

THE IMPORTANCE OF DEVELOPMENT FOR COMPARATIVE PRIMATOLOGY

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■ **Abstract** It is a truism to say that primates develop, but it is also important to acknowledge that development occurs across many domains, including motor behavior, socioemotional behavior, communication, and cognition. In this review, we focus on those aspects of development that impact social cognition outcomes in infancy. Triadic engagements, such as those of joint attention, cooperation, and intentional communication, develop in the first year of life in chimpanzees and humans. Joint attention, for example, occurs when infants coordinate their attention to a social partner while also attending to an object or event. Hominoids are strongly influenced by experiences during early development, especially experiences that are foundational for these coordinated triadic engagements. Purported species differences in triadic engagements are highlighted in current evolutionary theories of primate social cognition, but conclusions about species differences are unfounded when development is ignored. Developmental experiences must be matched, controlled, or systematically varied in experimental designs that make cross-species comparisons. Considerations of development, across species and across rearing experiences, would contribute to more accurate evolutionary theories of primate social cognition.

DEVELOPMENTAL CONSIDERATIONS IN PRIMATE SOCIAL COGNITION

Since the 1960s, scientists have offered different theories to explain the evolution of primate social cognition. Beginning with [Jolly \(1966\)](#), investigators proposed a distinct evolutionary path for social intelligence because social intelligence was based on the need to function in complex societies and both supported social learning and depended

on it. [Humphrey \(1976\)](#) was also interested in the adaptations that allowed for learning flexibly during ontogeny, in particular, learning the complexities of sociality. [Parker & Gibson \(1979\)](#) presented one of the first evolutionary theories of primate cognition, and it was explicitly developmental ([Table 1](#)). Recent influential theories of the evolution of primate social cognition, however, neglect to consider development in nonhuman primates; ignoring development is a significant problem because primates and their social cognition develop as a result of social and emotional experiences. For example, many theories consider only the abilities of adults in species other than human and disregard the influence of developmental experiences on outcomes (but see [Boesch 2012](#); [Jablonka & Lamb 2007](#); Suomi 2004 for alternative perspectives). The shared intentionality model ([Tomasello et al. 2005](#)), the cultural intelligence hypothesis ([Herrmann et al. 2007](#)), the Vygotskian intelligence theory ([Moll & Tomasello 2007](#)),

Table 1 Developmental considerations in selected theories of primate social cognition

Theory/model	Is development considered for		
	Humans? ^j	Apes? ^j	Monkeys ^j
Social intelligence ^a	Yes	Yes	Yes
Piagetian development ^b	Yes	Yes	Yes
Theory of mind ^c	Yes	No	na
Machiavellian intelligence ^d	No	No	No
Social brain ^e	No	No	No
Shared intentionality ^f	Yes	No	na
Cultural intelligence ^g	Yes	No	na
Vygotskian intelligence ^h	Yes	No	na
Cumulative culture ⁱ	Yes	No	No

References: ^a[Jolly 1966](#), [Humphrey 1976](#); ^b[Parker & Gibson 1977, 1979](#); ^c[Premack & Woodruff 1978](#); ^d[Byrne & Whiten 1988](#), [Whiten & Byrne 1988](#); ^e[Dunbar 1998](#); ^f[Tomasello et al. 2005](#); ^g[Herrmann et al. 2007](#); ^h[Moll & Tomasello 2007](#); ⁱ[Dean et al. 2012](#), [Tennie et al. 2009](#).

^j“Yes” indicates that developmental change in this group was considered specifically in the indicated paper; “no” indicates that development, developmental experiences, and/or developmental change for this group was not considered in the indicated paper; “na” (not applicable) indicates that this group was not considered in the indicated paper.

and the cumulative culture model ([Dean et al. 2012](#); [Tennie et al. 2009](#); [Tomasello et al. 1993a](#)) are offered as theoretical and evolutionary explanations of “human-unique” social cognition. Unfortunately, the study designs upon which these theories are built cannot identify social cognition that is unique to humans, undermining the core premises of these theories. These studies have the following three fatal flaws, which are the subject of this article: (a) a reliance on an experimental design that inaccurately depicts group-specific differences as “species” differences because the design neglects the impact of developmental experiences as confounds; (b) a lack of consideration of development in nonhuman primates; and (c) exclusive reliance on a single human group without evidence that their social cognition outcomes are universal, especially among humans from different ecocultural settings (e.g., [Keller 2007](#)).

HOW NEGLECT OF DEVELOPMENT IN PRIMATE SOCIAL COGNITION IMPACTS THE DATABASE: INVALID EXPERIMENTAL DESIGNS

Consider the hypothetical research design proposed by [Leavens et al. \(2008\)](#). Neonatal representatives of two closely related, but genetically distinct groups, human boys and human girls, are assigned to two different treatment groups. Boys are assigned to rearing circumstances like those of institutionalized Romanian orphans, experiencing daily social and physical impoverishment and neglect. In contrast, the girls are assigned to a treatment in which they are raised by their biological families, experiencing frequent daily episodes of laughter, shared joy, cuddling, joint attention, and responsive care. At 9--12 months of age, we assess each group’s ability to engage in joint attention with adults. We would likely find that the girl group outperformed the boy group (see the next section for brief review of the consequences of deprivation on social cognition). The interpretive question of vital importance not only to this paper, but to the comparative evolutionary discipline is, Can we conclude that there is a genetically based sex difference in joint attention between human boys and human girls given this research design?

