Emotional Engagement: How Chimpanzee Minds Develop

Kim A. Bard, PhD

Professor of Comparative Developmental Psychology

Centre for the Study of Emotion

Department of Psychology

University of Portsmouth

Portsmouth UK

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Comparative developmental psychology is a perspective with which we can view the similarities and differences in developmental processes that occur across primate species. My developmental area of specialty is infancy, and I find topics involving emotion particularly interesting. As a developmental psychologist, I ask questions about how the emotional system of chimpanzees develops, and in particular, I am interested in how developmental outcomes change as a function of social-cultural environments (e.g., Bard, 2005). Comparative psychologists are interested in similarities and differences across species in order to address questions of species-unique characteristics or characteristics shared by species based on evolutionary history. The last common ancestor (LCA) of humans, chimpanzees, and monkeys lived approximately 30 million years ago and the LCA of humans and chimpanzees lived approximately 7 million years ago (e.g., Steiper & Young, 2006), which means that humans and chimpanzees have 23 million years of shared evolutionary history. In fact, I am interested in how developmental processes of chimpanzees compare to developmental process of humans. To determine those characteristics that are uniquely human, those that are uniquely chimpanzee, or those shared by humans and chimpanzees, a comparative approach must be combined with the study of development across species (Bullowa, 1979; Johnson-Pynn, Fragaszy, & Cummins-Sebree, 2003).

The most common question that I am asked is 'How does the development of chimpanzees compare to that of humans?'. The desired answer is typically a cross-species comparison on a single dimension, e.g., 'the chimpanzee' is like a 2-year-old human. The scientific answer, however, is quite a bit more complex, because it depends upon which dimension is chosen, both for control and for comparison. Chimpanzees, like humans, show developmental changes in motor skills, in emotionality, in cognition, and in social skills. The outcomes within these domains vary as a function of 'lived experiences' (i.e., sometimes called

rearing, or learning, or eco-cultural experiences, or simply environment). Moreover, outcomes

in infancy form the foundational skills for adult competencies. In this chapter, I provide the

broad strokes of a comparative developmental answer to the question of how the development of

chimpanzees compares to that of humans, with a special focus on the role of engagement.

The study of young infants makes somewhat easier the task of comparing development

across species, and of understanding common developmental processes (which is my main goal).

To understand developmental processes, we need to understand the influences of maturation,

social-cultural environments, and of evolutionary history on outcomes (e.g., Jablonka & Lamb,

2007). Combining a comparative perspective with truly developmental study allows us to

address the flexibility and plasticity in outcomes. In this chapter, I review a number of studies

highlighting the relevance of this developmental approach to topics that are of interest to

comparative psychologists, primatologists, evolutionary biologists, etc.. The conclusion is that

social cognition has an important developmental history of lived experiences.

The idea that one can pinpoint an age for 'the chimpanzee' to equate them to 'the human'

of a certain age is perpetuated (repeatedly) in the comparative literature (Leavens & Bard, 2010).

Part of the problem is that outcomes from 'chimpanzees', usually adults, are compared to

outcomes of 'humans', typically 2 year-old infants (e.g., Herrmann, Herrnandez-Lloreda, Call,

Hare, & Tomasello, 2009). When authors find that chimpanzees performed less well on a

particular task than 2.5 yr humans, the assumption is that 'chimpanzees' are not as good as 2.5

yr-old humans. Of course to make conclusions of species differences (if one could control the

additional confounds of rearing, for example), the addition of adult humans and chimpanzee

infants are required (to have an appropriate experimental design to test for main effects of

species and age at testing, and to test for the interaction of species by age: Leavens, Hopkins, &

Bard, 2005, 2008). I resolve this problem by testing chimpanzees and humans at the same developmental age, choosing to equate the groups on duration of post-natal lived experiences. In this review, I discuss the effects of early experiences (i.e., engagement) on numerous milestones in development: 1) newborn neurobehavioral integrity; 2) early social cognitive processes such as primary intersubjectivity, neonatal imitation, and mutual gaze; 3) emotional expressions and social referencing; 4) attachment; and 5) self-awareness. With this database, I highlight the relevance of rearing histories (of lived experiences) to the development of social cognition in chimpanzees, and hence, the importance of developmental studies to comparative psychology (see also Boesch, 2007; Bjorklund, 2006; Burghardt, 2009; Suomi, 2006).

Characteristics of newborns

In this section, I address the question of how chimpanzees and humans compare at birth. First, we should compare gestational age. Full-term age in humans is approximately 266 days, or 38 weeks, when measured from conception to birth, and average full-term age for chimpanzees is approximately 225 days, or 32 weeks from the day of ovulation to birth (e.g., Wallis, 1997). This is corrected for that fact that typically, for humans, the length of pregnancy is measured from the last menstrual period until birth (adding 2 weeks = 40 weeks of pregnancy), whereas for chimpanzees (as in most non-human animals) pregnancy is measured from ovulation to birth. So, when compared from conception to birth, humans have a longer period of *in utero* development than chimpanzees, on the order of 6 weeks.

Secondly, we should compare the sizes of infants at birth. Newborn chimpanzees weigh 1.5kg on average or 3% of their adult weight (Fragaszy & Bard, 1995). Newborn humans weigh 3.25kg (7 lbs 4oz) on average or 4% of their adult weight (approximated for US males and females combined).   It is interesting to note that DeSilva & Lesnik (2006) estimate that

chimpanzees' brains have reached 35-40% of their adult growth at birth, and that the brain size of human newborns is 25-30% of their adult size. Thus, chimpanzees have a shorter in utero period, weigh less at birth, but have relatively more brain growth than human newborns.

Chimpanzees have inborn capacities for emotional engagement with caregivers, and possess developmental processes, such as neonatal imitation and primary intersubjectivity, by which emotional experiences become integrated in communication and cognition. The remainder of this section reviews these inborn capacities in chimpanzees and comes to the surprising conclusion that from birth through the first month, the neurobehavioral integrity and other expressions of inborn capacity of newborn chimpanzees are not easily distinguished from newborn humans (see review in Bard, Brent, Lester, Worobey, & Suomi, in press).

Neonatal Neurobehavioral Integrity

This section concerns neonatal neurobehavioral integrity, as measured by the Neonatal Behavioral Assessment Scale (NBAS:, also known as 'the Brazelton', most recently Brazelton & Nugent, 1995). The NBAS is a widely used instrument for clinical and for research purposes. The NBAS is used to assess many realms of newborn organization and functioning, including orientation, motor performance, reflexes. I find it particularly useful because it assesses the early functioning of emotional systems, specifically related to behavioral state arousal and behavioral state regulation. Additionally it is useful because it is designed to assess the current functioning of the newborn, in response to the challenges of the post-uterine environment. The NBAS test is a tool to observe early adaptations by infants to the demands of different environments.

Initially, I compared human newborns with the first 13 chimpanzee infants that I tested with the NBAS, from 1987-1990. These infants were raised in the standard care nursery (for details see Bard & Gardner, 1996, and below). The most important finding was that newborn

chimpanzees were measurable with the NBAS test, without modification. I had trained on the

NBAS with human newborns and on a modified 'monkey brazelton' (from Suomi's lab) which

included modified items from the NBAS, but also included some modified items from the

Bayley Scales of Infant Development (Bayley, 1969), i.e., items used for 3-5month-old human

infants. I expected that the monkey version would be more useful with chimpanzees than the

human version. But, I was wrong. The human version of the NBAS was the one that I used with

chimpanzee newborns, without a single administrative change. Here I review five clusters of

behavioral organization: orientation, motor performance, range of state, state regulation, and

autonomic nervous system stability. Of course, a requirement of all NBAS examiners is that the

tester be sensitive to the newborn and work to obtain their best performance (for more details and

review of previous studies see Bard, Brent, Lester, Worobey, & Suomi, 2010).

