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Primate Sociality to Human Cooperation

Why Us and Not Them?

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Abstract Developmental psychologists identify propensities for social engagement in human infants that are less evident in other apes; Sarah Hrdy links these social propensities to novel features of human childrearing. Unlike other ape mothers, humans can bear a new baby before the previous child is independent because they have help. This help alters maternal trade-offs and so imposes new selection pressures on infants and young children to actively engage their caretakers' attention and commitment. Such distinctive childrearing is part of our grandmothering life history. While consequences for other cooperative activities must surely follow, the novel rearing environments set up by helpful grandmothering can explain why natural selection escalated preferences and motivations for interactivity in our lineage in the first place, and why, unlike other aspects of infant development, social sensitivities are not delayed in humans compared with genus *Pan*.

Keywords Human evolution · Life history · Genus *Pan* · Grandmothers · Infant development

In the past decade or so, prosocial emotions and cooperative capacities have become a major focus of researchers seeking to identify primary distinctions between humans and other primates (Cartmill 2010). Yet an increasing wealth of evidence shows social relationships to be major concerns of other primates as well (e.g., Aureli and de Waal 2000; Cheney 2011; Cheney and Seyfarth 2007; de Waal 2000, 2011; Dunbar 2010; Dunbar and Shultz 2007; Kappeler and van Schaik 2007; Seyfarth and Cheney 2007, 2012). Many social abilities once seen as uniquely human have been documented among our near relatives (e.g., Bard 2012; Call and Tomasello 2008; de Waal 2012; Hare and Tan 2012; Rosati et al. 2010). We belong to an order of remarkably gregarious and socially sensitive animals.

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Most assume that features shared with our cousins were the phenotypic foundation for directional selection (Fisher 1958; West-Eberhard 2003) that eventually led to the economic interdependencies and elaborate social constructions that now set living humans apart (Kappeler and Silk 2010). But contemporary differences in social accomplishments and our modern capacities and tendencies required step-by-step changes. All we see now was not present at the initial divergence of our genus. What was? Here I follow Sarah Hrdy's (1999, 2009, 2013) hypothesis that our distinctive motivations for cooperation and mutual understanding initially evolved in a socially sophisticated ancestor as a consequence of selection on mothers and infants in novel childrearing environments.

Hrdy builds on Michael Tomasello and colleagues' findings that shared intentionality distinguishes humans from other apes (Call 2009; Tomasello 2008; Tomasello and Carpenter 2007; Tomasello and Herrmann 2010; Tomasello et al. 2005). The evolutionary benefit they identify for this capacity is the widespread cooperation that it enables, the Cultural Intelligence Hypothesis (Herrmann et al. 2007). But as Hrdy notes, those benefits do not explain why shared intentionality evolved in our lineage and not in other genera of the hominid radiation. In contrast, the selection pressures that accompanied the shift away from independent mothering to our distinctive childrearing might explain why shared intentionality evolved in our lineage in the first place. Immediate survival advantages could have selected infants more effective at engaging caregivers long before the evolution of more elaborate cultural interdependencies—establishing the social preferences that are then their foundation.

If selection on infants in novel rearing environments accounts for the initial evolution of distinctively human prosociality, what accounts for the origins of those rearing environments? As known ethnographically, human mothers and dependent children get help from many sources (Howell 2010; Hrdy 1999, 2009; Sear and Mace 2008). Older siblings contribute (e.g., Kramer 2011; Kramer and Ellison 2010), and the fact that humans form pair bonds and the fathers sometimes help has an especially venerable place in ideas about the evolution of our lineage (e.g., Hill and Hurtado 2009; Kaplan et al. 2000, 2010; Lancaster and Lancaster 1983; Lovejoy 1981; Washburn and Lancaster 1968). Men's work contributes substantially to what mothers and children consume, but men often spend time and energy supplying collective goods rather than directly provisioning their mates and offspring (Hawkes 1990, 1993a, b, 2004; Hawkes and Bliege Bird 2002; Hawkes et al. 1991, 2001, 2010). What and how much men do as husbands and fathers varies widely both within and between ethnographic communities (Gray and Anderson 2010; Hawkes et al. 2001; Hrdy 1999, 2008; Marlowe 2003). Neither facultative fathering nor male ontogeny and sexual dimorphism (Bribiescas 2006; Puts 2010:161–163 and references therein) are consistent with an evolutionary history of obligate paternal care.

The argument I pursue here is that the distinctive dependence of human mothers on rearing help initially evolved with grandmothering. Proposed to account for the increased longevity, delayed maturity, and early weaning of humans compared with our closest living relatives (Hawkes 2003; Hawkes et al. 1997, 1998; O'Connell et al. 1999), helpful grandmothering allows human mothers, unlike other ape mothers, to have next babies before the previous ones are independent. Grandmothering sets up the novel selection pressures on mothers and infants identified by Hrdy. Those pressures make social engagement advantageous to infants, so natural selection favors early social development despite delays in other aspects of life history.