The answer to this question is obvious: No. This research design cannot support the conclusion that girls are superior to boys in joint attention (i.e., generalizing to all girls and all boys or identifying genes as the critical variable). The differences in developmental experiences (i.e., rearing history) between the boy group and the girl

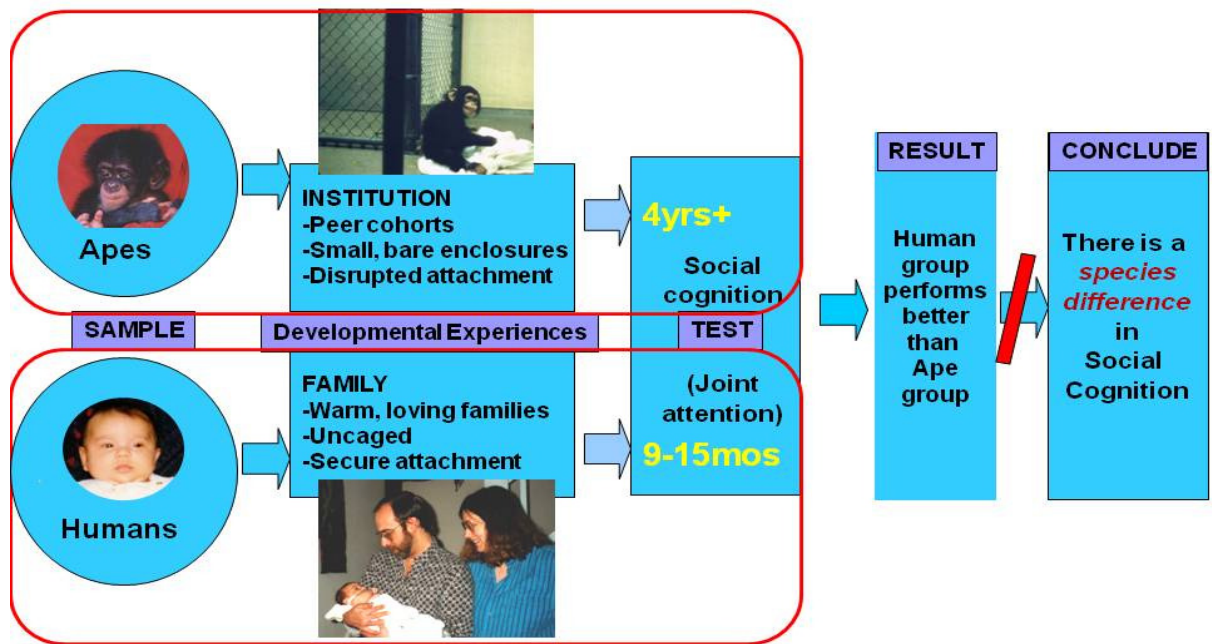
group are irretrievably confounded with their systematic genetic differences. Certainly, there is no reason to think that we would find the same superiority of girls in joint attention if the assignments to the two different rearing conditions was reversed, i.e., if the girls were assigned to the impoverished rearing condition.

Now consider **Figure 1**, which depicts precisely the same flawed research design. It depicts two groups of organisms whose genetic profiles systematically differ, although here, by simple substitution, the groups comprise human and ape neonates. It assigns the two groups to the same two rearing conditions as above: the ape group to experience impoverishment and neglect during development and the human group to experience warm, loving family life during development. Using the same outcome measure of joint attention, the likely result is a significant group difference, the human group displaying superior performance. Can we conclude from this research design that there is a genetically based species difference between apes and humans in joint attention? Of course not, for all the reasons outlined above.

In this experimental design, a third variable reflects yet another way in which development in nonhumans is disregarded. Added to the groups' systematic differences in genes and developmental experiences is the third confound: age at testing. In this design, the human group is tested during infancy (9--12 months), but the chimpanzee group is tested as juveniles (~4 years in captivity; [Fragaszy & Bard 1997](#)). Clearly, because no rational investigator would assert that there is a sex difference in the first research design with a two-way confound, we might reasonably expect, on logical grounds, that no contemporary researcher would assert that there is a species difference in the second research design, especially with a three-way confound (**Figure 1**). Unfortunately, this is far from the case: The results of such confounded experimental studies form the database for many of the contemporary evolutionary theories that claim "human-unique" social cognition (**Table 1**).

No amount of pleading can rehabilitate the illogical conclusion that girls (or humans) are innately superior to boys (or apes) in joint attention on the basis of these experimental designs (**Figure 1**). We cannot, for example, argue that because it would be really difficult or very expensive to equate the developmental experiences of these boys and girls (or apes and humans) that we should accept at face value the conclusion of sex (or species) difference. We have no basis on which to conclude that it is more

natural for girls (or humans) to be raised with positive affective experiences and for boys (or apes) to be raised in institutional settings. The design presented in **Figure 1** can never isolate genes as the explanatory factor accounting for the observed group differences in social cognition outcomes.