Orientation: Newborn chimpanzees and newborn humans are able to follow visually

presented stimuli across two 30 degree horizontal movements. Newborn chimpanzees and

newborn humans are able to alert to, turn their head toward, and search for auditory stimuli. In

general, visual and auditory orientations are better to social stimuli than to inanimate stimuli, for

both species. Initially, it appeared that chimpanzee newborns were alert more often and for

longer durations (up to 30 seconds each period) than human newborns (who sustained alertness

up to10-15 seconds each period). The 7 items were averaged into an Orientation Cluster score.

There was no group difference and no developmental change from 2 to 30 days of age.

Motor: In the five motor items and the Motor Performance Cluster scores part of the

NBAS, I was surprised to find only one species difference in head control. Newborn human and

chimpanzees had muscle tone that increased when handled but was neither hyper- or hypotonic.

In terms of motor maturity, amount of spontaneous and elicited activity, and specific motor

movements (defensive reaction), there were no species differences noted, but there was significant development from 2 to 30 days of age (for both humans and chimpanzees).

Arousal: Nursery-reared chimpanzees rarely cried for 15 seconds, and if they did cry, it was at the end of the exam (humans cried with handling in the first 8 minutes of the exam, and they tended to cry more than twice). In these early analyses, we found that chimpanzee newborns were significantly less aroused than humans.

State Regulation: Chimpanzee newborns are incredibly responsive to being held. Whereas human newborns typically mold and relax into the arms of the examiner, chimpanzee newborns additionally nestle their face into the examiner's neck and cling to the examiner. Some chimpanzee newborns, like some human newborns, are also able to bring their hand, fist, or thumb to their mouth for sucking and self-quieting. There were no group differences on the scores of self-quieting, consolability, or hand-to-mouth ability. Initially, however, I found a difference in the State Regulation cluster scores, with nursery chimpanzees have significantly better state regulation than human newborns.

Autonomic Stability: This cluster includes signs of stress affecting the autonomic nervous system, specifically the number of startles, and tremors (changes in skin color was not measured). Chimpanzees and humans showed different patterns of developmental change.

Comparing the one group of chimpanzee newborns to the one group of human newborns, I summarized differences in terms of differences in behavioral state organization. But recently, my colleagues and I conducted a sort of meta-analysis, statistically comparing NBAS data collected from chimpanzee newborns raised in four different environments to human newborns, and arrived at different conclusions (Bard et al., 2010). There were three nursery-raised chimpanzee groups, two from the Yerkes Research Center nursery at Emory University (standard

care- ST- and responsive care- RC), and one group raised at the Southwest Foundation for

Biomedical Research (SW). The three nursery settings (for chimpanzee infants whose mothers

did not have sufficient maternal skills) differed in terms of their rearing practices and

socialization goals. Briefly, the ST nursery consisted of groups of 4 to 6 infants of the same age

together constantly (24/7), with intermittent contact with human animal care technicians for

feeding & cleaning (scheduled once every 4 hours). In the RC nursery, there was an additional

contact with specially trained research assistants (for 4 continuous hours per day, 5 days a week),

who nurtured the socio-emotional and communicative development of each infant (Bard, 1996).

The SW nursery was similar to the Yerkes ST nursery, with infrequent contact, but animal care

technicians consistently wore biosafety masks and gloves, and had very limited cradling contact

with the chimpanzees. An additional group of chimpanzees were reared by their biological

mothers (Mo), with constant cradling contact (24/7), except for the 2 times that they were

temporarily 'borrowed' from their mothers and given NBAS tests at 2 and 28 days (Hallock,

Worobey, & Self, 1989). The chimpanzees groups were compared with one human group,

reared by their biological mothers, in a middle- to upper middle-class, urban part of Providence

RI, USA (see Lester et al., 1989 for full details). All infants were assessed using the same tool,

the NBAS, tested by certified examiners, at the same ages, 2 day and 28 days.

This cross-species analysis with multiple chimpanzee groups revealed very different

findings from the original comparison between a single group of chimpanzees and of humans.

On the second post natal day, the human group was significantly different from all the

chimpanzees groups in only 3 of 25 scores, specifically in alertness, in muscle tone, and pull-to-

sit (from 8 scores in orientation, 6 scores in motor performance, 5 scores in range of state, 5

scores in state regulation, and the single score of smiling). On day 30, there was only a single

difference that distinguished the human group from all the chimpanzee groups, and it was muscle tone, with the chimpanzees significantly more hypertonic than the human newborns. On the remaining 24 of 25 NBAS scores at 30 days, the human group was not distinct. Moreover, there was not a simple explanation for the pattern of group differences.   This range in chimpanzee neonatal behavioral outcomes encompassed the neonatal behavioral outcomes found in the human group. "In terms of describing chimpanzee newborns, we conclude that how they performed depended to a large degree on what they have experienced. " (Bard et al., 2010).

Therefore, in comparing chimpanzee newborns to human newborns, now I would summarize by saying that it is very difficult to find species differences. In fact, in the analyses that I report above, only a single human group was used to compare with the multiple chimpanzee groups. There are significant cross-group differences in humans as well (e.g., Nugent, Lester, & Brazelton, 1989), especially in range of state, state regulation, and some motor performance. Therefore, the degree to which the neonatal system matures in interaction with specific features of the post-natal environment illustrates the flexibility inherent in the genome of chimpanzees and humans to respond to particular types of emotional engagements.

Neonatal imitation

Imitative behaviors differ across primate species: There are a few examples of imitation in newborn rhesus monkeys (see chapter by Ferrari), but quite a lot of instances of imitation in chimpanzees from infancy through adulthood (see review by Myowa-Yamakoshi, 2006). Additionally, it's clear that imitative abilities differ across development: newborns don't copy their parent banging a hammer, for example, but 2-year-olds just might. Imitative abilities in nonhuman primates need to be viewed from both comparative and developmental perspectives. Here, I present an overview of research on neonatal imitation in chimpanzees (from Bard, 2007).

We used two procedures to assess imitation in healthy full-term chimpanzee newborns: one was very rigid and standardized, the other was both communicative and interactive. In the structured procedure, the chimpanzee infant was placed facing the adult human demonstrator. The adult human followed a predetermined order of demonstration: either Mouth Opening (MO) first and Tongue Protrusion (TP) second, or TP first and MO second. There were 4 presentations of the first demonstrated action within a 20-second period, followed by a passive face for 20 seconds, and this lasted for the first 4 minutes. Immediately thereafter, the second demonstrated action was given in the same cycle of 4 demonstrations within a 20-second period, followed by 20 seconds of a passive face. From the beginning through the entire 8-minute session, the actions of the adult human were completely determined by the structure of the test and did not change regardless of the actions of the infant. Using the Structured procedure, all 5 chimpanzees matched one of the modeled actions, but none matched both actions (see Table 1).

In the Interactive procedure, the infant was either held or laid comfortably within arm's reach. The order of modeled actions were determined in advance, just like in the Structured procedure. However, the number of presentations depended on the infant's response. The first demonstrated action was presented and a 5s pause allowed the infant to respond. If the infant emitted <u>any</u> of the target actions, then this was considered the infant's response, and the demonstration concluded. If the infant did not respond, up to five repetitions of the demonstrated action were given. After the infant responded, or after 5 demonstrations, there was a 10s pause, before the next action was demonstrated. The series of modeled actions was provided twice, so that the infants had two opportunities to exhibit imitation of each action.

In the Interactive procedure, we used three modeled actions: MO, TP, and Tongue Clicks (TC). The MO and TP models were identical to those in the Structured procedure. One

demonstration of a TC included three rhythmic clicks, a rather complex model of both sound production and a series of three actions. Using the Interactive procedure, one subject matched one modeled action, three subjects matched two modeled actions, and one subject matched all three modeled actions (Table 1).