This notion of early social development in human infants may seem mere fantasy in light of still-influential views such as those of Montague (1961) about the first year of human life. He said, "the human infant is quite as immature at birth as is the little marsupial immaturely born into its mother's pouch, there to undergo its exterogestation until it is sufficiently matured" (161:157). But comparisons between humans and chimpanzees contradict claims of unique helplessness in human babies (Matsuzawa 2012; Schultz 1969).

The hypothesis that social capacities are shaped by selection on infants as a result of novel rearing environments makes the developmental timing of social cognition and emotions a crucial line of evidence about our evolution. Brian Hare (2011) and colleagues (Wobber et al. 2010) recently highlighted the evolutionary importance of timing shifts in the cognitive ontogeny of humans and genus *Pan*. My argument shares their assumption that foundational abilities for human sociality must have been present in our last common ancestor with the other great apes. However Hare and collaborators cite the Cultural Intelligence Hypothesis to explain the evolution of human social cognition: benefits are "participating and exchanging knowledge in cultural groups" (Herrmann et al. 2007:1360). Since natural selection is blind to future consequences, what evolved later cannot explain initial selection for our distinctive prosociality, but selection exerted by rearing environments might. If elevated social sensitivities evolved in humans because they gave survival advantages in infancy, social skills and emotions should develop earlier in humans than in genus *Pan*.

After summarizing Tomasello and colleagues' findings about shared intentionality, Hrdy's arguments about the novel selection pressures of human rearing environments, and the hypothesized role of grandmothering in the evolution of human life history, I consider some comparative evidence about the developmental timing of social abilities in humans and genus *Pan*. The evidence, though varied, disputed, and incomplete, shows human babies to be socially engaging and discriminating—perhaps right from birth. Although this early development could have come after cultural propensities that evolved in our lineage for other reasons, a simpler alternative reverses the causal arrow. That reversal makes the evolution of our distinctive prosociality an aspect of our grandmothering life history, which laid the foundation for the subsequent evolution of language, vastly expanded the range of venues for male status competition (Coxworth 2013), and escalated the social and economic interdependence of our cultural lives.

Tomasello and Colleagues' "Shared Intentionality"

Tomasello's observations and experiments in the 1980s identified differences in social cognition between children and chimpanzees. Subsequent work continued to build evidence for and improve characterization of those differences. Recently Tomasello and Call (2010:249) said:

> the totality of current evidence strongly suggests that . . . the fundamentals are the same for chimpanzees and humans: a perception-goal psychology enabling the understanding of important aspects of intentional, rational action and perception. . . . Most of human cognitive uniqueness derives . . . from some species-unique social-cognitive skills and motivations for sharing intentional states with others in special types of cooperative and communicative activities.

Tomasello (e.g., 1999) has also written at length and persuasively about the fundamental role of shared intentionality in human life. It is "what is necessary for engaging in uniquely human forms of collaborative activity in which the plural subject 'we' is involved: joint goals, joint intentions, mutual knowledge, shared beliefs—all in the context of various cooperative motives" (Tomasello 2008:6–7).

The arguments and ever-growing evidence for this human distinction and about its consequences for human language, social learning, cultural transmission, and cooperation are persuasive. Less so are the answers as to why these capacities and motivations evolved in humans and not in other apes. As Hrdy (2009) asks, "Why us and not them?" Tomasello (2009:75, and further elaborated in Tomasello et al. 2012) pins the shift on cooperation in foraging activities. Hrdy's analysis of the cooperative childcare that distinguishes humans from the other great apes is noted as one possibility to explain why we seem to be "more socially tolerant and less competitive over food" (2009:84). But selection on infants as a consequence of novel rearing environments is mentioned only in passing. Here I assemble reasons to make it central.

Hrdy's Analysis of Rearing Environments

In *Mother Nature* (1999:177ff) Hrdy drew attention to contrasts between the "discriminating solicitude of human mothers" and the nearly "unconditional devotion characteristic of mother monkeys and apes." She noted that because humans bear the next baby before the previous one reaches independence, they cannot focus unconditionally on their new infant. A mother's reproductive success will depend on how she distributes attention among multiple dependents. This predicament inevitably puts selection pressures on her capacities and motivations to calibrate costs and benefits and shift investment accordingly. Moreover, the ability to rear overlapping dependents can only evolve if help is usually available. This implies selection on mothers both for situation-dependent commitment and for capacities to juggle the additional tasks of recruiting and maintaining helpers.

Hrdy took initial steps in 1999 toward exploring the consequences of these shifts in maternal strategies for selection on the social abilities of infants and children. In subsequent papers, and especially in *Mothers and Others* (2009), she highlighted those important effects, not only canvassing findings in developmental psychology but also making explicit links to Tomasello's arguments about shared intentionality.

