humans (18 to 20/hr; Ling & Ling, 1974) and 3-month-old chimpanzees (17/hr; the current study). Moreover, mutual gaze in chimpanzees develops within a prosocial context, nurtured by some chimpanzee mothers through intuitive parenting behaviors (Bard, 1994, 2002). Of course, there are notable differences between chimpanzees and humans. These include (a) the duration of mutual gaze: Twenty percent of mutual gaze bouts with 3-month-old humans last longer than 6 s (Stern, 1974), whereas it appears that chimpanzees had no bouts longer than 6 s; (b) the amount of maternal looking at the infant: 100% for some human mothers (Adamson, 1995: Bullowa, 1979), compared with 25% for the chimpanzees in this study (Bard, 1994); and (c) the likely developmental course after 3 months (Tomonaga et al., 2004).

Intuitive parenting systems differ across cultures (Keller et al., 1988; Lavelli & Fogel, 2002; Papousek & Papousek, 1987; Trevarthen & Aitken, 2001) and across primate species (Bard, 2002; de Waal, 2001; Kaplan & Rogers, 2002: Kummer, 1968; Whitham & Maestripieri, 2003), which may support the observed group differences in mutual gaze in humans (Keller et al., 2004) and in chimpanzees (this study). If only one group of chimpanzees is compared with one group of humans, then all differences tend to be attributed to species differences. It is crucial to consider more than one group of each species, especially as plasticity is a hallmark of development in humans and great apes. When substantial overlap among groups is found, then one can gain a better understanding of the contributions of the gene–environment interaction in development (Garcia Coll, Bearer, & Lerner, 2004)

Mutual gaze between infant and caregiver is not unique to humans. It appears in chimpanzees (Bard, 1994; this study), in other apes (Kaplan & Rogers, 2002; Yamagiwa, 1992), and also in some monkeys (Ehardt & Blount, 1984; Kummer, 1968). Thus, we conclude that mutual gaze is species typical for chimpanzees, as it is species typical for humans. The amount of mutual gaze found in different primate species may be linked with the richness of early communication. Chimpanzees and humans share high degrees of facial expressiveness (e.g., de Waal, 2003) and of communication (e.g., Bard, 2003; van Lawick-Goodall, 1968), and they also share the highest amounts of mutual gaze.

Mother–infant chimpanzees at PRI exhibited significantly more mutual gaze than those at Yerkes. Group differences in mutual gaze are not a by-product of maternal visual attention or visual exploration in humans (e.g., Lavelli & Fogel, 2002) or in chimpanzees (this study). Rather, maternal cradling was found to be inversely related to mutual gaze in chimpanzees, such that when mother and young infant are in constant physical contact, there is little mutual gaze. Reduced face-to-face interactions, including reduced amounts of mutual gaze, are found in human cultures that have increased physical contact with infants compared with Western norms (Keller et al., 2004; Ochs & Schieffelin, 1984; Sorenson, 1979). In an experimental study, when mother and young infant were in constant physical contact, there was little mutual gaze, but mutual gaze increased when infants were placed out of contact (Lavelli & Fogel, 2002). The developmental pattern of mutual gaze influenced by changes in physical contact in chimpanzees (see Figure 1) is remarkably similar to that for humans (see Figure 2).

Mutual engagement can be primarily tactile, arguably the more basic pattern, as it is found in most nonhuman primates (Bard, 2002). Mutual engagement takes the form of high cradling contact in humans, specifically those in rural ecocultural environments (Keller et al., 2004; Sorenson, 1979; Stack, 2001). With reduced physical contact found in Western societies, mutual engagement shifts to the visual system, arguably a very recent shift from an evolutionary perspective. Rethinking mutual engagement within a framework of the interchangeability between visual and tactile