The best performance in neonatal imitation was given by Lindsey, when she was 7 days old. During the first presentation of TC, she listened and occasionally looked at the model during the first 4 demonstrations, and then with the fifth demonstration, after a pause, she emitted a single tongue click. During the second pass, and again after the fourth demonstration of TC, she responded. But this time, she imitated the series of three actions, (2 MOs) and matched a TC.

When chimpanzees are 7-11 days of age, imitation was exhibited in both the Structured and Interactive procedures by all 5 chimpanzees (Bard 2007: Table 1). Imitation of facial expressions by chimpanzee neonates appears to represent a capacity to engage in intersubjectivity that is similar to that of human infants. Furthermore, 4 of 5 subjects performed better in the Interactive paradigm, indicating that chimpanzees share with humans a developmental mechanism (i.e., neonatal imitation) that may allow outcomes to be highly influenced by early interactive experiences.

Emotional Expressions

How do chimpanzees and humans compare in their development of emotional expressions? In the first 30 days of life, chimpanzees, like humans, express happiness with movements of the mouth. We call this smiling if matching the emotion across species. We call the facial expressions something different, however, if we are matching on facial movement morphology (i.e., with a standardized coding of facial action units, such as with ChimpFACS: Vick, Waller, Parr, Smith Pasqualini, & Bard, 2007). Chimpanzee infants express happiness

with an open mouth expression, a playface, whereas human infants express happiness most often with lip corners being raised, although humans also have open mouth smiles (e.g., Messinger, 2002) and chimpanzees also raise their lip corners (Thorsteinsson & Bard, 2009; Vick et al., 2007). Given the same positive context, say of a caregiver vocalizing to an infant while tickling, the prototypic facial movements of human and chimpanzee infant might look very much the same (compare the large smile of the human infant in Oster, 2005, p.281 with the big playface of the chimpanzee infant in peek-a-boo in Bard, 2005, p.47). But note that these are 3 month-old infants, although newborns also smile (see Table 2). Of course, chimpanzee newborns and human newborns cry and fuss with distinctive facial expressions and vocalizations (see Bard, 2000 for details of crying in chimpanzees). We found species-typical chimpanzee vocalizations of greeting, threat bark, and alarm call occurred in some chimpanzees during the newborn period, although not all occurred in appropriate contexts (see Bard 2003, 1996 for more details).

We know that the chimpanzee emotional system, like the human emotional system, develops in interaction with the social environment (Bard, 2005). Beginning in the neonatal period, chimpanzee infants, like human infants, smile in response to familiar caregivers in face-to-face contexts (see also Tomonaga, 2006). By 30 days of age, chimpanzees raised in a nursery by humans smile significantly more often than do mother-raised chimpanzees, when tested by a human examiner (Bard, 2005). Perhaps most interesting is that human infants (from middle-class American) smile more than mother-raised chimpanzees but less than nursery-raised chimpanzees at 30 days of age (Bard et al., 2010).

Socio-emotional experiences can impact the development of negative emotional expressions. The amount of crying and fussing in chimpanzees varies as a function of rearing experiences: Two groups of nursery-reared chimpanzees differed significantly in the amount of

fussing and crying evident in the second month of life (Bard, 2000); and extended periods of crying occurred much more rarely in nursery-raised chimpanzees compared to mother-raised chimpanzees, when given the NBAS standardized test (e.g., Bard et al., 2010). Interestingly, by 21 days of age, on average, some chimpanzee newborns displaying angry faces, although there was a significant difference in occurrence as a function of the early rearing environment (Bard, 2003). Therefore, it is clear that a variety of emotional expressions, both facial and vocal, occur in young chimpanzees, but the prevalence or even the age of onset may vary widely as a function of the socio-emotional environment in which chimpanzees are developing.

Characteristics of 3 month-olds

Intersubjectivity is Trevarthen's (1979) term for the human infants' ability to adapt their own purposeful acts to the subjectivity of others. Primary intersubjectivity is most often seen in face-to-face interactions of parents with their very young infants. One question that has motivated much of my research relates to whether chimpanzee infants, like human infants, are born with this capacity for intersubjectivity. Four strands of evidence are required to conclude that humans, or chimpanzees have primary intersubjectivity, including: 1) neonatal imitation ; 2) mutual gaze; 3) the extent to which emotional behaviors can acquire communicative meaning; and 4) the degree of flexibility in emotional and/or communicative meanings (i.e., based on differences in early rearing). If we find evidence of each in chimpanzees, then we might conclude that primary intersubjectivity was a capacity common to the great ape – human lineage (for further discussion of this topic see Bard, 2009).

In order to enter into a communicative system, it is required than an individual has behaviors that can assume communicative meaning. These meaningful behaviors can develop from the most basic elements of neonatal behavior, such as crying, and alert attention. I

observed chimpanzee mothers with their newborn infants, and found that they spend time engaged in face-to-face interactions with their infants. They spend lots of time in communicative, tactile games (Bard, 1994; Bard, 2002). Primary intersubjectivity appears to be expressed in social games in chimpanzees. For example, Sheena, when she was 3 months of age was assessed with a NBAS exam, the item where a cloth is placed lightly covering the face. She pulled the cloth down and smiled at us, initiating a game of peek-a-boo. We replaced the cloth over her face and when she pulled it down the second time, her smile was even broader. Nursery chimpanzees are active partners in social games (see Figure 2.8 in Bard, 2005).

So, there is evidence that young chimpanzees have neonatal imitation, have behaviors that assume communicative meaning (i.e., emotional expressions), and there is some evidence already from the newborn period that socialization exerts a powerful influence on the development of emotional expressions in chimpanzees. What about one other marker of primary intersubjectivity, that is mutual gaze?

Mutual gaze

In chimpanzee mother-infant interactions at the Yerkes Research Center, there are between 8 and 10 instances of mutual gaze in an hour. That level is steady as the infant grows from 2-4 weeks, to 6-8 weeks, and 10-12 weeks of age. This is in marked contrast to my observation of the skills of infant chimpanzees raised in the Yerkes nurseries, that is, interacting with human partners. In the nursery, I was impressed with infant chimpanzee's ability to engage in emotionally meaningful, face-to-face interactions, with extended periods of mutual gaze.

By using an approach that combined a developmental perspective (describing changes in mutual gaze in the first 3 months of life) with comparative data (documenting mutual gaze and intuitive parenting behaviors across different groups and across species), my colleagues and I

explored developmental prerequisites and correlates of mutual gaze in chimpanzees (Bard et al., 2005). This study confirmed previous evidence that mutual gaze occurs in mother-raised chimpanzees (16.9 times per hour). Moreover, mutual gaze occurred in chimpanzees at all ages sampled, and at both centers, but, we found different developmental of mutual gaze in the two groups of chimpanzee mother-infants pairs. There was a significantly higher rate of mutual gaze in the mother-infant pairs residing at the Primate Institute of Kyoto University (PRI) compared with mother-infant pairs residing at the Yerkes Research Center of Emory University (PRI: M = 22 $\pm$3.4 mutual gaze bouts per hour; Yerkes M = 11.8 $\pm$2.1 mutual gaze bouts per hour).

It appeared that mothers at PRI were actively encouraging mutual gaze by tilting or holding up the infant's chin with her finger while looking into her infants eyes. This behavior occurred in each of the PRI mothers with their 3-month-old infant, but was not observed to occur in any Yerkes chimpanzee mother.   We found that the rate of mutual gaze was significantly and inversely correlated with percent of time spent cradling 3-month-old infants.   Reduced face-to-face interactions, and reduced amounts of mutual gaze are reported in some human cultures that have increased physical contact with infants, compared with Western norms (reviewed in Bard et al., 2005; Keller, 2007).   In an experimental study (Lavelli & Fogel, 2002) with human infants, mutual gaze increased when 2- and 3-month-old infants were out-of-contact compared with being held by their mothers. Thus, the enculturation process of intuitive parenting behavior in chimpanzees, thus, appears strikingly similar to the process used by humans.