Drawing widely on both ethnography and primatology, Hrdy documented contrasts between the problems faced by human and other ape infants. Whereas other ape infants are inseparable from their mothers, each having its mother's undivided attention, human babies often spend substantial amounts of time away from their mothers right from birth. The combination of mothers' distributed concerns and the importance of other helpers puts a premium on the capacities of infants themselves to engage both mothers and others (Chisholm 2003).

The "why us and not them?" question has not been Tomasello's central concern. In contrast, Hrdy has focused on the very particular adaptive advantages conferred on human infants and youngsters who are better at engaging their mothers and other potential caretakers (Chisholm 2003). Payoffs for slight improvements in attracting commitment will be greatest, and selection strongest, where that commitment is most crucial. In humans as in other primates, mortality is highest in infancy. That is when caretakers' attentions are a matter of life or death.

Grandmothering and Human Rearing Environments

The Grandmother Hypothesis (Hawkes 2003; Hawkes et al. 1997, 1998; Kim et al. 2012; O'Connell et al. 1999) addresses the evolution of human rearing environments. It proposes that ancestral populations faced ecological changes in the Plio-Pleistocene that restricted the availability of the foods just-weaned juveniles could handle for themselves. Mothers who did not follow the retreating forests had to provision their weanlings, and this longer period of juvenile dependence presented a novel opportunity for any older females still surviving as their fertility was ending. They could enhance their own fitness by helping provision their dependent grandchildren and allowing daughters to have their next babies sooner without reductions in previous offspring survival. As a consequence, our lineage evolved greater longevity, later maturity, and earlier weaning from an ancestral life history that was like that of the other living great apes, all without altering the age at which female fertility ends.

The hypothesis was initially stimulated by observations of high levels of economic productivity by women past childbearing among East African Hadza hunter-gatherers (Hawkes et al. 1989, 1997), but grandmother effects have been looked for and usually found in an array of human populations (e.g., Lahdenperä et al. 2004; Sear and Coall 2011; Sear and Mace 2008; Voland et al. 2005). Formal modeling has shown that when resources produced by the older generation are important to reproductive success, it is production and not fertility that determines selection against senescence, so humanlike productivity can maintain humanlike aging rates (Lee 2003, 2008).

A mathematical simulation (Kim et al. 2012) now shows that grandmothering alone can evolve an apelike life history into a humanlike one. Verbal arguments about the ancestral shift in life history (Hawkes 2003; Hawkes et al. 1997, 1998) assumed that regularities observed among life history traits across the living primates held in the past as well: greater adult longevity favored later maturity and later ages at independence (Charnov 1993; Charnov and Berrigan 1993; see Hawkes 2006a for review). Peter Kim's mathematical model (Kim et al. 2012) assumes that too. The simulation begins with a population at an apelike equilibrium for longevity, age at maturity, and age at independence. The addition of helpful grandmothering favors greater longevity in both sexes and shifts that equilibrium. Apelike longevity evolves into the human range, with increased age at first birth and lengthened duration of juvenile dependence. When adult lifespans are apelike, very few can be helpful grandmothers—less than 1% of the caregivers in this simulation. Nevertheless, those few are enough for helpful grandmothering to drive the evolution of increased longevity and expand the fraction of grandmothers into the human range. That happens because longer-lived grandmothers can help more descendants, and their help gives greater benefits to longer-lived mothers.

The model makes no assumptions about shifts in caretaker preferences. Hrdy has described notable "donative intent" in elder female monkeys (1999, and see Wroblewski 2008 for chimpanzees). This, plus widespread "baby lust" in primates, suggests that attraction to infants has deep phylogenetic roots with maternal protectiveness the main impediment to infant sharing (Hrdy 2009). Mothers might most trust their own mothers with access to dependents, and grandmother effects would have the largest fitness impact through help to daughters' offspring because assurance of shared genes through sons is uncertain. But initial critiques of the Grandmother Hypothesis cited female natal dispersal throughout our lineage that would have kept mothers and adult daughters apart. Now evidence is plentiful that hunter-gatherers do not show the presumed patrilocal bias (Alvarez 2004; Hill et al. 2011; Marlowe 2004; Wilkins and Marlowe 2006). Nevertheless Peter Kim's mathematical model (Kim et al. 2012) is deliberately conservative, allowing grandmothers to help any dependent juvenile, not just daughters' children.

The model is, of course, an extreme simplification, aimed to see whether (very weak) helpful grandmothering could propel the evolution of a humanlike life history from an apelike one. It does not include the maternal problem of distributing attention among newborns and older dependent juveniles because model mothers can only start a new pregnancy when not caring for a dependent. Model juveniles do not vary in how likely they are to receive care, except that grandmothers take older dependents first and cannot take them before they reach age two. Caretakers—both mothers and grandmothers—are only allowed to care for one dependent at a time. All these constraints obviate the distributed attention problem for model mothers. But there are never enough grandmothers in the model to take on all the juveniles eligible for non-maternal help. If juveniles varied in their ability to engage that help, the mothers of those better able to do so would have shorter birth intervals and higher reproductive success. Even without considering differential allocation of maternal investment, a rearing environment with helpful grandmothers has ample room for selection on youngsters' social abilities.