Adapted from Leavens, Hopkins, & Bard, 2005; 2008

Figure 1 Design flaws of current comparative studies. In this experimental design, developmental experiences and age at testing are not matched across groups and are confounded with genetic differences. Because developmental experiences strongly influence social cognition outcomes in apes and humans, this design can never isolate species as the explanatory factor accounting for group differences in social cognition.

THE DEVELOPMENT OF SOCIAL COGNITION IN HUMANS

Few theories deny the importance of development for social cognitive outcomes in humans. We find it surprising, however, that development is often ignored for nonhuman primates, especially when considering that apes, our closest evolutionary relatives, have a long period of infancy during which they are responsive to environmental stimuli. For human infants, we have known for decades that engagement with social partners and engagement with objects are essential developmental precursors for joint attention (e.g., [Bakeman & Adamson 1984](#); Trevarthen & Aitken 2001). For

chimpanzees, we have known for decades that outcomes vary as a function of developmental experiences (see reviews by [Bard & Leavens 2009](#); [Leavens & Bard 2011](#)), but these developmental effects have generally been ignored in theory building ([Table 1](#)). There is a puzzling and widespread bias toward attributing poor performance in nonhuman primates to genetic factors (e.g., the species lacks a capacity) and yet attributing similar poor performance in humans to developmental factors (e.g., infants lack a capacity). In the following sections, we review early development of joint attention in humans and chimpanzees, identifying differential outcomes as a function of early developmental experiences. Using this evidence, we discuss why the consideration of development is absolutely essential when building meaningful and valid theories of the evolution of primate social cognition.

We focus on the prototypical form of infant social cognition, that is, joint attention. Joint attention is a triadic ability, known as a “referential triangle,” “coordinated joint engagement” ([Bakeman & Adamson 1984](#)), or “intentional co-orientation to a common focus” ([Leavens & Racine 2009](#)), in which infants coordinate their attention to a social partner with their attention to an object or event. According to one of the most widely cited theories of primate social cognition, joint attention marks the developmental onset of shared intentionality ([Tomasello et al. 2005](#)). This form of social cognition is thought by some to be a precursor to “theory of mind” ([Nelson et al. 2007](#); [Tomasello et al. 2005](#)) or second-order intentionality (e.g., [Rakoczy 2009](#)).

Human Normative Development

Figure 2 illustrates the development of joint attention. In humans, joint attention emerges between 9 and 12 months and depends on a developmental history of early mutual engagement with social partners (peaking at 3 months) and a developmental history of early engagement with objects (from 5 months of age). In many urban and Western cultures, young human infants engage in face-to-face interactions with caregivers, with positive affective exchanges (i.e., primary intersubjectivity: [Trevarthen 1979](#); interpersonal engagement: [Adamson 1996](#)). By five months of age, human infants in these settings tend to shift their attention away from *en face* interactions with caregivers and toward exclusive interaction with objects. There appears to be a universal developmental milestone of increased manipulation of objects around 5--7 months of age (e.g., [Bakeman et al. 1990](#)).

The Development of Joint Attention

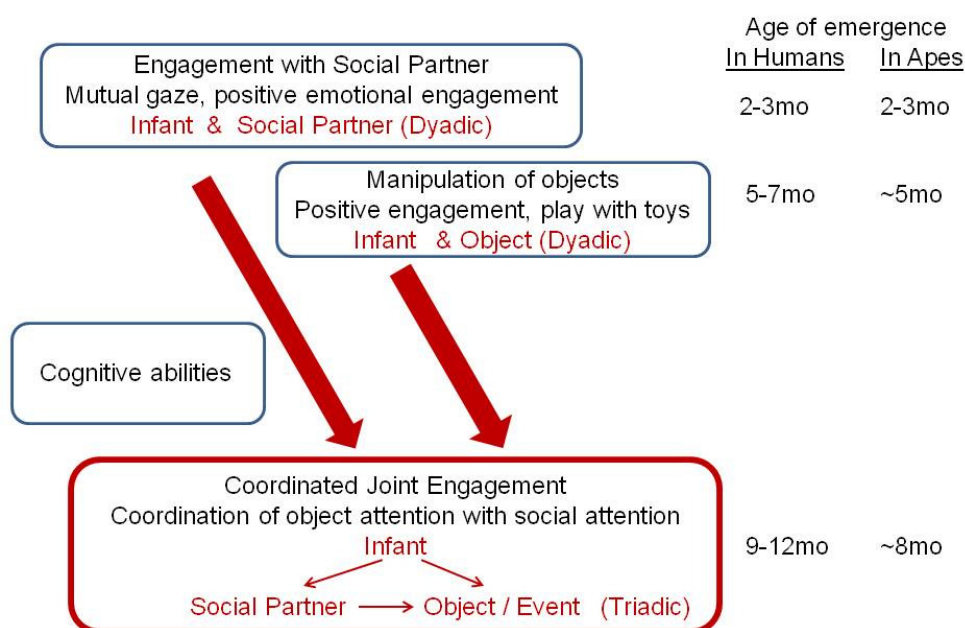


Figure 2 Social cognition develops in human and in chimpanzee infants. Joint attention is a triadic skill that develops from cognitive abilities entwined with developmental histories of previous dyadic engagements with social partners and with objects (Bard et al. 2014b). Ages of emergence in these dyadic and triadic skills follow similar timelines in human and chimpanzee infants.