We proposed The Interchangeability Hypothesis (Bard et al., 2005) to explain variations of mutual engagement based in physical contact without mutual gaze (the basic primate system, also found in traditional human societies: Keller, 2007), or on mutual gaze without high levels of physical contact (an evolutionary derived system, found in middle-class human societies. My

observations of nursery chimpanzees fits in nicely as those chimpanzees raised by human caregivers are most often out of physical contact, and they have the highest levels of mutual gaze among 3-month-old chimpanzees studied to date. There is a range in mutual engagement, explainable by the same development mechanism, active in chimpanzees and humans (e.g., Bard et al., 2005: Keller, 2007: Plooij, 1984). Furthermore, by identifying a similar developmental process that accounts for higher (and lower) amounts of mutual gaze, we confirm further evidence for primary intersubjectivity in chimpanzees.

Early cognition and social cognition (6-9 months of age).

The most widely used assessment of early cognition in human infants is the Bayley Scales of Development (reviewed in Bard & Gardner, 1996). My research team administered the Bayley test to chimpanzee infants raised in the three nursery settings of the Yerkes Research Centre of Emory University (Bard & Gardner, 1996; van IJzendoorn, Bard, Bakermans-Kranenburg, & Ivan, 2009). At 3-5 months of age, chimpanzees oriented well to sights and sounds, and grasped and mouthed object, scoring significantly well above human infants of the same age (humans $M = 100$ SD 16; chimpanzees $M > 130$). By 6-7 months, the chimpanzees from both ST and RC nurseries were still scoring significantly above humans of the same age. At 8-9 months the chimpanzees overall were not different from 8-9 month human infants. But by 10-12 months, when turn-taking, pointing to the parts of a doll, and completing puzzle boards were required, the chimpanzees scored significantly lower than 10-12 month-old humans.

Once again, we found differences among the chimpanzee nursery groups. At 9 months, for example, the responsive care (RC) chimpanzees scored higher than 9-month-old human infants, but the standard care (ST) chimpanzees score lower than the humans (van IJzendoorn et al., 2009). Moreover, the chimpanzees that experienced early stress performed significantly less well on the BSID throughout the first year of life, with a spike of fearful anxiety during testing at

6-7 months. It is evident that the institutionalized rearing was responsible for many of the poor cognitive outcomes in year-old chimpanzees, as their rearing was impoverished (see e.g., van IJzendoorn et al., 2009; Racine, Leavens, Susswein, & Wereha, 2008), especially compared to that of typical middle-class urban human infants, for whom the Bayley tests were devised.

Object manipulation & cooperative motivations

It is interesting that the extent to which parents use objects in their interactions with young human infants varies widely across eco-cultural contexts. Keller and colleagues (2007) have demonstrated that for 3-month-old infants living in rural subsistence eco-cultures, objects are much less often the focus of interactions (less than 1% of waking time v 2.5 % in urban settings), and body contact is much more often experienced (~80% in rural Nso v 43% in urban German infants: p.258). Bakeman, Adamson, Konner, & Barr (1990) found !Kung caregivers most often gave objects to their infants as a distraction, so that the caregivers can carry on with their work undisturbed by infants. Menzel (1964) found that chimpanzees raised in isolation exhibited extreme fear when they first encountered novel objects, and early rearing had an impact on tool use (Menzel, Davenport, & Rogers, 1970). Thus, it is clear that (the lack of) previous experience with objects has a long-term effect on chimpanzee emotional engagement with objects. The need to habituate captive apes to novel objects is a constant reminder of this fact in experimental contexts.

Caregivers to chimpanzees raised in biomedical nursery environments do not typically nurture object manipulations (e.g., Vauclair & Bard, 1983), however, inanimate objects are usually provided to stimulate well-being in captive chimpanzees from a very young age (e.g., Bard & Nadler, 1983). In the Bayley (cognitive) tests, we scored the degree to which in young chimpanzees manipulated objects with their hands. There were significant improvements from

3-5 mo through 10-12 months in manipulations (Figure 1), and significant differences among the different nursery rearing groups, beginning at 6 months, and continuing through the first year of life (Bard & Gardner, 1996). The RC infants performed significantly better than the ST infants, but the LA did not differ from the ST. Even in relatively basic skills, such as object manipulation, the early lived experiences of chimpanzees have a significant impact.

Characteristics of 12-month-olds

Locomotor Ability

Chimpanzee infants begin to walk on (hands and) feet around 5 to 7 months of age. This early locomotor ability may have an important influence on the chimpanzees developing social cognition (Vauclair & Bard, 1983). Human infants begin to walk (crawling then taking first steps) around 12 months of age. This means when humans first begin to coordinate their engagement with objects and with social partners (i.e., coordinated joint attention: Adamson & Bakeman, 1991) at 9 months, they are not yet able to independently locomote. Therefore they engage in a lot of referential communication (e.g., asking caregivers to give them out-of-reach objects). Chimpanzees at 9 months appear also to be coordinating their engagement with objects and with social partners (along with other tertiary circular reactions: see overview in Bard, 1992), but since chimpanzee are able to independently locomote, they appear to bypass the Referential Problem Space, and typically engage is less referential communication (Leavens et al., 2005: see also Vauclair & Bard, 1983). Therefore understanding developmental processes, here the interplay between locomotor (in)ability and the lack of need for using referential communication, e.g., pointing, helps us to make sense of the findings of comparative studies.

Attachment

A major factor of early rearing, with long term consequences for social cognition, is the

quality of attachment bonds. Van IJzendoorn, Bard, Bakermans-Kranenberg, & Ivan (2009) found that 1-year-old chimpanzee exhibit the balance of exploration (play with toys when the caregiver is present) and security seeking (distress when separated from their caregiver) that is found in 1-year-old humans when tested in the Strange Situation Procedure. The chimpanzee infants from Yerkes were primarily secure (54%), but 33% were classified with insecure-ambivalent, and 7% with insecure-avoidant, when classifications were conducted.   This compares favorably to Ainsworth, Blehar, Waters, & Wall's (1978) original sample of US middle-class human infants who were 57% secure (and 42% insecure), but the relatively higher ambivalent classifications relative to avoidant classifications in the chimpanzees compares more favorably to Japanese samples with limited experiences in being alone and encountering strangers (e.g., Miyake et al., 1985).

Children with disorganized attachment systems have serious problems in childhood, and can continue to have 'poor emotional health' later in life. One cause of disorganized attachments is a developmental history of neglect or abuse (van IJzendoorn et al., 2009). Whereas 15% -20% of non-clinical and daycare human samples have disorganized attachments, the percentage rises to over 60% for children living in Romanian, Hungarian, or Greek orphanages (see Figure 2). By 1 year of age, the attachment system of nursery-raised chimpanzees was more like that of human infants raised in Romanian orphanages, than like that of human infants raised in middle-class families (van IJzendoorn et al., 2009). At 1 year of age, chimpanzees with dysfunctional attachments were more likely to exhibit stereotyped rocking, and tended not to contact the caregivers during reunion episodes but rather clutched towels (van IJzendoorn et al., 2009). Raising chimpanzees in biomedical centers significantly and negatively impacts their emotional and cognitive systems, with potentially long-lasting effects (e.g., Brune, Brune-Cohrs, McGrew,

Preuschoft, 2006; Kalcher, Franz, Crailsheim, & Preuschoft, 2008).

It is important to note explicitly that the attachment system is highly influenced by early rearing. Chimpanzees raised in the enriched RC nursery, compared to those raised in the standard care nursery at Yerkes, had significantly fewer dysfunctional attachments, had significantly higher 9-month cognitive scores, and were significantly less likely at 9 months, to exhibit an attachment to a towel. Early experiences with caregivers during the first year of life have important and long-lasting effects on developmental outcomes in chimpanzees.