Cognitive Ontogeny

On these grounds, grandmothering would have consequences for the ontogeny of social cognition. More than 30 years ago, in *Ontogeny and Phylogeny*, Stephen J. Gould was especially interested in "the immediate significance of acceleration and retardation in the evolution of life-history strategies for ecological adaptation" (1977:8). He noted especially the long childhoods and delayed maturation of our own species. Although Gould recognized there must be diversity in patterns of development, he concluded that "Neoteny has been a (probably the) major determinant of human evolution" (1977:57).

Aspects of human life history are unassailably slow relative to those of other great apes. Adult lifespans are longer, the beginning of adulthood is later, and juveniles are dependent longer. But weaning age is earlier, and subsequent work has mostly falsified global neoteny for growth and development (e.g., Godfrey and Sutherland 1996; Leigh and Park 1998; McKinney and McNamara 1991; Minugh-Purvis and McNamara 2002; Parker et al. 2000; Shea 1989; Thompson et al. 2003, see Hawkes 2006b for review). Still, developmental timing shifts remain likely mechanisms for the evolution of differences. Gould (1977) cited King and Wilson's (1975) demonstration that the genetic differences between humans and chimpanzees are small compared with the many organismal differences between the two species. He endorsed their hypothesis that the phenotypic differences must be largely due to regulatory mutations.

"Heterochronic changes are regulatory changes; they require only an alteration in the timing of features already present" (Gould 1977:9).

Gene Expression and Brain Imaging

Gene expression studies now reveal regulatory changes making the neoteny hypothesis again a useful guide to research. Somel et al. (2009) studied gene expression in postmortem brain tissue from rhesus macaques, chimpanzees, and humans. They found slightly more than 3,000 genes expressed in all three species. Using rhesus as an out group they could assign about 10% to four developmental categories based on whether there were timing changes in humans or chimpanzees and whether the changes were delay or acceleration. Of these, 38% showed timing changes in humans that were delayed relative to chimpanzees, about twice as many as they found in any of the other three categories. While the phenotypic consequences of the genes expressed are unknown, correlations between age of expression and observed differences in development at those ages are suggestive. They reported that "at least in one of the two cortical regions studied, the neotenic shift is most pronounced at the time when humans approach sexual maturity, a process known to be delayed in humans relative to chimpanzees or other primates" (2009:5746).

Somel et al. (2012) noted an array of hypotheses to link delayed maturity in humans to our notable longevity. Here I privilege the Grandmother Hypothesis to explain it. As noted, the addition of Hrdy's arguments about rearing environments also connects grandmothering to selection for accelerated development in infant social cognition. That connection implies early expression in genes associated with social sensitivities. Even though the phenotypic effects of the genes in Somel and colleagues' gene expression study remain unknown, their results could provide an initial test of whether any genes show accelerated expression in human babies' brains compared with brains of baby chimpanzees.

Approximately 22% of the genes with expression changes in Somel et al. (2009) do show acceleration in human brains, but the authors do not report the ages at which acceleration is most prominent. What they do say is not encouraging for the expectation of early social acceleration: "human-chimpanzee expression divergence is relatively small after birth" (2009:4746). But perhaps a focus especially on the first few years would show different results. That possibility is suggested by a report from Sakai and colleagues (2011), who used brain imaging to compare the development of white matter (WM) between chimpanzee and human infants and found "the rate of prefrontal WM volume increase during infancy was slower in chimpanzees than in humans" (2011:1397). Their conclusion, consistent with the expectations developed here, is that "the lineage leading to modern humans has undergone substantial evolutionary modifications, resulting in the rapid development of the prefrontal connections during infancy. This likely facilitates the development of complex social interactions" (2011:1401).

Behavior in the Wild

Frans Plooij (1984) studied six chimpanzee mother-infant pairs at Gombe, noting that mothers were alone (with their infants) most of the time, with infants on their mother's body for the first 3 months. By 8 months infants spent 80–90% of their time in physical contact with their mothers, and still the majority of their time by 12 months (1984:97). Initially mothers paid little visual attention to their babies. Until about 9 months the baby would grasp the mother's food and initially she allowed this. "Soon, however she passively prevented the baby from taking the food by not letting go of it or by withdrawing her hand from its advance. In such cases the baby (or young infant) kept trying to obtain the food directly, without even looking up into the mother's face" (1984:116).

Contrast that description with Melvin Konner's account (1972:292–293) of human infant development among Ju/'hoan hunter-gatherers:

> From their position on the mother's hip . . ., the infant's face is just at the eye-level of desperately maternal 10-to-12-year-old girls who frequently approach and initiate brief, intense, face-to-face interactions, including mutual smiling and vocalization. . . . [Infants] are passed from hand to hand around the fire for similar interactions with one adult or child after another. . . . Objects are often used to distract fretting babies. They become regular targets for the phrase "look at that" by the second week. . . . Crying, the pucker face, and sub-cry vocalizations are the infant's most powerful survival weapons. They appear on the first day of life and remain prominent items in the behaviour repertoire throughout early childhood.