These two strands of dyadic engagement (infants with social partners and infants with objects) intertwine with emerging cognitive abilities to allow infants to engage triadically in the final three months of the first year of life. Around 12 months of age, infants respond to adult bids and initiate joint attention by showing, offering, pointing to, and requesting objects, amid other shared practices (Racine & Carpendale 2007). Studies from the Western middle-class perspectives emphasize the independent agency of the one-year-old infant who is given the lead role in interactions (child-centered parenting style).

Cultural Variation in Human Infants

Infants' phenotypic expression of engagement with caregivers and engagement with objects varies across human cultures. Human infants from different cultures have different socioemotional experiences, i.e., different developmental histories. It should not be surprising, therefore, that the effects of particular human settings can be seen as early as the first several weeks of life (e.g., Bard 2005), and in many social, emotional,

and interactional outcomes. For example, in rural and interdependent cultures, high value is placed on body movement and physical contact with young infants ([Abels et al. 2005](#); [Keller et al. 2005a](#); [Rogoff et al. 1993](#)). Therefore, the amount of mutual gaze between infants and caregivers is reduced compared with Western norms ([Keller 2007](#)). There is also cultural variation in socialization practices surrounding object manipulation (e.g., [Bakeman et al. 1990](#)). In two rural settings in India, for example, three-month-olds were not given any toys ([Abels et al. 2005](#)), and in many traditional subsistence and hunter/gatherer cultures, there is very little caregiver encouragement, support, or attention paid to infant object manipulation ([Bakeman et al. 1990](#); [Hewlett & Lamb 2009](#); [Rogoff et al. 1993](#)).

Infants in traditional, agrarian communities are socialized to value social harmony and obedience and to follow the caregiver's lead (adult-centered parenting style: [Greenfield et al. 2003](#), [Keller et al. 2004](#)). In these cultures, infants are expected to comply with adult demands, and they do not command adults to follow their wishes (e.g., [Gaskins 2006](#)). Not only do infants in non-Western and rural settings spend significantly less time in joint attention activities, but they also exhibit significantly fewer pointing and showing gestures than do infants from Western, urban settings ([Bakeman et al. 1990](#), [Carpenter et al. 1998](#); [Clarke-Stewart 1973](#); [Salomo & Liszkowski 2012](#)).

Human Infants Raised in Severely Deprived Environments

Owing to government policies in the 1960s, many Romanian infants were raised in orphanages that did not provide the kinds of emotional and other interactive experiences that human children typically experience. In these orphanages, infants spent 17.5 hours per day alone in their cribs ([Vorra et al. 2003](#)). Studies have shown deleterious effects on cognitive, socioemotional development and attachment relationships in tragically impoverished and neglected populations [[Hennighausen & Lyons-Ruth 2006](#); [Nelson et al. 2007](#); [Rutter et al. 1999, 2010](#); [Rutter & Engl. Rom. Adopt. \(ERA\) Study Team 1998](#); [Spitz 1946](#)]. Human infants reared in Romanian orphanages had severely impaired or absolutely no joint attention skills ([Kaler & Freeman 1994](#)), and [Rutter & ERA \(1998\)](#) found between 30 and 300 times the background incidence of autism-like symptoms and severe deficits in communicative competence. The effects of early institutional care were still evident in follow-ups at 11 years ([Rutter et al. 2007](#)).

A prospective, randomized controlled experiment confirmed the earlier associations between prolonged privation and developmental outcomes ([Nelson et al. 2007](#)). Children randomly assigned to foster care (FCG) performed significantly better than did children randomly selected to remain in institutional care. For the FCG, adoption at two years of age or less was associated with better mental development scores than those associated with later adoption. Thus, both retrospective and prospective studies of human children exposed to unusual amounts of deprivation and neglect have identified long-term deleterious effects on cognitive functioning and socioemotional development, as well as an apparent dose-dependent response to institutional rearing (albeit with some remarkable potential for developmental catch-up, given subsequent good foster care; see, e.g., [Rutter & ERA 1998](#)).

THE DEVELOPMENT OF SOCIAL COGNITION IN CHIMPANZEES

Although we have known for decades that developmental experiences impact cognitive development in chimpanzees, few studies have provided information on the role of experience in the development of social cognition in apes. In this section, we review the studies that support our conclusion that chimpanzee infants, like human infants, develop joint attention and cooperation (among other triadic skills), based on developmental histories of engagement with social partners and engagement with objects (Figure 2).