Social referencing & cooperative motivations

In social referencing experiments, when the infant looks to the caregiver, seeking information about the novel object, the caregiver is instructed to give an emotional message about the object. Joint Attention is demonstrated when the infant (chimpanzee in this case) is influenced in his or her behavior toward the novel object as a result of the caregiver's emotional message (e.g., Bard & Leavens, 2009; Leavens & Bard, in press). In social referencing, the key is whether the chimpanzee associates the caregiver's message, with his or her actions on the object. Russell, Bard & Adamson (1997) reported that 1) all the chimpanzees, from as young as 14 months, looked to their favorite caregiver, and engaged in alternating gaze between the caregiver and a novel object. This indicates that the young chimpanzees, like human infants, actively seek information about the novel object from their caregiver ; 2) Moreover, their behavior is regulated by the emotional message that they receive. Young chimpanzees withdraw from a novel object when the caregiver gives a distressed facial expression and chimpanzees look longer at the toy when the caregiver gives a happy expression. Note that early rearing does not appear to influence the basic ability to follow another's gaze (Pitman & Shumaker, 2009).

Social referencing is a form of secondary intersubjectivity, in which the infant

demonstrates the ability to coordinate engagement with a social partner (attending to the

emotional message given by the caregiver) with engagement with an object (to regulate

interactions with the novel toy: Russell et al., 1997). Clearly there can be wide individual

differences in caregiver's natural emotions toward objects in the world, and individual

differences in infants' sensitivity to emotional messages. For example, in general, the nursery-

raised chimpanzees of the Russell et al study were more wary of the novel objects than were

middle-class human infants. Therefore, this developmental system of social referencing,

common to chimpanzees and humans, can account for individual differences, as well as rearing

group differences in outcomes for human and chimpanzee infants.

Characteristics of 2 to 2.5 year-olds

Mirror self-recognition (Bard, Todd, Bernier, Love, & Leavens, 2006)

The identification of the self is a cognitive ability found in humans and great apes.

Evolutionarily, mirror self recognition is a cognitive capacity shared by chimpanzees and

humans – but is not present in any species of monkey, and so it is thought to have evolved in the

past 30my (for reviews see Bard et al., 2006; Inoue Nakamura, 2001). Developmentally, mirror

self recognition appears to develop around 2 years in humans and in chimpanzees, although there

has been some debate concerning the age of acquisition for chimpanzees (see Bard et al., 2006).

An objective methodology to index self awareness in nonverbal or preverbal primates,

the mark-and-mirror test was proposed by Gallup (1970) for comparative psychologists, and

independently by Amsterdam (1972) for developmental psychologists. The methods involve

application of make-up (as used by Amsterdam for human children) or dye (as used by Gallup

for nonhuman primates) to the face and placement of the marked individual in front of the

reflective surface of a mirror. If the individual used the mirror image to touch the marked area

on his or her <u>own</u> face, then this constituted behavioral evidence of understanding that the image in the mirror was the self, distinct from any other being.

In order to be more precise about age of onset, Bard et al., (2006) conducted a replication an earlier study, extending the age range to include more young chimpanzees. In the design of this experiment, we were faced with a comparative/development dilemma: Do we treat infant chimpanzees as if they were infants (and use the methods developed by developmental psychology), or do we treat infant chimpanzees as if they were adult chimpanzees (and use the methods developed by the comparative psychologists)? We decided to take a primarily developmental approach, choosing to minimize distress and not to render them unconscious during the marking. In fact, we marked the chimpanzees with Halloween make-up, and tested them while they remained with their normal social partners, in their social groups and in their familiar rooms. The question was whether the infants could be exhibiting mark-directed behavior when they in fact did not have the cognitive ability, labeled false positives'.

Specifically, we proposed that the method of overt marking with make-up, while awake and in a social group, did not cause false positives. Two groups of human infants were tested, one group of 15-mo- olds (none expected to pass), and a group of 24-mo-olds (all expected to pass). Did this method create self awareness in 15 month-olds? No, it did not! Even though the mark was placed on each child's face with their full awareness, not a single 15 month-old touched the mark while looking the in the mirror, or passed the mark test by any criteria, whether mark directed or self labeling. Even when the infants were prompted to respond, when their mother asked 'Who's that in the mirror?', none of the 15 month olds said their name, or gave any other self label. Yet, 4 of the 5 15-month-old children demonstrated that they understood the task, by wiping the mark on the doll when asked to do so by the mother.

In contrast, half of the 24-month-olds passed the mark test, all of the 2 year-olds labeled the self, and all understood the task. Viewing the data on mirror-guided mark directed behavior separately from verbal self labels present another interesting finding. Only half of the 24-month-olds actually touched the mark, when the literature suggests that most, if not all 2 year olds possess self-awareness. The amount of mark touching was comparable in the 24-mo children and the 28 mo chimpanzees.   This study raises questions about the age of onset of mark touching distinct from self labeling in the human literature, and about the influence of the social-cultural environment on the development of self naming in the mirror (e.g., does playing 'naming the self games' during the first 18 months of life faciliatate passing the test?).

With a comparative developmental perspective applied to studies of self recognition, we learn that self awareness is a cognitive characteristic shared by humans and chimpanzees. Moreover, there are similarities in the developmental patterns, age of onset, mirror behavior, and probably socio-communicative variables that culminate in self awareness for both human and chimpanzee infants (Bard et al., 2006). However, it appears that mirror self recognition is a relatively robust phenomenon in humans, as it may well be found across all human cultures (but see Keller et al., 2005), and little evidence exists to date that rearing environment influences age of onset of self recognition in chimpanzees.

<u>Advanced cognitive skills (e.g., language)</u>

The literature on ape language and ape cross-fostered projects presents overwhelming evidence of the impact of early experiences on social and cognitive outcomes (see review in Leavens & Bard, in press). Young chimpanzees have learned symbol systems comparable to those learned by 2- to 4-year-old human infants (e.g., Fouts, 1997; Savage-Rumbaugh, 1986).

Young chimpanzees show self-recognition comparable to 2 year-old human infants (reviewed in Bard, Todd, Bernier, Love, & Leavens, 2006). There are additional reports of triadic engagement in chimpanzees who do not learn symbol systems. For example, at Yerkes in the responsive care program (Bard, 1996), young chimpanzees often worked jointly in activities such as opening a padlock with a key. Kellogg & Kellogg (1933) reported that their son, Donald at 18.5 months and their chimpanzee Gua at 16 months, often engaged in cooperative games, such as rolling a ball back and forth. These examples illustrate commonly observed instances of mutual triadic engagements when chimpanzees are raised with warm relationships and industrially manufactured objects. In contrast, when young chimpanzees are tested in conditions in which there are few triadic engagement opportunities with human testers, outcomes can be relatively poor (e.g., Tomonaga et al., 2004).

Summary

Emotional engagement plays a critically important role in the development of social cognition skills, by providing foundational motivation for the expression of competencies, or by actually co-constituting social cognition. Chimpanzees have inborn capacities for emotional engagement with caregivers, and possess developmental processes, such as neonatal imitation and intersubjectivity, by which emotion becomes integrated in communication and cognition. In making cross-species comparisons, it is important to note the effects of early experiences and socialization practices, as they have a major impact on the nature and developmental trajectories of emotional engagements in primates, with potentially long-lasting effects. Socialization effects on expressions of emotion and on regulation of emotion are evident within the first month of life in chimpanzees (Bard et al., 2010), and by 3 months, socialization has an impact on many social, emotional and interactional outcomes, such as mutual gaze (Bard et al., 2005). By 6 months, the

effects of early experiences become evident in cognitive outcomes in chimpanzees (e.g., early stress compromises attention, leading to poor cognitive performance whereas positive emotional experiences enhance cooperation, leading to enhanced cognitive outcomes: Bard & Gardner, 1996). At 8-10 months, chimpanzees spontaneously exhibit joint engagement with caregivers and objects, and by 1 year, emotional attachments with specific caregivers have developed. When caregivers are emotionally responsive, chimpanzees' cognitive and emotional development is positively stimulated (van IJzendoorn et al., 2009) Many chimpanzees raised in institutional settings, however, do not develop secure attachments, impairing their ability to emotionally engage, that can seriously compromising performance on tests of social cognition later in life. The study of development in primates is important for understanding cross species comparisons in communication and cognition, especially social cognition.