Konner reports that an infant "is born with the basis of social behavior. . . . By smiling he can make [his mother and others] smile and vocalize, or even make his surroundings explode with human sounds. By dint of these powers he is a social animal at birth" (1972:294).

These accounts suggest more interactivity, earlier, in human than in chimpanzee infants. But Plooij noticed "aversive reactions" to strangers at 6 months in his chimpanzees whereas Konner's summary in his recent broad synthesis of *The Evolution of Childhood* (2010:229) suggests it may be slightly later in human infants. Across a wide range of cultural and socioeconomic contexts, "the growth of social fears with the concomitant growth of attachment appears to be a universal feature of the second half year."

Observations and Experiments with Captive Chimpanzees

Results from measurements on captive chimpanzees indicate notable similarities to humans in both attachment and its developmental timing. van IJzendoorn et al. (2009) evaluated the attachment behavior of 12-month-old chimpanzees using the Strange Situation Procedure (SSP) designed to reveal the quality of attachment in human infants. In the SSP infants are placed an unfamiliar environment and confronted by a stranger with two brief separations from their caregiver. The researchers found that "Expert coders trained on hundreds of human infant attachment SSP's were readily able to independently identify individual attachment patterns in chimpanzee infants with a high level of inter-coder reliability" (2009:180). They concluded that "the attachments of infant chimpanzees appear surprisingly similar to those of human infants" (2009:181).

Van IJzendorn and colleagues (2009) also reported results from the Bayley Scales for Infant Development (Bayley 1969) on captive chimpanzee infants and compared them with results from human infants. The Bayley scales are used to assess the development of motor, language, and cognitive skills in human infants. Chimpanzee scores at 3.5 months were higher than the human standard (Bard and Gardener 1996) and then declined with age relative to human norms, overlapping them at about 9 months. Investigators found that "In comparison with normed human US samples, 9-month-old nursery-reared chimpanzees would be considered to show typical cognitive development, apart from the lack of language skills" (van IJzendoorn et al. 2009:181). But, "by 12 months, the chimpanzees were not combining objects or using objects in functional ways, including tools . . ., [whereas] at 10–12 months, human infants began to exhibit turn-taking, tool use, and other object-object combinations" (Bard and Gardener 1996:240–241).

Another standard measure of social abilities that has been applied to both human infants and captive nonhumans is Gallup's (1970) Mark and Mirror Test. The test is whether subjects recognize the surreptitiously marked reflection in the mirror as themselves. Lewis and colleagues (1989) found that the development of self-recognition in human infants at about a year and a half indicates a "social self" with the capacity to experience self-conscious emotions such as embarrassment, pride, empathy, and jealousy. Chimpanzee infants pass this test after the age of two (Lin et al. 1992; see Bard et al. 2006 for more nuanced discussion of protocols with more subjects).

Kim Bard and colleagues (2011) used the Brazelton Neonatal Behavioral Assessment Scale (NBAS) to compare newborn development between humans and chimpanzees and to investigate differences among chimpanzees by captive care regimes. The NBAS was developed by Brazelton (1984) to evaluate infant adjustment to life outside the womb. Of the 21 items and four cluster scores, Bard et al. (2011:48) found the "human group was distinct in only 1 of the 25 NBAS scores (the human group had significantly less muscle tone than all the chimpanzee groups)."

Care Regimes and Standards of Comparison

Infant developmental norms and studies of human infants have largely relied on Western middle-class babies. Captive chimpanzee subjects (both babies and adults) have usually been tended as infants by humans in nurseries (Bard 2012). Neither subject pool is representative (e.g., Henrich et al. 2010; Leavens et al. 2010). Apparent differences may be inflated because the human babies tested have had early experiences that—unlike in some (but not all) cultural settings (Lancy 2007; Liu and Tronick 2011; Super 1981)—explicitly promote early social interaction, whereas the chimpanzees mostly have not (Bard 2012).

Responsive care (Bard 1996) was an innovation at the Yerkes nursery in the early 1990s in which all chimpanzees under 1 year of age had an additional 4 h a day, 5 days a week of active interaction with specially trained research assistants. van IJzendoorn et al. (2009) distinguished cohorts of chimpanzee infants that had received standard nursery care from those that had received responsive care. Although "disorganized attachment" was less frequent at 12 months among the responsive care cohort, records from scores on the composite Mental Development Index of the Bayley Scale showed no difference by care regime at 3 months or 4 months (van IJzendoorn et al. 2009:176). When, at 9 months, the chimpanzee subject pool overlapped human norms, those with responsive care scored significantly higher than both the standard care cohort and the human standard (2009:180).