Social Engagement in Chimpanzee Infants

It is in the realm of socioemotional development that we find a high degree of comparability between chimpanzees and humans and the earliest effects of developmental experiences in chimpanzees ([Bard 2000, 2003](#); [Bard et al. 2011](#)). Like human newborns, chimpanzee newborns smile with a play face to familiar sights and sounds at about four weeks of age and laugh in response to tickles in the second month of life (e.g., [Bard 2003, 2005](#)). Newborn chimpanzees imitate facial actions of caregivers ([Bard 2007](#)). By 30 days of age, the specific rearing environment impacts the affective quality and amount of face-to-face interactions ([Bard et al. 2011](#)). For example, the number of smiles seen in chimpanzee infants was significantly higher (given positive interactive experiences with humans) or significantly lower (given little or no exposure

to en face interactions with humans) than in a group of human infants (raised in Providence, RI; [Bard et al. 2011](#)). If the chimpanzee infants experienced 30 days of interaction with their biological mother, then they did not smile during interactions with a human examiner but did smile in interactions with their mother ([Bard 1994](#); [Bard et al. 2011](#)). Thus, the types of social stimuli with which chimpanzee infants engage (*a*) develop, (*b*) differ depending on developmental experiences, and (*c*) are evident from very early in life, i.e., by 30 days of age.

By three months of age, the amount of face-to-face interaction between infants and their chimpanzee mothers differs as a function of the caregiving environment ([Bard et al. 2005](#); see [Lavelli & Fogel 2002](#) for similar findings with human infants). Developmental experiences have dramatic effects in the preferred modality of mutual engagement; in some chimpanzees, face-to-face interactions emerge from six to eight weeks of age, whereas in other groups, close physical contact is the preferred modality for mutual engagement ([Bard et al. 2005](#)). There is a range in phenotypes of preferred mutual engagement between infants and social partners among primates (e.g., [Abels et al. 2005](#); [Bard 1994, 2009](#); [Bard et al. 2005](#); [Bard & Russell 1999](#); [Keller et al. 2005a,b](#); [Plooij 1984](#); [Rogoff et al. 1993](#)).

Chimpanzee Infant Engagement with Objects

Chimpanzee infants and human infants engage with objects in similar playful and manipulative ways, in rearing environments in which object play is valued and nurtured ([Bard & Vaclair 1984](#); [Fouts & Mills 1997](#); [Hayes & Hayes 1954](#); [Kellogg & Kellogg 1933](#); [Savage-Rumbaugh et al. 1998](#); [Temerlin 1976](#)). “Enriched” chimpanzee infants experience warm and available caregivers who scaffold, praise, and comment on infants’ explorations with objects (e.g., [Bard et al. 2013](#); [Fouts & Mills 1997](#)); mother-reared chimpanzee infants experience continuous physical contact, enriched social experiences, and infant-led explorations of the physical world independent of social interactions (e.g., [Boesch, 2012](#); [Goodall 1986](#); [van Lawick-Goodall, 1968](#)); human-reared nursery chimpanzee infants have extremely limited experiences, restricted access to objects and to caregivers, and poor-quality and low levels of interactions surrounding object manipulation even when caregivers are present (see [Bard et al. 2014b, figure S4](#); [van IJzendoorn et al. 2009](#); [Vaclair & Bard 1983](#)). A lack of exposure to objects in infancy can cause chimpanzees to be extremely fearful of new objects and avoid new objects

even many years later ([Menzel 1964](#)). These rearing experiences can also impact object manipulations that require more cognitive complexity, e.g., using objects as tools. For example, [Furlong and colleagues \(2008\)](#) compared tool use performance in chimpanzees from three backgrounds: those that had highly enriched rearing for most of their lives; those that had standard laboratory nursery experiences throughout their lives (from [Povinelli 2000](#)); and those with standard laboratory nursery for the first one to two years of life, followed by eight years at a highly enriched US sanctuary. Tool use performance varied systematically, with more sophisticated performance displayed by those chimpanzees with more enriched backgrounds. Thus, in chimpanzees, developmental experiences with object engagement have long-term effects, including effects on more complex abilities such as using objects as tools.

Triadic Skills (Joint Attention/Shared Attention) in Chimpanzee Infants

For chimpanzees, as well as humans, the dyadic engagements with social partners and with objects serve as the foundation for the emergence of joint attention and other triadic skills (**Figure 2**) ([Bard et al. 2014a,b](#)). A recent study demonstrated the presence of both joint attention and cooperation in chimpanzees as young as five months of age ([Bard et al. 2014b](#)). Joint attention was evident when young chimpanzees watched demonstrations or tried to imitate the object-related actions of social partners. The triadic skill of coordinated joint engagement in the social domain, i.e., cooperation, was evident when young chimpanzees anticipated actions (or reactions) of social partners in regular social games such as peek-a-boo or actively participated in the give-and-take of objects with a social partner. Previous developmental experience was a major, highly significant, factor predicting success in both types of social cognition ([Bard et al. 2014b](#)).