Primary intersubjectivity, moreover, provides the foundation for the development of secondary intersubjectivity. Secondary intersubjectivity is when an infant can coordinate attention and action on an object with the attention and action with a social partner (reviewed in Trevarthen & Aitken, 2003). We have evidence that chimpanzees engage in at least two different forms of secondary intersubjectivity: intentional communication and social referencing. Intentional communication is evident when chimpanzees point to an object while gaze alternating between the object and the person (Leavens et al., 2005, 2008). Although Leavens and colleagues have not conducted developmental studies of intentional communication, fieldwork strongly suggests that referential behavior is evident as early as 9-12 months in wild chimpanzees, the same age as in human infants (van Lawick-Goodall, 1968).

I use the comparative developmental perspective to compare results from my own studies with those reported in the literature to arrive at an informed view of how development milestones

in chimpanzees compare with those in humans, and how developmental history of engagements might impact outcomes. Overall, these studies show that young chimpanzees compare favorably to humans as newborns through to 2.5 year-olds. Chimpanzees earlier development of motor skills, independently locomoting by 5-6 months in contrast to the 11-12 months of humans, has consequences in their developmental entry into the Referential Problem Space (Leavens et al., 2005, 2008), and their advanced manipulative ability has consequences in assessments of early cognition. However, even early developmental milestones in chimpanzees, as in humans, are significantly influenced by early experiences.

Much of our scientific knowledge of 'universal' psychological outcomes of humans is based on mono-cultural data (e.g., Henrich, Heine, & Norenzayan, 2010). Across many domains of adult cognition, western adults were found to be extreme outliers when compared with humans raised in non-western cultures (Henrich et al., 2010). Leavens, Hopkins, & Bard (2010) suggest that conclusions drawn from studies using laboratory chimpanzees similarly be viewed with caution. As reviewed in this chapter, emotional and cognitive outcomes of chimpanzees are sensitive to socio-emotional engagement experiences. The search for universal or species-unique social cognition in chimpanzees must be conducted with consideration of groups raised across many different 'lived experiences'.

Acknowledgements

Table 1: Emotional expressions found in neonatal chimpanzees (Bard, 1998, 2003)

INTEREST	JOY	UPSET/DISTRESS	ANGER	FEAR
Brightening	Greet	Pout	Mad face	Alarm
Effort Grunt	Smile	Fuss	Threat	
Tongue Click	Laughter	Cry		
		Cry face		

Table 2: Imitative performance of newborn chimpanzees in two test paradigms (adapted from Bard, 2007)

First Test when chimpanzees were 7-11 days old

Structured paradigm

No response/no match	Match 1 model	Match both models
	Lindsey	
	Rosemary	
	Wilson	
	Claus	
	Nugget	

Interactive paradigm

None	Match 1 model	Match 2 models	Match all 3
	Wilson	Rosemary	Lindsey
		Claus	
		Nugget	

Figure 1: Levels of object manipulation found in 3 different groups of nursery chimpanzees during their first year of life (adapted from Bard & Gardner, 1996). Group differences indicate that object manipulation varies as a function of early socio-emotional experiences. Object manipulation also varies as a function of age.
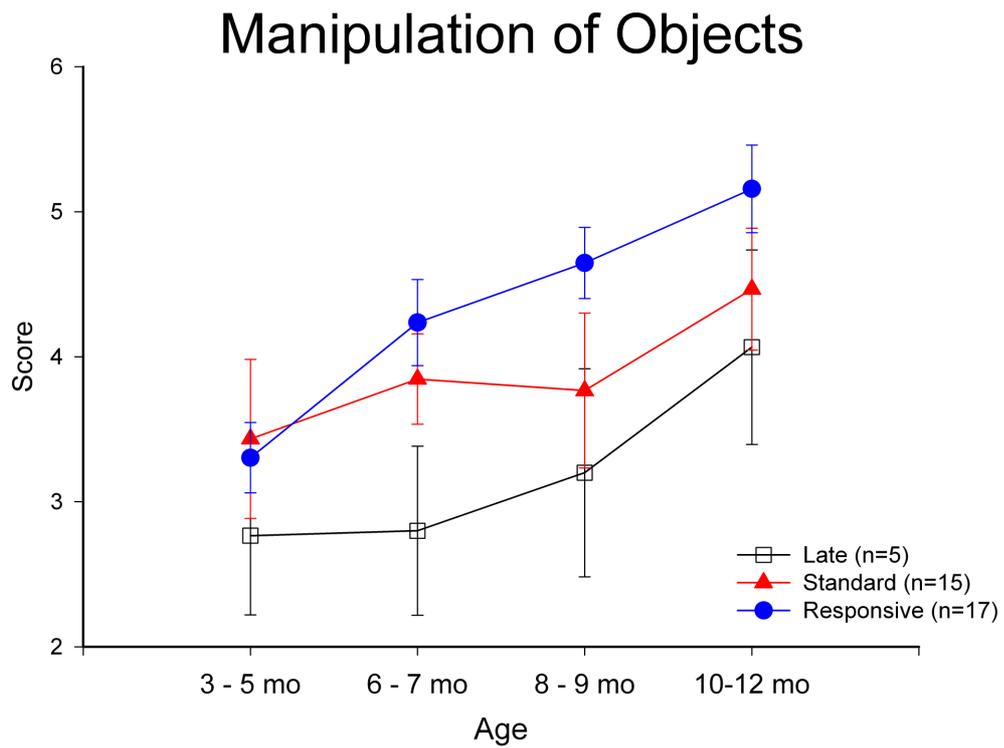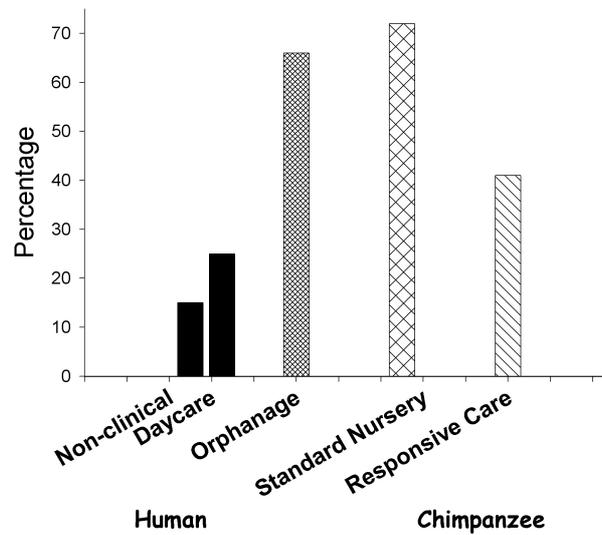
Figure 2: Percentage of human and chimpanzee 1-year-olds that have disorganized attachments with favorite caregivers (measured in the Strange Situation Procedure, SSP) as a function of early rearing environments (adapted from van IJzendoorn, Bard, Bakermans-Kranenberg, & Ivan, 2009).

Disorganized attachment in SSP

References

Adamson, L. B., & Bakeman, R. (1991). The development of shared attention during infancy. In R. Vasta (Ed.), *Annals of child development, Vol. 8* (pp. 1-41). London, England: Jessica Kingsley Publishers.

Ainsworth, M. D. S., Blehar, M. C., Waters, E., & Wall, S. (1978). *Patterns of attachment*. Hillsdale, N.J.: Lawrence Erlbaum.