Captive care regimes might lead to overestimating differences between human and chimpanzee infants, but they might also lead to underestimation of differences. In captivity, even with mother-rearing, babies can be set down safely, unlike the wild where babies must cling all day long as their mothers travel and forage (Plooij 1984). Takeshita et al. (2009:252) noted that the human pattern of placing babies down on their backs "promotes face to face communication. . . . Moreover, infants in the supine position can interact with other nearby individuals in the same manner from an early age." As captivity seems to expose similar sensitivities between human and chimpanzee newborns, so too a shift from independent mothering could have revealed these capacities in ancestral populations (Hrdy 2013), providing phenotypes for directional selection to modify (Chisholm 2003; Fisher 1958; Gould 1977; West-Eberhard 2003). Has it done that?

At the Kyoto University Primate Research Center, where trusting relationships with chimpanzee mothers have allowed researchers to monitor social capacities in mother-reared infants, Tomonaga and colleagues (2004) found remarkable similarities to humans in chimpanzee infant and mother mutual gaze and infant gaze-following through the first 2 months of life. Initially infants matched facial expressions with caregivers as human babies do (Myowa-Yamakoshi et al. 2004), but this declined to chance levels by 2 months of age. The "9 month revolution" when human infants begin to seek joint attention with others on objects of interest "does not seem to occur in chimpanzees. . . . The chimpanzee infants never displayed 'object showing' or 'object giving,' indicative of referential communication in a triadic relationship in human infants" (Tomonaga et al. 2004:232).

Human infants draw others into joining them in paying attention to things by pointing, behavior labeled shared or "joint attention," or "triadic engagement." One hypothesis about why children do this by 9 months or before whereas chimpanzee infants do not is that earlier locomotor competence allows chimpanzee infants to get what they want themselves, whereas human babies must use social means (Leavens et al. 2008). Bard (2012:243) reports that "when chimpanzees are raised with warm relationships and industrially manufactured objects," mutual triadic engagements are common. Her appraisal is that, in captivity, "young chimpanzees compare favorably to humans as newborns through to 2.5 years olds" (2012:244).

A widely used measure of what youngsters understand is the False Belief Test. The subject and a confederate of the experimenter together watch the experimenter hide a treat. Then the confederate leaves, and the subject sees the experimenter move the treat to a new hiding place. The test question is whether the subject will expect the confederate to look for the treat where they saw it hidden, or where it was moved and rehidden while the confederate was away. Children generally fail to pass it until about 4 years of age, but chimpanzees do not pass it even as adults (Call and Tomasello 2008; Ruiz and Santos 2012). Yet careful experiments show that chimpanzees do know that others can know different things, and they behave accordingly (e.g., Kaminski et al. 2008; Schmelz et al. 2011)—something Hare (2011) called "chimpanzee chess." The developmental timing of such capacities remains to be determined in chimpanzees. But just as protocols other than the False Belief Test show that chimpanzees recognize that others can know different things than they know, findings with (Western) human infants show they can too—by at least 12 months of age, long before they pass the False Belief Test (Baillargeon et al. 2010; Reddy 2008; Tomasello and Haberl 2003).

Human Developmental Psychology

Most human infant development studies are not cross-species comparisons and instead aim to document how and when human babies begin to understand the world and participate in social life. Because language is so central to human interactions, developmentalists are often especially interested in the role of language learning in cognitive ontogeny (e.g., Spelke 2009; Spelke and Kinzler 2007). But many have argued persuasively that the evolution of human language depended on the preceding evolution of distinctive human preferences for shared intentionality (including Tomasello [following Grice 1957] and Hrdy 2009 [following Tomasello]). If so, the focus on language learning leads away from preexisting social appetites that are its foundation.

Observations and systematic protocols to probe the minds of prelinguistic babies reveal very early social sensitivities (e.g., Gopnik et al. 1999; Hamlin et al. 2010, 2011; Reddy 2003, 2008; Sommerville et al. 2005; Trevarthen 1979; Trevarthen and Aitken 2001; Woodward 1999; Wynn 2008). However Konner (2010:214) is not alone in his skepticism about such inferences from similar observations, criticizing Nagy's (2008) inference of "innate intersubjectivity" from newborn reactions to unresponsively still faces. Instead, Konner concludes that, "our newborns are less competent motorically, socially, and even perceptually than ape newborns" (2010:216).

Motorically, yes (Gómez 2004; Kellogg and Kellogg 1933; van Lawick-Goodall 1968; Takeshita et al. 2009). Plooij (1984) found that even at 8 weeks of age chimpanzee babies had some body-position control and could sit and push off to a standing position from the mother while supporting themselves on her. But the evidence touched on here does not support claims that humans are delayed socially. The developmental timing of attachment may not be very different in chimpanzee and human infants (van IJzendoorn et al. 2009). Human infants also pass the Mark and Mirror Test earlier than chimpanzee infants do (Bard et al. 2006; Lin et al. 1992), and developmental psychologists find evidence that human infants are self-conscious long before they can pass that test (see Reddy 2008: chap. 7 for references and discussion). "Results from many studies suggest that infants treat intentional agents—or, at least, the specific category of *human* agents—differently from other entities, even in the first days and weeks of life" (Wynn 2008:331, and see further discussion and references therein).