Developmental experiences during the first year of life have meaningful and large impacts on joint attention, cooperation, attachment, and communication ([Bard 2000](#), [2003](#); [Bard et al. 2014a,b](#); [van IJzendoorn et al. 2009](#); [Vauclair & Bard 1983](#)). For example, a chimpanzee toddler raised in an enriched family home exhibited pretend play with objects similar to that found in two-year-old humans (e.g., [Hayes 1951](#)). Young chimpanzees given explicit tuition have learned symbol systems comparable to those learned by 2--4-year-old human infants (e.g., [Fouts & Mills 1997](#); [Gardner et al. 1989](#); [Savage-Rumbaugh et al. 1993](#)).

Older chimpanzees exhibit this cognitive triadic capacity in many behaviors, such as intentional communication, cooperation, pointing, and social referencing ([Bard et al. 2014a](#); [Boesch 2012](#); [Hobaiter et al. 2014](#); [Leavens et al. 1996, 2004, 2005a,b, 2009](#); [Leavens & Hopkins 1998, 1999](#); [Russell et al. 1997](#)). Developmental experiences have long-lasting effects on the triadic social cognition skills involved in communication, imitation, and social cognition (e.g., [Carpenter et al. 1995](#); [Davenport et al. 1973](#); [Horowitz 2003](#); [Leavens et al., 2009](#); [Leavens & Hopkins 1998](#); [Lyn et al. 2010](#); [Menzel 1964](#); [Rumbaugh et al. 2008](#); [Russell et al. 2011](#); [Savage-Rumbaugh 1986](#); [Tomasello et al. 1993a,b](#)). Not surprisingly, differential developmental experiences are evident in brain structures of adult chimpanzees ([Bogart et al. 2014](#)), similar to those proposed for humans ([Fox et al. 2010](#)). Group-specific variants of tool use and intentionally communicative gestures have been documented in wild chimpanzees (summarized in [Whiten et al. 1999](#)) as well as captive chimpanzees ([Bard et al. 2014a](#); [Call & Tomasello 1997](#); [Pika & Liebal 2006](#); [Pollick & de Waal 2007](#)). Thus, there can be no doubt that chimpanzees exhibit joint attention and also exhibit a significant amount of phenotypic variation in social cognition.

Chimpanzee infants, like human infants, develop emotional responses to caregivers, to examiners, and to objects, and these developmental experiences influence chimpanzees' motivations to engage, their pleasure (or fear) in cooperation, and their ability to perform cognitively complex activities (e.g., [Bard 1998, 2005](#); [Bard & Gardner, 1996](#); [Bard et al. 2014b](#); [de Waal & Ferrari 2010](#); [Fouts & Mills 1997](#); [Menzel 1964](#); [Menzel et al. 1970](#); [Russell et al. 1997](#); [Savage-Rumbaugh et al. 1993](#)). We have known since the mid-1990s that young chimpanzees, like human toddlers, seek emotional messages about objects from favorite caregivers using a triadic skill known as social referencing ([Russell et al. 1997](#)). In social referencing, the chimpanzee's emotional bond with a caregiver supports the sharing of affective information about objects. Therefore, when the caregiver gives a negative message about the object (I don't like that object; it's scary), then the infant avoids the object. Alternatively, when the caregiver gives a positive message about an object (I like that object; it's a happy toy), the infant approaches and engages with the object. Additionally, some young chimpanzees may exhibit empathetic responses (comforting the caregiver when she expresses fear of the object) or spontaneous "showing" of objects (sharing attention to

objects for no reason other than mutual interest; [Carpenter et al. 1995](#), [Russell et al. 1997](#)). [Boesch \(2012\)](#) argued that social referencing was a component of theory of mind that occurred regularly in wild chimpanzees and furthermore presents convincing evidence of the chimpanzees' world "being 'transformed' by the social culture to which an infant belongs" (pp. 149--50).

Chimpanzees Raised in Institutional Nurseries

Institutional nursery rearing of chimpanzees produces many deficits in emotional and cognitive development, just as similar rearing negatively influences cognitive development in humans ([Smyke et al. 2007](#); [van IJzendoorn et al. 2009](#); [Zeanah et al. 2005](#)). The conditions of the great ape nursery at the Yerkes Primate Center from 1956 to 1991 are briefly described in [van IJzendoorn et al. \(2009\)](#). In the period from 1956 to 1961, some laboratory chimpanzees were raised in isolation from birth through two years of age, but few, if any, of these subjects have been used for comparative studies of social cognition. Isolation rearing produced individuals with severe and persistent stereotyped behavior (rocking, self-clasping, eye poking, etc.; [Davenport & Menzel 1963](#)), extreme fear of and avoidance of novel objects (e.g., [Menzel 1964](#)), an inability to cope with stress, persistent social deficits, and sexual deficits in adulthood (e.g., [Rogers & Davenport 1969](#)). Isolation rearing, even if begun at two or three years of age (in wild-born chimpanzees) can cause persistent stereotypies and long-term deficits in social behavior ([Kalcher et al. 2008](#)).