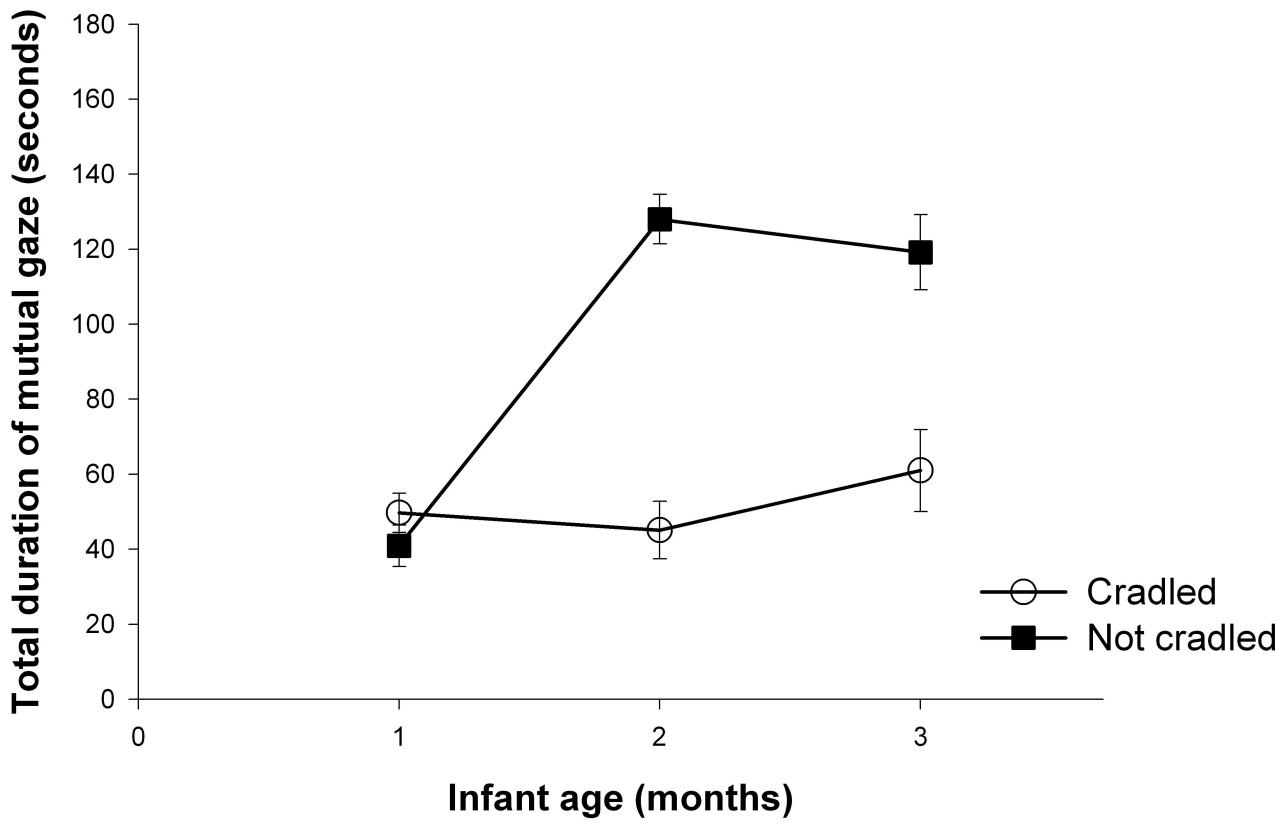

Figure 2. In human infants ($n = 16$) studied by Lavelli and Fogel (2002), there is less mutual gaze in face-to-face interactions (mean + standard error) when infants are placed on a sofa than when they are held in mother's arms.

modalities (c.f. Robson, 1967) allows for an integration of the human, cross-cultural, and nonhuman primate data with regard to mutual gaze. Evidence to support this interchangeability hypothesis converges from cross-species comparisons (as in the current study) and from cross-cultural data (e.g., reported by Greenfield, Keller, Fuligni, & Maynard, 2003; Keller, 2003).

The current study is based on 11 chimpanzees. The number of subjects is small, especially in comparison with human mother–infant studies, but it is important to note that this results from naturally occurring small groups and is not due to selection. Although each chimpanzee mother–infant pair was observed for 60 min at each of three ages, caution is warranted. Significant differences were found; the average effect size for the significant findings was moderately large (.41). In contrast, the average effect size for the nonsignificant results was small (.09). The effect size distributions are distinct (nonoverlapping 99% confidence intervals) and converge with results of the statistical probability tests. The low levels of mutual gaze found at Yerkes (with 8 infants) are comparable with those reported for chimpanzee mother–infant pairs in the wild (Plooij, 1979, with only 3 infants; van Lawick-Goodall, 1968). Chimpanzee infants can develop high levels of mutual gaze when actively encouraged, as when they are raised by humans (see Bard, Platzman, Lester, & Suomi, 1992, for a study with 10 infants) or by chimpanzee mothers (PRI mothers in this study). The current study has the largest number of chimpanzee mother–infant pairs of any mutual gaze study, from either captive or wild settings.

Infant chimpanzees, by 3 months of age, engaged in the pattern of eye gaze practiced by their mother. Chimpanzee infants might learn group-specific differences through interactions with their mothers, as, for example, human infants learn through intuitive parenting behaviors (Keller et al., 2004). Group differences might also be explained by parity (all PRI mothers gave birth to live infants for the first time, whereas 3 of the 8 Yerkes mothers were first-time mothers) or by cohort effects (Yerkes infants were born in 1988 and 1989, whereas PRI infants were born in 2000). The current study cannot rule out the influence of humans on the existence of mutual gaze, especially in the adults at PRI (Matsuzawa, 2001); however, the mutual gaze pattern was maintained during exclusively chimpanzee mother–infant interactions. When there is evidence that behaviors are passed on to the next generation through learning and not genetics, then claims of culture (Bonner, 1980) or cultural evolution (de Waal, 2001; Whiten et al., 1999) are supported.

In Western industrialized cultures, the function of eye gaze changes with age from mutual gaze in support of social–emotional engagement found in early infancy to triadic gaze in support of communicative engagement about objects found in 1-year-olds. Mutual gaze appears to be a human universal, although the amount of mutual gaze varies across cultures as a function of parenting

practices (Bullowa, 1979; Keller et al., 2004). Mutual gaze is not unique to the human species. Although triadic gaze is species typical in humans (e.g., Adamson, 1995), it is not clear whether triadic gaze is a human universal (Keller, 2003). Triadic gaze is also species typical for great apes, as it is found in intentional communication (e.g. Bard, 1992; Boesch & Boesch-Achermann, 2000; Hare, Call, & Tomasello, 2001; Leavens, Hopkins, & Thomas, 2004; Okamoto, Tanaka, & Tomonaga, 2004; Pika, Liebal, & Tomasello, 2003; Tanner & Byrne, 1996; but see Tomasello, 1999, for a different interpretation). Comparative developmental studies of mutual and triadic gaze are needed to identify species-typical and species-unique characteristics in the socialization of attention (Keller et al., 2004; Langton, Watt, & Bruce, 2000; Rogoff & Morelli, 1989).

We confirm that mutual gaze occurs between chimpanzee mothers and infants. Moreover, mother–infant chimpanzee pairs exhibited higher rates of mutual gaze in the PRI center than in the Yerkes center, demonstrating flexibility in the development of mutual gaze in chimpanzees and suggesting that chimpanzee infants learn group-specific patterns. Group differences in mutual gaze were associated with group differences in physical contact and motor stimulation in chimpanzees, as is found in humans. We propose that mutual engagement in primates is supported via an interchangeability of tactile and visual modalities. Mutual gaze is best studied within a cross-species and cross-cultural developmental perspective.

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