Our Other Closest Living Relative

In his review of the history of ideas around hominid social capacities, Brian Hare (2011) suggested that we might gain insight into "what changed and why" in human cognitive ontogeny by comparing not just humans with apes, but also apes with each other. Of the two species with which we share a most recent common ancestor, bonobos are notably more socially tolerant than chimpanzees (de Waal 2012; Hare et al. 2012; Herrmann et al. 2010b), more like humans on that score. If our higher social tolerance is due to similar shifts in cognitive ontogeny, then developmental timing in humans and bonobos should be shifted in the same direction from chimpanzees, either because similar shifts are derived in both humans and bonobos or because chimpanzees are more derived than either of us.

Wobber et al. (2010) investigated development of the social tolerance difference between chimpanzees and bonobos by running experiments on feeding tolerance, social inhibition, and social learning with similarly aged pairs. With youngest subjects 2 to 4 years old, the experimenters found bonobo development to be delayed relative to chimpanzees in all three tasks. Similar tests on human subjects would be confounded by language. But prelinguistic infants show a preference for helpful versus hindering actors by the age of 2 months (Hamlin et al. 2011). That human babies discriminate social opportunities and threats at astonishingly young ages (Gopnik 2009; Reddy 2008) can only be an indirect comparison because directly parallel measures are unavailable for either species of *Pan*. But Wobber and colleagues (2010:229) are likely right to say that "The crucial cognitive adaptation of humans relative to other apes is the accelerated development of social skills in infants."

If social discrimination is delayed in more tolerant bonobos compared with chimpanzees, but accelerated in even more tolerant humans compared with either species of *Pan*, then higher social tolerance goes with timing shifts in opposing directions. The Self-Domestication Hypothesis (Hare et al. 2012) linking selection for reduced aggression and higher social tolerance to developmental delays fits bonobos but not humans. In both *Pan* species, infants have their mother's undivided attention as she rears them one at a time without help. According to the hypothesis favored here, accelerated social development in humans evolved along with our distinctive rearing environments. Motivations and capacities for shared intentionality were favored in us and not the other apes as concomitants of our grandmothering life history. While grandmothering propelled delays in other aspects of development, it accelerated development of social emotions and motivations in infancy.

Discussion and Conclusions

Based on behavioral experiments with young (Western) human children and older apes, Tomasello and colleagues continue to add evidence consistent with their argument that shared intentionality is distinctively human. Other comparativists contributing to behavioral experiments usually use adults of each species. Recent reviews of this growing field are numerous, identifying an array of features as the distinctive scaffolding of human prosociality. Some nominate escalated altruistic preferences (Fehr and Fischbacker 2003; House et al. 2012; Silk 2009) or multiple differences in prosociality, tendency to punish, and concern for fairness (Silk and House 2011). Others highlight punishment (e.g., de Waal and Suchak 2010; Melis and Semmann 2010) or disgust (Sheskin and Santos 2012). Some identify proactive cooperation and reactivity (Jaeggi et al. 2010), emotional reactivity and social tolerance (Hare 2007; Melis et al. 2006), or recognition of benefit from mutualistic endeavors in a wide range of situations (Hare and Tan 2012).

Lack of agreement reflects the difficulty of the comparisons. Even carefully documented differences in social comprehension (Herrmann et al. 2007, 2010a) can be contested on grounds of experimental logistics (de Waal 2011; de Waal et al. 2008). Protocols are carried out in contexts constructed by humans, and usually with human participants. Developmental (Bard et al. 2011) and socioecological (Boesch 2012; Wrangham 2010) confounds are continuing issues. The same should be noted for the use of experiments to characterize human sociality since behavior in the lab does not mirror human life outside it (e.g., Kahneman 2012; Wiessner 2009). Concerns about ecological validity, as well as other interpretive difficulties (e.g., Burton-Chellew and West 2013; Leavitt and List 2007; Shettleworth 2010), should be noted more often for our own species. Interpretation is even less straightforward with nonhuman primates (Penn and Povinelli 2007; Penn et al. 2008; Povinelli 2000; Povinelli and Vonk 2003) and prelinguistic infants (Scarf et al. 2012).

Despite the complexity of this literature, there is seeming agreement that humans differ from other apes in our prosocial tendencies, whether or not that difference is best characterized by distinctive human preferences for shared intentionality. Along with general if not universal agreement about this conclusion goes a widely shared assumption that is contested here. Primatologists and developmental psychologists generally attribute the evolution of the human difference to evolutionary benefits conferred in cultural transmission and cultural cooperation. This circularity offers no leverage for explaining why shared intentionality evolved in us and not the other apes. An especially promising alternative hypothesis locates the initial evolution of our distinctive social appetites in the ancestral shift from independent mothering to reliance on help.