In the 1970s and early 1980s, many nursery-reared chimpanzee infants were raised in pairs or triads. Peer-group rearing was a major improvement over isolation rearing in terms of psychological health, as chimpanzees formed attachments, albeit with peers (e.g., [Bard & Nadler 1983](#)). In the late 1980s, with a new focus on psychological well-being (e.g., [Fritz 1986](#)), larger peer groups were formed, allowing 4--6 same-aged peers to live together continuously in enlarged spaces. This practice is known as standard care because it typifies institutional nursery care at the Yerkes Center and other institutional ape nurseries in the United States and Europe. During the average day, infant chimpanzees raised in a standard laboratory nursery spent ~2 of every 24 hours with an adult human caregiver ([Bard et al. 2011](#); [Bard et al. 2014b](#); [Spijkerman et al. 1996](#)). At Yerkes, this human-raised nursery care resulted in 59% of 9-month-old chimpanzees having an abnormal attachment to an inanimate object (usually a towel) and 72% of 1-

year-olds having disorganized attachment systems with their favorite human caregivers ([van IJzendoorn et al. 2009](#)). Secure, insecure-avoidant, and insecure-ambivalent classifications represent the various organized strategies emerging from an infant--caregiver attachment system that allows infants to adapt to their environments. In contrast, disorganized attachment represents the absence of or major dysfunction in this system, an unfortunately common result when infants experience a neglectful or abusive environment (e.g., [van IJzendoorn et al. 2009](#)).

Only at the Yerkes Primate Center, from 1991 to 1995, was a responsive care (RC) nursery in place ([Bard 1996](#)). For four hours of each weekday, chimpanzees younger than one year had a specially trained human researcher/caregiver who was dedicated to nurturing the chimpanzees' species-typical communicative, social, and motor development ([Bard et al. 2014a](#)). Infants raised in RC, compared with standard care, had significantly higher levels of joint attention success and significantly higher cognitive scores ([Bard et al. 2014b](#)). However, even with the reduced caregiver--infant ratio (1.5 to 1 in RC versus 12.5 to 1 in the standard nursery) and the increase in caregiver contact (300 more minutes in RC), RC infants spent most of their time with same-aged peers in the absence of adult caregivers (16 of every 24 hours during the week and 22 of 24 hours during weekends and holidays). This rearing environment resulted in 42% of RC chimpanzees having a disorganized attachment system, significantly less than was found in the standard nursery group ([van IJzendoorn et al. 2009](#)) but substantially more than we find in human nonclinical populations.

Implications

A substantial amount of evidence speaks to the power of early developmental experiences in shaping the social cognition of chimpanzees, an area that has received very little attention (but see [Bard & Leavens 2009](#); [Boesch 2007, 2012](#); [Brüne et al. 2006](#); [Kalcher et al. 2008](#); [Leavens & Bard 2011](#)). Current comparative studies may state that the chimpanzee subjects were “human-raised,” but typically, this designation means that they were raised in standard laboratory nurseries as described above (as were infants in the 1980s and 1990s). The percentage of disorganized attachment in human-raised nursery chimpanzees (72% in standard care) is comparable to that of human infants raised in very poor Greek or Romanian orphanages (~67%; see [Bard 2012, figure 14.2](#), based on data derived from [van IJzendoorn et al. 2009](#); [Smyke et al. 2007](#); [Zeanah et al.](#)

2005). Human-raised nursery-reared chimpanzees at 1 year of age had cognitive scores around 75, significantly lower than typically developing humans (with norms of 100; [Bard et al. 2014b, figure S6](#)) and remarkably similar to scores reported for human infants reared in substandard orphanages (an average of 66; [Smyke et al. 2007](#)). Raising chimpanzees in institutional nurseries significantly and negatively impacts their emotional and cognitive systems, with potentially long-lasting effects ([Bard et al. 2014b](#); [Brüne et al. 2006](#); [Clay et al. 2012](#); [Lyn et al. 2010](#); [Menzel et al. 1963](#); [Russell et al. 2011](#); [van IJzendoorn et al. 2009](#)), prompting [Menzel \(1964\)](#) to argue that the effects of raising chimpanzee infants in isolation were not noticeably different from the effects of any nursery rearing on chimpanzees. Even chimpanzees living as adults in physically enriched sanctuaries suffer long-lasting effects of early trauma and institutional care ([Ferdowsian et al. 2011](#); [Kalcher et al. 2008](#)).

CONSEQUENCES OF IGNORING DEVELOPMENT IN PRIMATE SOCIAL COGNITION

Current evolutionary theories of social cognition rely on monocultural data for humans, i.e., collected from educated and well-off people from Western, industrialized, democratic countries (known as WEIRD; [Henrich et al. 2010](#)). In many domains of adult cognition, ranging from basic perception to complex social cognition, WEIRD adults are extreme outliers. Current mainstream comparative theories tend to ignore variations in social cognition, even from human infants raised in non-Western, rural cultures. It is vital to incorporate cross-cultural developmental data into theories of social cognition to determine the precursors and sequelae of joint attention that are universal in humans across the full range of ecocultural contexts (e.g., [Vinden 1999](#)). In building evolutionary scenarios, it is important to acknowledge that Western industrialized society is extremely unlike the environment(s) of evolutionary adaptedness (e.g., [Foley 1996](#); [Hewlett & Lamb 2009](#); [Hrdy 2009](#); [Symons 1992](#)). Consideration of the diversity in outcomes among humans is essential in building meaningful and valid evolutionary theories of social cognition.