Bakeman, R., Adamson, L.B., Konner, M., & Barr, R. (1990). !Kung infancy: the social context of object exploration. *Child Development, 61*, 794-809.

Bard, K.A. (1992). Intentional behavior and intentional communication in young free-ranging orangutans. *Child Development, 63*, 1186-1197.

Bard, K. A. (1994). Evolutionary roots of intuitive parenting: Maternal competence in chimpanzees. *Early Development and Parenting, 3*, 19-28.

Bard, K. A. (1996). *Responsive care: A behavioral intervention program for nursery-reared chimpanzees*. Tuscon, AZ: The Jane Goodall Institute.

Bard, K. A. (2000). Crying in infant primates: Insights into the development of crying in chimpanzees. In R. G. Barr, B. Hopkins & J. A. Green (Eds.), *Crying as a sign, a symptom, & a signal: Clinical emotional and developmental aspects of infant and toddler crying* (pp. 157-175). New York, NY: Cambridge University Press.

Bard, K. A. (2002). Primate parenting. In M. H. Bornstein (Ed.), *Handbook of parenting: Vol. 2: Biology and ecology of parenting (2nd ed.)* (pp. 99-140). Mahwah, NJ: Lawrence Erlbaum Associates Publishers. L. Erlbaum.

Bard, K. A. (2003). Development of emotional expression in chimpanzees (*Pan troglodytes*). *Annals of the New York Academy of Sciences, 1000*, 88-90.

Bard, K. A. (2005). Emotions in chimpanzee infants: the value of a comparative developmental

approach to understand the evolutionary bases of emotion. In J. Nadel & D. Muir (Eds.),

Emotional development: Recent research advances (pp. 31-60). New York, NY: Oxford

University Press.

Bard, K. A. (2007). Neonatal imitation in chimpanzees (*Pan troglodytes*) tested with two

paradigms. *Animal Cognition, 10*, 233-242.

Bard, K.A. (2009). Social cognition: Evolutionary history of emotional engagements with

infants. *Current Biology, 19(20)*, R941-R943.

Bard, K. A., & Gardner, K. H. (1996). Influences on development in infant chimpanzees:

Enculturation, temperament, and cognition. In A. E. Russon, K. A. Bard & S. T. Parker

(Eds.), *Reaching into thought: The minds of the great apes* (pp. 235-256). New York, NY:

Cambridge University Press.

Bard, K.A. & Leavens, D.A. (2009). Socio-emotional factors in the development of joint

attention in human and ape infants. In L. Roska-Hardy & E. Neumann-Held (Eds.),

Learning from animals? Examining the nature of human uniqueness (pp. 89-104). London:

Psychology Press.

Bard, K.A. & Nadler, R.D. (1983). The effect of peer separation in young chimpanzees (*Pan

troglodytes). American Journal of Primatology, 5*, 25-37.

Bard, KA, Brent, L., Lester, B., Worobey, J. & Suomi, SJ. (2010). Neurobehavioral integrity of

chimpanzee newborns: Cross-group and cross species comparisons. *Infant and Child

Development.*

Bard, K. A., Todd, B. K., Bernier, C., Love, J., & Leavens, D. A. (2006). Self-awareness in

human and chimpanzee infants: What is measured and what is meant by the Mark and

Mirror Test? *Infancy, 9*(2), 191-219.

Bard, K.A., Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., Costall, A., & Matsuzawa, T. (2005).   Group differences in the mutual gaze of chimpanzees (*Pan troglodytes*). *Developmental Psychology, 41*, 616-624.

Bayley, N. (1969). *Bayley Scales of Infant Development.* New York: Psychological Corporation.

Bjorklund, D. F. (2006). Mother knows best: Epigenetic inheritance, maternal effects, and the evolution of human intelligence. *Developmental Review, 26*(2), 213-242.

Boesch, C. (2007). What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison. *Journal of Comparative Psychology, 121*, 227-240.

Brazelton, T. B., & Nugent, J. K. (1995). *Neonatal behavioral assessment scale, 3rd Edition*: Mac Keith Press.

Brune, M., Brune-Cohrs, U., McGrew, W. C., & Preuschoft, S. (2006). Psychopathology in great apes: Concepts, treatment options and possible homologies to human psychiatric disorders. *Neuroscience and Biobehavioral Reviews*, *30*, 1246-1259.

Bullowa, M. (1979). (Ed.), *Before Speech: The beginnings of interpersonal communication*. New York: Cambridge University Press.

Burghardt, G. (2009). Darwin's legacy to comparative psychology and ethology. *American Psychologist, 64*, 102-110.

Call, J. & Tomasello, M. (1996). The effect of humans on cognitive development of apes. In A. E. Russon, K. A. Bard & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 371-403). New York, NY: Cambridge University Press.

DeSilva, J. & Lesnik, J. (2006). Chimpanzee neonatal brain size: Implications for brain growth in *Homo erectus. Journal of Human Evolution, 51,* 207-212.

Fouts, R. & Mills, S. (1997). *Next of kin: What my conversations with chimpanzees have taught me about intelligence, compassion, and being human.* London, UK: Michael Joseph.

Fragaszy, D.M. & Bard, K.A. (1997). Comparisons of development and life history in *Pan* and *Cebus*. *International Journal of Primatology, 18*, 683-701.

Gardner, B.T., & Gardner, R.A. (1971). Two-way communication with an infant chimpanzee. In A. M. Schrier & F. Stollnitz (Eds.), *Behavor of nonhuman primates: Modern research trends*, Vol. 4 (pp. 117-184). New York: Academic Press.

Gardner, R. A., & Gardner, B. T. (1989). A cross-fostering laboratory. In R. A. Gardner, B. T. Gardner, & T. E. Van Cantfort (Eds.), *Teaching sign language to chimpanzees* (pp. 1-28). Albany: State University of New York Press.

Hallock, M. B., Worobey, J., & Self, P. (1989). Behavioral development in chimpanzees (Pan troglodytes) and human newborns across the first month of life. *International Journal of Behavioral Development, 12*, 527 - 540.

Hayes, K. J., & Nissen, C. H. (1971). Higher mental functions of a home-raised chimpanzee. In A. M. Schrier & F. Stollnitz (Eds.), *Behavor of nonhuman primates: Modern research trends*, Vol. 4 (pp. 59-115). New York: Academic Press.

Henrich, J., Heine, S.J., & Norenzayan, N. (2010). The weirdest people in the world? *Behavioral and Brain Sciences, 33*, 61-135.

Hermann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, *317*, 1360-1366.

van IJzendoorn, M.H., Bard, K.A., Bakermans-Kranenburg, M.J. & Ivan, K. (2009). Enhancement of attachment and cognitive development of young nursery-reared

chimpanzees in responsive versus standard care. *Developmental Psychobiology, 51,* 173-185.

van Lawick-Goodall, J. (1968). The behavior of free-living chimpanzees of the Gombe Stream Nature reserve. *Animal Behavior Monographs, 1*, 161 - 311.

Jablonka, E. & Lamb, M. (2007). Bridging the gap: The developmental aspects of evolution. *Behavioral and Brain Sciences, 30*, 353-365. Keller, H. (2003). Socialization for competence: Cultural models of infancy. *Human Development, 46*, 288-311.

Johnson-Pynn, J., Fragaszy, D.M., & Cummins-Sebree, S. (2003). Common territories in comparative and developmental psychology: Quest for shared means and meaning in behavioral investigations. *International Journal of Comparative Psychology, 16,* 1-27.

Kalcher, E., Franz, C., Crailsheim, K., & Preuschoft, S. (2008). Differential onset of infantile depreivaiton produces distinctive long-term effects in adult ex-laboratory chimpanzees (*Pan troglodytes*). *Developmental Psychobiology, 50*, 777-788.

Keller, H. (2007). Cultures of infancy. Mahwah, NJ: L. Erlbaum.