In conflict with the idea that human babies are in a uniquely helpless state of exterogestation (Montague 1961), chimpanzees babies are helpless too (Matsuzawa 2012; Schultz 1969). Plooij (1984:56–57) noted that “chimpanzee and man (and possibly the other apes) seem to stand apart from the remainder of the order primates in this respect” and said, “I venture to think that the early development of chimpanzee babies and human babies are almost equally retarded.” We share a broadly apelike helplessness in thermoregulation or “proper clinging” compared with monkeys, and humans have notably slower motor development. But investigators looking for social engagement and interactive participation in human infants find them soon after birth. This sensitivity, like the self-recognition detected by the Mark and Mirror test, may be earlier in humans than in chimpanzees, and likely much earlier than in bonobos.

Hrdy’s hypothesis that distinctively human sociality evolved in response to novel challenges faced by ancestral infants converges with the suggestion that Konner made 40 years ago. Perhaps “characteristic features of adult human behavior have evolved not because they are an ideal adaptation [in adulthood], but because they are the result of an ideal adaptation in infancy” (Konner 1972:302). If infant sociality is the foundation of human cooperative capacities, it also makes sequences of mutual attention and intention with particular others central concerns in our lineage alone. This preference for mutual attention can account for our distinctive enthusiasm for doing things “our way” (Nagell et al. 1993; Nielsen and Tomaselli 2010) as well as the in-group bias toward similar others that is present in very young children (Gopnik 2009; Mahajan and Wynn 2012). Although concerns about human cooperation were not central when Konner (1972) focused on Ju/’hoan infant development, he anticipated the speculation that it is these capacities that provide the foundation for the subsequent evolution of human pair ponds when he said, “some adult behavior patterns (for example marriage) may be in part the result of selective forces favoring certain infant behaviors” (1972:302).

Hypotheses that make selection on infants due to rearing environments central to distinctly human cooperative tendencies contrast with other current ideas about human prosociality. I note especially contrasts with hypotheses that appeal to some form of group selection to explain the human difference (e.g., Boehm 1999; Bowles and Gintis 2011; Haidt 2012; Richerson and Boyd 2005; Sober and Wilson 1998; Wilson 2012). Although those arguments are varied, they often cite Darwin's 1871 discussion of the evolution of human moral faculties and use his own words as an authoritative source for the need to rely on group selection. Darwin said:

> When two tribes of primeval man, living in the same country, came into competition, if one tribe included . . . a greater number of courageous sympathetic and faithful members, who were always ready to warn each other of danger and to aid and defend each other, this tribe would without doubt succeed best and conquer the other. . . . A tribe possessing the above qualities in high degree would spread and be victorious over other tribes; but in the course of time it would, judging from all past history, be in its turn overcome by some other still more highly endowed tribe. Thus the social and moral qualities would tend to slowly advance and be diffused throughout the world (1981:162).

But he continued:

> How, it might be asked . . . did a large number of members first become endowed with these social and moral qualities, and how was the standard of excellence raised? . . . It is extremely doubtful whether the offspring of the more sympathetic and benevolent parents, or those which were most faithful to their comrades, would be reared in greater number than the children of selfish and treacherous parents of the same tribe. . . . It seems scarcely possible (bearing in mind that we are not speaking of one tribe being victorious over another) that the number of men gifted with such virtues, or that the standard of their excellence, could be increased through natural selection (1981:163).

Having established the challenge, he proceeded to meet it, suggesting solutions that have a remarkably modern ring. First he suggested reciprocity, but,

> there is another and much more powerful stimulus to the development of the social virtues, namely the praise and blame of our fellow-men. The love of approbation and the dread of infamy, as well as the bestowal of praise or blame, are primarily due . . . to the instinct of sympathy; and this instinct no doubt was originally acquired like all other social instincts, through natural selection (1981:164; see also Williams 1966:93–94).

Although there is much yet to learn of social ontogeny in our great ape cousins, developmental psychologists find evidence of sensitivity to praise and blame in very young human babies (Gopnik et al. 1999; Hamlin et al. 2011; Reddy 2003, 2008). It appears well before they have language, even longer before they participate in cooperative foraging (Tomasello 2009; Tomasello et al. 2012), let alone lethal aggression between groups (Bowles and Gintis 2011). Just as these sensitivities appear earlier in development, the survival advantages they confer on infants are independent of cooperative opportunities at older ages. Their early development is consistent with the hypothesis that distinctively human prosociality is a legacy of natural selection on ancestral infants facing the novel rearing environments that came with grandmothering. These links may explain why it was only our lineage that evolved the intersubjective appetites that, once evolved, became foundation for our relationships, our imaginations, and the social and economic interdependence of our lives (Tomasello and Rakoczsy 2007).

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