We cannot measure the universality of a characteristic, or the cognitive capacity of a species, by investigating only members living in a single environmental niche. For example, some investigators assumed that the initiation of joint attention by pointing

was universal and species-unique to humans, but this conclusion was based on studies with only Western middle-class infants (e.g., [Butterworth 2003](#)). People in some human cultures do not point with their fingers (therefore manual pointing is not universal in our species), and pointing reliably occurs in chimpanzees and other apes (therefore, pointing is not species-unique; [Hobaiter et al. 2014](#); [Leavens 2004](#); [Leavens et al. 2005b](#); [Wilkins 2003](#)). It is only by documenting phenotypic variation in outcomes across groups that we can determine whether a characteristic is universal and/or species-unique (see [Figure 3](#)).

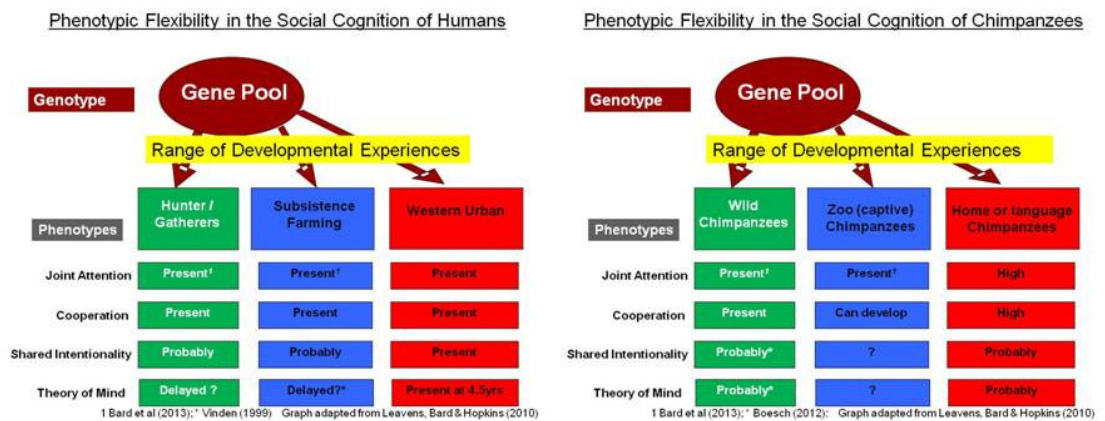


Figure 3 Phenotypic plasticity in social cognition. For future comparative studies we suggest this design that embraces the impact of developmental experiences on social cognition phenotypes (adapted from Leavens et al. 2005a, 2008, 2010). Species differences may be concluded if phenotypic outcomes do not overlap between chimpanzees and humans, given there is overlap in their developmental experiences.

On the basis of the data from studies of humans raised in Romanian orphanages and of apes reared in institutional nurseries, we purport that no researcher would assume that the institutionalized child is representative of the human species at large, and we argue that no researcher should assume that apes raised in institutional nurseries are the best representatives of their species ([Leavens et al. 2010](#)). Developmental experiences of such institutionalism clearly results in deficiencies in cognition, communication, and other socioemotional characteristics. One cannot generalize from the developmental profiles of these impoverished groups to the entire species. Unfortunately, very few contemporary researchers in comparative psychology give explicit consideration to how well their sample generalizes to the species (for exceptions, see [Bard et al. 2014b](#); [Boesch 2007](#); [Furlong et al. 2008](#); [Hayes 1951](#); [Leavens 2004](#); [Leavens et al. 2005a, 2008, 2010](#); [Lyn et al. 2010](#); [Racine et al. 2008](#)).

PROPOSING A STUDY DESIGN THAT EMBRACES DEVELOPMENTAL EXPERIENCES

We offer a research design that embraces development by documenting phenotypic variation in outcomes as a function of different developmental experiences (**Figure 3**) ([Leavens et al. 2005a](#), [2008](#), [2010](#)). When discussing social cognition outcomes, it is critical, yet a surprisingly uncommon practice, to consider the effects of development (especially, developmental experiences or rearing) in describing the capacities of apes, our closest evolutionary relatives. In the many ways we have identified here, the field would benefit from observing phenotypic variation in social cognition as a function of developmental experiences in humans and all other primates.

Multigroup comparisons are essential to specify whether types of social cognition are universal or species-unique because social cognitive outcomes of chimpanzees and humans are sensitive to developmental experiences. It remains a major task to systematically construct a model of the evolution of social cognition that builds on species comparisons containing developmental data (e.g., [Deák et al. 2013](#); [Jablonka & Lamb 2007](#); [Syal & Finlay 2011](#)). With this design, species differences could be concluded if there is no overlap in the phenotypic outcomes of chimpanzees and of humans, given that there is overlap in their developmental experiences. We propose that the use of this design (**Figure 3**), documenting the diversity and flexibility in outcomes and replacing the flawed experimental designs of the past (**Figure 1**), would support the construction of valid, logical, and grounded evolutionary theories of primate social cognition.

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