Kellogg, W. N., & Kellogg, L. A. (1933). *The ape and the child: a study of environmental influence upon early behavior*: NY, Whittlesey House. (1933). 341 pp.

Lavelli, M., & Fogel, A. (2002). Developmental changes in mother-infant face-to-face communication. *Developmental Psychology, 38*, 288-305.

Leavens, D.A. & Bard, K.A. (in press). Environmental influences on joint attention in Great Apes: Implications for human cognition. Special Issue on "Culture and Cognition", edited by H. Keller for *Journal of Cognitive Education and Psychology*.

Leavens, D.A., Bard, K.A. & Hopkins, W.D. (2010). BIZARRE chimpanzees do not represent

"the chimpanzee". Commentary on target article by Henrich, Heine & Norenzayan, 'The

weirdest people in the world?', *Behavioral and Brain Sciences, 33(2/3)*, 100-101.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005). Understanding the point of chimpanzee

pointing: Epigenesis and ecological validity. *Current Directions in Psychological Science,

14*(4), 185-189.

Leavens, D.A., Hopkins, W.D., & Bard, K.A. (2008). The heterochronic origins of explicit

reference. In J. Zlatev, T. P. Racine, C. Sinha & E. Itkonen (Eds.) *The Shared Mind:

Perspectives on Intersubjectivity,* pp.185-214. Amsterdam, John Benjamins.

Lester, B.M., Anderson, L.T., Boukydis, C.F.Z., Garcia Coll, C.T., Vohr, B., & Peucker, M.

(1989). Early detection of infants at risk for later handicap through acoustic cry analysis.

In N. Paul (Ed.) *Research in infant assessment*. New York: March of Dimes Birth Defects

Foundation.

Menzel, E.W. (1964). Patterns of responsiveness in chimpanzees reared through infancy under

conditions of environmental restriction. *Journal of Psychological Research, 27*, 337-365.

Menzel, E., Davenport, R.K., & Rogers, C.M. (1970). The development of tool use in wild-born

and restriction-reared chimpanzees. *Folia Primatologica, 12*, 273-283.

Messinger, D. (2002). Positive and negative: Infant facial expressions and emotions. *Current

Directions in Psychological Science,11(1),* 1-6.

Myowa-Yamakoshi, M. (2006). How and when do chimpanzee acquire the ability to imitate?

In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds), *Cognitive development in

chimpanzees, (pp 214-232).* Tokyo, Japan: Springer-Verlag

Nugent, J. K., Lester, B. M., & Brazelton, T. B. (1989). *The cultural context of infancy*. New

Jersey: Ablex.

Ogden, C.L., Fryar, C., Carroll, M., & Flegal, F. (2004). Mean body weight, height, and body

    mass index, United Stated 1960-2002. Advance Data from Vital and Heath Statistics,

    347,1-18.

Oster, H. (2005). The repertoire of infant facial expressions: An ontogenetic perspective. In J.

    Nadel & D. Muir (Eds.), *Emotional development: Recent research advances* (pp. 261-292).

    New York, NY: Oxford University Press.

Papousek, H., & Papousek, M. (1987). Intuitive parenting: A dialectic counterpart to the infant's

    integrative competence. In J. Osofsky (Ed.), *Handbook of infant development* (Second ed.,

    pp. 669-720). New York: Wiley.

Piaget, J. (1952). The o*rigins of intelligence in children*. New York: Basic.

Pitman, C & Shumaker, R. (2009). Does early care affect joint attention in great apes (*Pan

    troglodytes, Pan paniscus, Pongo abelii, Pongo pygmaesu, Gorilla gorilla*)? *Journal of

    Comparative Psychology, 123,* 334-341.

Plooij, F. (1984).

Racine, T.P., Leavens, D.A., Susswein, N., & Wereha, T.J. (2008). Conceptual and

    methodological issues in the investigation of primate intersubjectivity. In F. Morganti, A.

    Carassa, & G. Riva (Eds), *Enacting intersubjectivity*. Amsterdam, NL: IOS Press.

Reissen, A.H. & Kinder, E.F. (1952). *Postural development of infant chimpanzees.* New

    Haven: Yale University Press.

Russell, C. L., Bard, K. A., & Adamson, L. B. (1997). Social referencing by young chimpanzees

    (Pan troglodytes). *Journal of Comparative Psychology, 111*(2), 185-191.

Savage-Rumbaugh, E. S. 1986. *Ape Language: From Conditioned Response to Symbol*. New

    York: Columbia University Press.

Suomi, S.J. (2006). Risk, resilience, and gene X environment interactions in rhesus monkeys. *Annals of the New York Academy of Science, 1094*, 52-62.

Susswein, N. & Racine, T. (in press). Sharing mental states: Causal and definitional issues in intersubjectivity. In J. Zlatev, T. P. Racine, C. Sinha & E. Itkonen (Eds.) *The Shared Mind: Perspectives on Intersubjectivity.* Amsterdam, John Benjamins.

Steiper, M.E., and Young, N.M. (2006). Primate molecular divergence dates. Mol. Phylogenet. Evol. *41*, 384-394.

Thorsteinsson, K. & Bard, K.A. (2009). Coding infant chimpanzee facial expressions of joy. In E. Banninger-Huber & D. Peham (Eds). *Current and future perspectives in facial expression research: Topics and methodological questions. Proceedings of the International Meeting at the Institute of Psychology, University of Innsbruck/ Austria, (pp. 54-61).* Innsbruck, Austria: Innsbruck University Press.

Tomasello, M., & Carpenter, M. (2005). The Emergence of Social Cognition in Three Young Chimpanzees. *Monographs of the Society for Research in Child Development, 70*, 1-136.

Tomonaga, M. (2006). Development of chimpanzee social cognition in the first 2 years of life. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds), *Cognitive development in chimpanzees, (pp 182-197).* Tokyo, Japan: Springer-Verlag.

Tomonaga, M., Tanaka, M., Matsuzawa, T., Myowa-Yamakoshi, M., Kosugi, D., Mizuno, Y., Okamoto, S., Yamaguchi, M., & Bard, K.A. (2004). Development of social cognition in infant chimpanzees (*Pan troglodytes*): Face recognition, smiling, gaze, and the lack of triadic interactions. *Japanese Psychological Research*, *46*, 227-235.

Trevarthen, C. (1979). Communication and cooperation in early infancy: A descriptive of primary intersubjectivity. In M. Bullowa (Ed.), *Before Speech: The beginnings of*

interpersonal communication. New York: Cambridge University Press.

Trevarthen, C., & Aitken, K. J. (2001). Infant intersubjectivity: Research, theory, and clinical

applications. *Journal of Child Psychology and Psychiatry, 42*, 3-48.

Tronick, E. Z., & Winn, S. A. (1992). The neurobehavioral organization of Efe (Pygmy) infants.

Developmental and Behavioral Pediatrics, 13, 421 - 424.

van IJzendoorn, M.H., Bard, K.A., Bakermans-Kranenburg, M.J. & Ivan, K. (2009).

Enhancement of attachment and cognitive development of young nursery-reared

chimpanzees in responsive versus standard care. *Developmental Psychobiology, 51,* 173-

185.

Vauclair, J. & Bard, K.A. (1983). Development of manipulations with objects in ape and human

infants. *Journal of Human Evolution, 12*, 631-645.

Vick, S-J, Waller, B., Parr, L., Smith Pasqualini, M., & Bard, K.A. (2007). A cross species

comparison of facial morphology and movement in humans and chimpanzees using FACS.

Journal of Nonverbal Behavior, *31*, 1-20.

Wallis, J. (1997). A survey of reproductive parameters in the free-ranging chimpanzees of

Gombe National Park. *Journal of Reproduction and Fertility, 109*, 297-307.

Yerkes, R.M. & Tomilin, M.I. (1935). Mother-infant relations in chimpanzee. *Journal of

Comparative Psychology, 20*, 321-359.